VOCAL CULTURE AND SOCIAL STABILITY IN RESIDENT KILLER WHALES (*ORCINUS ORCA*)

by

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ABSTRACT

The killer whale (*Orcinus orca*) is one of the few species for which vocal culture is actively involved in the development and maintenance of the social organizations of populations. In particular, the social structure of one form of killer whales, called *residents*, is a good example of this involvement. Resident societies are characterized by associations of groups with highly stable membership, which allow an in-depth examination of the association between vocal culture and the nested social hierarchy of that population. Resident killer whales live in small populations where inbreeding is a threat to their genetic diversity. Genetic and cultural evolution may be closely linked in killer whales, as has been proposed for a number of other cetaceans with matrilineal social structure. To test for a possible link between genetic and cultural evolution in killer whales, I investigated vocal similarities and differences among mixing and non-mixing resident groups and between two ecotypes, residents and transients.

First, I examined whether clans exist among resident killer whales in Southern Alaska. Vocal clans had been previously identified in British Columbia but not in Alaska. Two acoustically distinct clans were recognized, each of which was monomorphic for a different mitochondrial D-loop haplotype based on results of a separate genetic study. Thus, acoustic similarities within these cultural groups reflect common matrilineal ancestry, which suggests that clan-based social structure is a fixed characteristic of resident killer whales.

Second, I examined the similarity of vocal repertoires between residents and transients, and among clans and communities within residents. Call type similarity does not exist above the clan level. To investigate vocal similarity above the clan level, I split calls into *syllables*, and compared their distribution among population levels. Structural variation of upper frequency syllables characterized vocal variation among clans of the same community, while usage of distinct lower frequency syllables reflected divisions among communities and between residents and transients.

Third, I examined syntax, the ordered arrangement of syllables, among clans of resident communities. I found that vertical transmission of syllable order in matrilines is important for the distinctiveness of call type repertoires and leads to clan-specific syntax rules. Previous work has shown that mating mainly takes place between clans. Because syntax similarity appears to be negatively correlated with sociality among clans, resident killer whales may use syntax variation to choose mates with low levels of genetic relatedness.

The link between vocal culture and social structure likely influences mate choice in resident killer whales. This link leads to gene-culture co-evolution in killer whales and makes them excellent candidates for studies of cultural taxonomy.

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DEDICATION

I dedicate this thesis to my wife Jeanette Boily for her enormous support and patience and to our two children, Zara and Luca. Jeanette remained hopeful about the positive solution to this project when even I had my doubts.

CO-AUTHORSHIP STATEMENT

Chapter 2 is a revised version of the following paper:

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I designed the acoustic study and analyzed all acoustic data and wrote the paper. L.G. Barrett-Lennard conducted the genetic analysis. J.K.B. Ford and C.O. Matkin provided recordings, as well as assistance and advice throughout the study.

1. GENERAL INTRODUCTION

Culture is the transmission of traits within or between generations based on social learning through either teaching or imitation (e.g. Rendell & Whitehead 2001). Culture produces behavioural variation among isolated and non-isolated groups and populations. Depending on whether this variation influences the social structure and the fitness of individuals directly or through trade-offs with other traits, cultural traits can be considered adaptive or non-adaptive (Avital & Jablonka 2000). Vocal culture is that part of the cultural phenomenon that deals with the transmission of vocal patterns through vocal learning.

Vocal culture resulting from social learning has been identified in three groups of organisms: birds, humans and marine mammals (Janik & Slater 2003). There is the potential for vocal culture in bats, because *screech* calls of greater spear-nosed bats (*Phyllostomus hastatus*) are socially learned (Boughman 1998). However, long-term stability or divergence of group vocalizations of bats has yet to be assessed. Without detailed knowledge of vocal divergence one cannot assess the prevalence of vocal culture. For example, all male humpback whales (*Megaptera novaengliae*) of the same breeding area use a converged song type (Payne & McVay 1971). This song type changes progressively from the beginning to the end of the breeding season (Payne et al. 1983). However, the basic structure or song form remains recognizable over longer periods of time (e.g. 19 years: Payne & Payne 1985), making assessments of cultural changes possible (Noad et al. 2000).

In birds, humans and marine mammals, vocal cultures are often expressed as dialects, i.e. different repertoires of song types or call types, and human speech variations that have the potential to lead to different languages. A language split occurs when dialects become mutually unintelligible (Chambers & Trudgill 1980). Some anthropologists see dialects therefore as pre-cursors in the evolution of language (Hill 1978). In humans, dialects are considered to be adaptive because they lead to social barriers due to different mental concepts, i.e. how an individual sees and interprets its environment (Britain & Trudgill 1999). Dialects can also act as social barriers in some songbirds because of cultural innovations in locally adapted populations (e.g. Gammon & Baker 2004) or through male-male competition and territory defense, and when females select males with local dialects (Catchpole & Slater 1995; Searcy & Nowicki 2000; Lachlan et al. 2004). Dialect differences in songbirds (song types) and humans (languages) are therefore cultural icons of socially and sometimes geographically isolated groups.

Killer whales are one of the few mammalian species for which vocal culture plays a role in the evolution of social structure (Ford 2004). In particular, residents, which are characterized by matrilines, clans, and communities, are good candidates to examine the relationship of vocal culture and a nested social hierarchy. In order for this association to appear, vocal culture needs to be stable for some generations.

Cultural transmission of vocal patterns between generations leads to the formation of stable traditions, or *cultural lineages* (Mundinger 1980). When cultural lineages also reflect common ancestry, and/or are shared by individuals that live together, they are called clans (Murdock 1960). Many primate societies are characterized by clan-like structures due to female philopatry (Sterck et al. 1997), but only human clans, which include both males and females, are specifically characterized by cultural traits (Murdock 1960). Clans in other vertebrates are most often found among cooperatively breeding mammals (Frank 1986) and birds (Naske 1998; Price 1998).

Resident killer whales in the Northeastern Pacific are characterized by cultural clans based on shared vocal repertoires (Ford 1991). Killer whale clans result from the sharing of group-specific vocal dialects among matrilines. This form of dialect sharing is rare in mammals as are vocal clans with distinct dialects (Ford 1991). The only other reported occurrence of distinct acoustic clans in mammals has been for sperm whales (*Physeter macrocephalus*) (Rendell & Whitehead 2003). There is an important difference between killer whale and sperm whale clans. While vocal repertoires of killer whale clans are by definition completely distinct (Ford 1991 and Chapter 2), sperm whale clans are allowed to share some vocal patterns (Rendell & Whitehead 2003). This difference makes it more difficult to examine associations between vocal structure of clans and the social structure of sperm whale populations.

If cultural lineages or clans influence the spread of genes within populations, gene-culture co-evolution (Feldman & Laland 1996) is present in that species or population. Cultural traits that are beneficial for individuals and groups can affect the social structure of a population by creating barriers that influence mate choice, which ultimately can affect genetic diversity. This is called cultural hitchhiking, a process suggested to be responsible for low mtDNA diversity in matrilineal whales (Whitehead 2005).

The sharing of group-specific dialects among resident killer whales, which is suspected to lead to the formation of clans, could be a culturally selected trait that is beneficial for group survival. Alternatively, call repertoires of clans, which are the only completely distinct dialects of residents may be culturally selected to allow reliable clan recognition. Matrilines within clans are more closely related than between clans (Barrett-Lennard 2000), making cooperation among clan members more likely. Furthermore, mating predominantly takes place between clans, which may reduce inbreeding costs (Barrett-Lennard 2000). Resident killer whales only associate within their community and community sizes can be small (e.g. < 100 whales) (Bigg et al. 1990; Ford et al. 2000). Effective community or population sizes are smaller than census sizes because of assortative mating patterns. For example, the mating success of male killer whales is age-dependent due to female choice (Barrett-Lennard 2000). Killer whales must have developed an effective outbreeding mechanism (Barrett-Lennard 2000), and while this mechanism is not known, it could be based on vocal differences among groups.

Resident and transient killer whales: social structure, vocalizations and relatedness

Three different ecotypes of killer whales inhabit the Northeastern Pacific, *residents*, *transients,* and *offshores.* The three ecotypes have overlapping ranges (Fig. 1.1) but appear to be reproductively isolated (Barrett-Lennard 2000). While the call repertoires of residents and some transients are well known (Ford 1991 and Chapter 2 of this thesis; Ford & Morton 1991; Deecke 2003), call repertoires of the offshore ecotype are not well described. To examine stability and differences of vocal culture in association with group divergences, I focused on the call repertoires of three resident killer whale communities (Fig. 1.1). Call repertoires of one population of transients were compared to those of the resident communities because of their different social structure.

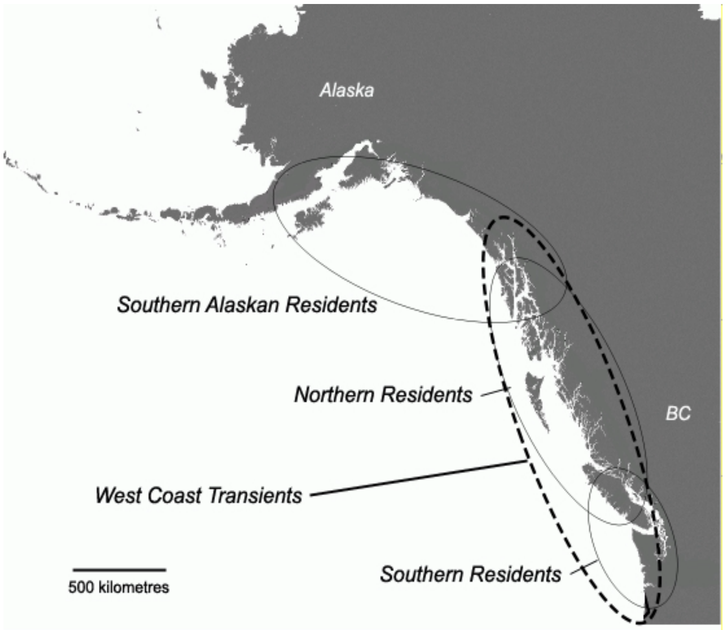

Figure 1.1: The summer distributions of three resident killer whale communities and one transient community. The range of the offshore ecotype is poorly known but overlaps with both the range of transients and residents

The structure of resident killer whale populations is characterized by the social and acoustic associations of groups of animals that are closely related by matrilineal descent. The basic social unit of resident killer whales is the matriline. Neither males nor females are known to disperse from their matriline (Bigg et al. 1990; Barrett-Lennard 2000). Whales of the same matriline use specific call-types as vocal signatures of their matriline (Ford 1991; Deecke et al. 2000; Miller & Bain 2000). Groups of matrilines that associate at least 50% of the observed time are called pods (Bigg et al. 1990). Matrilines within a pod are more closely related than matrilines of different pods (Barrett-Lennard 2000). The pod, however, is not as stable a social unit as the matriline (Ford & Ellis 2002). Matrilines and pods that share parts of their vocal repertoires form a vocal clan (Ford 1991). Clans that socialize belong to the same community (Bigg et al. 1990). The existence of stable matrilines, clans and communities, which is almost unique among mammals, makes resident killer whales an especially good candidate to study associations between vocal culture and social divergence.

In contrast to residents, transients have a more fluid social structure (Ford & Ellis 1999; Baird & Whitehead 2000). Transients travel and forage in groups that are typically smaller than those of residents but sometimes form larger aggregations that may serve social functions (Ford & Ellis 1999; Baird & Whitehead 2000). On the other hand, transients sometimes swim alone and join other groups only occasionally (Baird & Dill 1996). Especially larger group sizes may reflect the type and size of prey that transients are hunting rather than mirroring the social relationships among group members (Baird & Dill 1996; Ford et al. 1998; Ford & Ellis 1999; Ternullo & Black 2002). Animals in groups are not necessarily all closely related. While some transient killer whales stay within their matriline for extended periods of time, others seem to disperse temporarily or permanently. However, occurrence of transients in a particular area at a particular time is less predictable than the occurrence of residents, which makes it difficult to determine dispersal patterns of transients (Ford & Ellis 1999). Transient call repertoires also do not reflect social structure and transients do not have group-specific dialects (Ford & Morton 1991; Deecke 2003).

Vocalizations of killer whales fall into three categories, clicks, whistles, and calls. Clicks are heard in 95% of all recordings of residents and are used by whales in the detection and pursuit of prey, and during social encounters (Barrett-Lennard et al. 1996a). Transients use clicks less often than residents and have developed specific types that differ from those of residents (Barrett-Lennard et al. 1996a). Whistles of both residents and transients are mainly heard during social interactions when the whales are in close proximity to each other (Ford 1989; Thomsen et al. 2002; Deecke et al. 2005). After echolocation clicks, calls are the most common type of vocalization in residents (Ford 1989). Calls are stereotyped pulsed vocalizations. They are heard in approximately 90% of recordings, typically in situations where the whales are spread out foraging or when two or more pods meet. Ford (1989) suggested that the calls of resident killer whales serve as signals for maintaining contact between matrilines or pod members. Resident pods share a repertoire of 7-17 discrete call types and call variants, which appear to be stable over several generations (Ford 1991; Ford 2004). Similar to the rare use of echolocation clicks, transients also use fewer calls than do residents. The use of any vocalization appears to incur costs for transients because vocalizations can be detected by potential prey (Deecke et al. 2002; Deecke et al. 2005). This places a constraint on the ability of transients to communicate with each other (Deecke et al. 2005) and may also be responsible for smaller call repertoires than those of residents. The “West Coast” community of transients have call repertoires of 11-13 calls of which most are shared among all whales, while none of the calls are used by residents (Ford & Morton 1991; Deecke 2003).

Killer whale calls are complex structured vocalizations (Fig. 2.2 in Chapter 2) that can be divided into spectrographically distinguishable elements (Ford 1987; Strager 1995, Chapter 2 and 3). Calls produced by the same groups of whales have not shown variation in their stereotypic form for more than 25 years (Ford 2004), and some calls appear to have been stable for at least 47 years (Ford, pers. comm.). This stability allows observers to determine distinct call repertoires (Ford 1987). Ford also used distinct combinations of call elements to define sub-categories (sub-types). Subsequent studies of acoustic differences among killer whale matrilines have found structural differences within call categories and sub-categories (Deecke et al. 1999, 2000; Miller & Bain 2000; Miller 2002). Two studies concluded that structural variations reflect vocal differences among closely related matrilines (Ford 1987; Miller & Bain 2000). Variations of the stereotypic forms of calls, however, appear to reflect vocal differences among more distantly related matrilines (Ford 1991, and Chapter 2).

Call type divergence

Killer whale calls are most likely transmitted across generations by vocal learning (Ford 1991; Barrett-Lennard 2000; Janik & Slater 2003). Bigg et al. (1990) and Ford (1991) suggested that pod fission in residents and group-specific variation in calls occurs gradually over several generations. According to this hypothesis, newly formed sister pods initially spend a significant amount of time together and share most of the calls of their ancestral pod. Over time, because of copying errors of calls between generations and fewer contacts between sister pods, calls change progressively and repertoires diverge. Ford (1991) referred to pods that share parts of their repertoires as clans. He proposed that pods that share much of their call repertoire have split more recently than pods that have fewer calls in common.

Consequently, repertoire divergence could result from the social divergence of groups. Ford (1991) proposed that pods with very similar call repertoires are more closely related than pods that share only a few calls. The genetic analysis by Barrett-Lennard (2000) confirmed this association between genetic and cultural relatedness. He suggested that vocal similarities and differences function in mating preferences (i.e. call repertoire similarities or differences are under selection to function in assortative mating). Alternatively, vocal divergence could occur passively through cultural drift following social divergence or group splitting.

Thesis question and approach

In this dissertation, I examine proximate and ultimate mechanisms leading to vocal and social divergence among killer whales of the Northeastern Pacific. I focus on differences between clans, communities and populations, and compare the divergence of vocal culture among interacting groups and groups that are socially and reproductively isolated (Barrett-Lennard 2000; Ford et al. 2000). The results provide insights on how cultural traits can remain stable without continuous social contact and how they can affect the genetic population structure of killer whales. The goal of my study was to investigate whether vocal repertoires of killer whales have the stability to function in assortative mating and to create and maintain social barriers among communities and populations. To do so, I tested whether selection plays a role in the divergence of vocal repertoires among groups that socialize frequently and those that do not.

The dissertation consists of three main components. The first component (Chapter 2) is an analysis of the cultural transmission of call repertoires among pods of a resident community in Alaska. The vocal repertoire of this community had not been studied previously. By comparing the call repertoires of seven pods from southern Alaska to an earlier study of their genetic relatedness (Barrett-Lennard 2000), I tested whether clans exist among the resident type killer whales in Southern Alaska.

In the second component (Chapter 3), I examined acoustic similarities among resident killer whale clans and communities, and between resident and transient killer whales. Within resident clans, call repertoire similarities among matrilines are maintained through vertical or oblique transmission (parent or members of parent generation to offspring) of call structure (Ford 1991; Deecke et al. 2000). Call similarity among closely related matrilines has been explained by this mechanism (Miller & Bain 2000). However, repertoire similarity ceases to exist above the clan level (Ford 1991). Communities are often comprised of more than one clan making it necessary for clans to recognize each other. Chemical and optical markers are poor carriers of information in an aquatic environment. Acoustic signals are better suited as markers. Individual whales may learn all of the calls used by members of a community (range: 29 to 64 calls) or use vocal markers that are embedded in the call structure. To test for vocal markers, I will explore whether call elements exist that distinguish resident clans and communities and between residents and transients. If the number of distinct elements is lower than the number of calls and if elements can be reliably recognized, they should be used preferentially as vocal markers. If vocal markers exist, distribution differences of markers may distinguish among levels of the social structure. If marker differences are selected, they could act as social barriers and indicate gene-culture coevolution.

The third component (Chapter 4) is an analysis of the syntactical organization of syllables within calls. Many call types are produced by combining at least two syllables (Ford 1987). I examined the combinatorial variability of syllables to determine what influence syntax has on call type divergence. Furthermore, I assessed whether syntactical order of syllables results from social separation of groups, or whether syntax divergence is governed by clan, community, or population specific rules. Functional implications of syntax, such as group recognition and mate choice are discussed. Also, I determined whether the syntactical system fulfills the conditions of a ‘discrete combinatorial system’ that uses grammatical rules to combine discrete elements (Pinker 1998). Complex signals consisting of combinations of qualitatively-distinct acoustic elements are rare in birds and non-human mammals (Pinker 1994; Marler 1998).

2. CULTURAL TRANSMISSION WITHIN MATERNAL LINEAGES: VOCAL CLANS IN RESIDENT KILLER WHALES IN SOUTHERN ALASKA

2.1 Introduction

Traditions and cultural lineages

Traditions are expressions of conserved information that is not coded genetically but learned socially, and are stable for several generations (Mundinger 1980; Cavalli-Sforza & Feldman 1981). Cultural lineages are characterized by traditions, and commonly identify groups of individuals that inhabit the same area and/or belong to a consanguineal kin group (Murdock 1960). One advantage of culturally transmitted information over genetically transmitted information is that traditions can respond more rapidly than genetically formed traits in response to changes in the environment (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). However, traditions can also be maintained for long periods if they remain advantageous for individuals of a group, sub-population or population (Mundinger 1980). Unique social traditions can develop by a process of cultural drift and selection of behavioural traits that distinguish groups, while migration between groups is sufficiently low in frequency. The stability of those traits then allows individuals to use them as cultural identifiers of relatedness between groups as well as individuals.

Traditions can generally be divided into several categories, e.g. those that involve physical manipulation of objects, those that can be regarded as social customs, or those that involve vocalizations. Social customs such as complex greeting ceremonies and physical manipulation, such as tool use are common in apes, such as chimpanzees (Whiten et al. 1999) and humans. A well-known example of a tradition that involves physical manipulation but is outside the hominid family is that of the potato-washing Japanese macaques (Kawamura 1959). The behaviour was invented by an individual female macaque in 1958, and spread over a period of two years first to related members of the troop and later to non-relatives (Nishida 1987). The best-described examples of vocal traditions in animals are the commonly found learned structured song repertoires of birds (Payne 1988; Lynch & Baker 1993), and the rare group or sub-population specific learned dialects of some mammals, such as humans and certain cetaceans (Ford 1991; Payne & Payne 1985; Rendell & Whitehead 2003). Vocal traditions of songbirds contain recognizable themes, phrases and notes (Marler & Tamura 1962; Slater & Ince 1979), elements that are also used by male humpback whales to structure their song types and themes (Payne et al. 1983). Further examples of vocal traditions are discrete call-type repertoires produced by killer whales (Ford 1989), and discrete temporal patterns in click vocalizations of sperm whales (Weilgart & Whitehead 1997).

The specific vocal traditions of sympatric living or neighbouring groups or sub-populations of mammals are called dialects (Conner 1982; Ford 2002) (no single definition for dialects exists for birds). Vocal repertoire differences resulting from isolation between groups or sub-populations should be called geographically varying repertoires because they most likely resulted only from passive cultural or genetic drift due to that isolation (Conner 1982; Lynch 1996). The majority of mammalian dialects are learned within a social group by copying signals of a parent or other kin group member or through acoustic interaction between non-related individuals that are familiar with each other (Mundinger 1980; Conner 1982; Ford 1989). The humpback song, which is a tradition learned socially by males on the breeding ground, is an example of a vocal tradition that is however, not a dialect. Novel songs produced by singers new to a particular breeding ground appear to spread rapidly through a population. On the other hand, existent songs appear to disappear quickly when new songs are introduced (Noad et al. 2000). Therefore, the song does not identify a group or sub-population.

A vocal tradition is by definition a learned behaviour. However, even when mammalian dialects are learned, the question of how they are learned; vocally or contextually, is still important (Janik & Slater 2000). Potentially, dialects could arise from vocalizations whose acoustic structure is determined completely by genetic templates (Marler 1997). The calls could then either be the result of maturational processes of the individual, or the template usage could be contextually learned making the dialect a socially learned pattern. However, as Janik & Slater (1997) pointed out, the vocalizations comprising the dialect would not be vocally learned. An individual producing the same vocalizations as other members of the group would do so because of a learned social custom and every individual could potentially still produce all of the vocalizations typical for a population or species.

Dialects of resident type killer whales appear to be vocally learned because killer whales copy calls of distantly-related conspecifics in captivity (Bain 1988; Ford 1991). Killer whales also mimic calls in the wild, although the mimicked calls are easily recognizable as such by human observers and therefore possibly easily recognizable as mimics by other killer whales (Ford 1991). Dialects appear to be strongly associated with the recognition process of social groups within the hierarchical social organization of these whales (Bigg et al. 1990), implying that the vocalizations are also learned socially by selectively copying signals of group members.

The goals of our study were to investigate whether clans as mentioned by Ford (1991), hereafter called vocal clans because of their basis in vocalizations, exist among southern Alaskan resident killer whales. Furthermore, if vocally similar groups of pods are true clans, then vocal clans should be parallel cultural and genetic lineages. To test this hypothesis, we compared a representative sample of discrete calls produced by the seven pods in the study population (Matkin et al. 1999), and determined whether the variation in discrete call use among pods matched up with results of a pre-existing genetic study of maternal relatedness patterns among the same pods. The genetic study (by L.B.-L.) and the call repertoire assessments (by H.Y.) were performed independently and were blind to each other's results.

2.2 Methods

Acoustic Analysis

Recordings were made by a number of different observers (see Acknowledgements for details), and were analysed following the protocol of Ford (1987), Saulitis (1993), and Strager (1995). Data were collected under National Marine Fisheries Service scientific research permits No. 840 and No. 875-1401. Groups of whales were located in the field (Fig. 2.1) and photographed for individual identification from 4 m to 11 m vessels after visually searching for them and by listening for their vocalizations with a directional hydrophone. After photographing all of the whales present, the boat was then moved 500 metres ahead of the whales, and the engine was turned off. A hydrophone was then lowered over the side of the boat to a depth of 10-15 metres.

The recording systems varied, but most consisted of a Celesco BC-10/ BC-50 or an Offshore Acoustics hydrophone and a Sony WM-DC6 or Marantz PMD 221 cassette-tape recorder. The frequency responses of these recording systems were approximately linear between 100 Hz and 8 kHz and were still useful for call identification up to 14 kHz (± 10 dB). Some recordings with wider frequency responses were made with a Bruel & Kjaer 8101 hydrophone, and a Nagra IV-SJ reel-to-reel tape recorder (5 Hz – 35 kHz ± 1dB), or an Offshore Acoustics hydrophone and a TCD-D7 Sony DAT recorder (20 Hz – 22 kHz ± 1 dB).

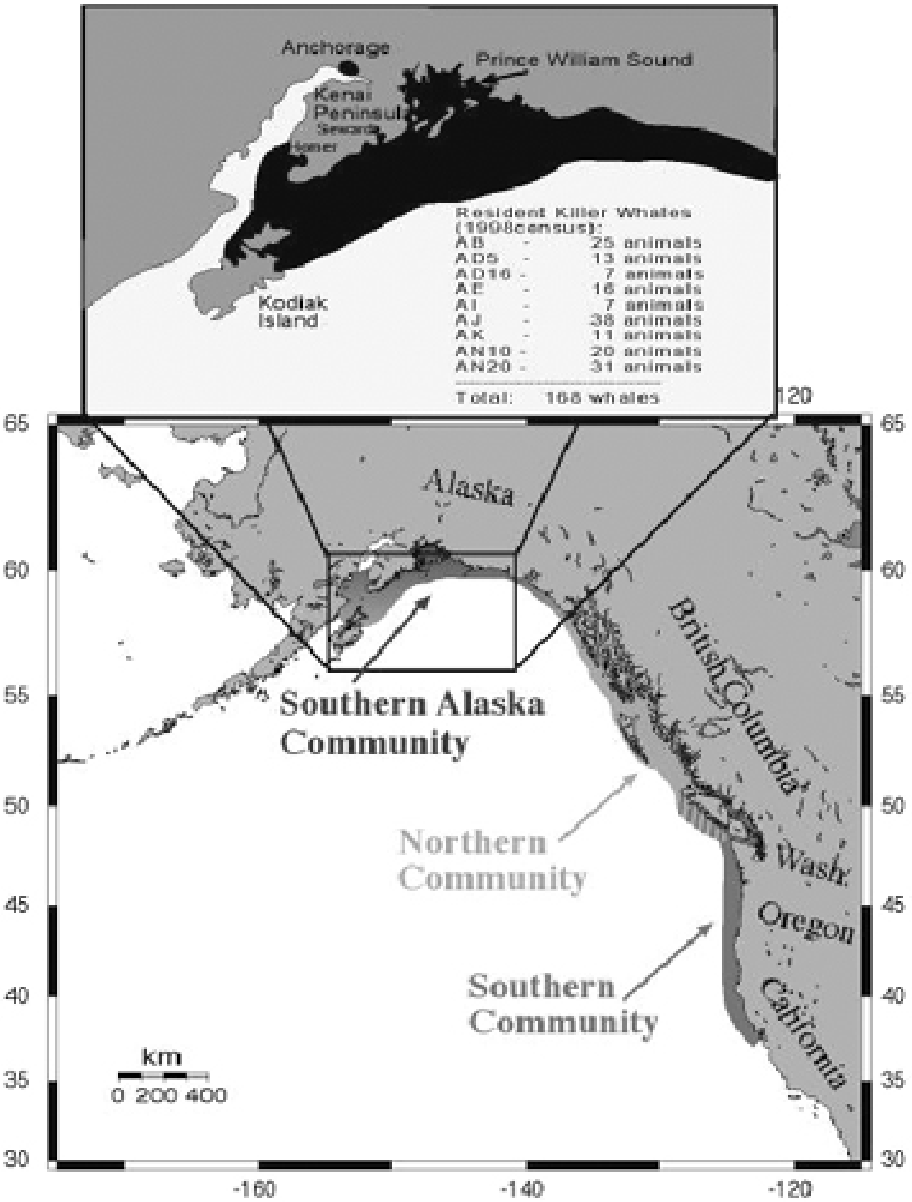

Figure 2.1: Distribution of the seven resident killer whale pods in Prince William Sound and adjacent waters during late spring/ summer and early fall. Distribution ranges of resident killer whales in the Northeastern Pacific.

Recording selection and discrete call description

We only analysed recordings of a pod when it was encountered alone or at such a distance from other pods (> 1 km) that the calls could be attributed unequivocally to that group. Vocalizations were recorded during a wide range of observable behaviours, such as travelling (slow and fast), feeding, resting (milling at surface), and socializing (pod gatherings) as described by Ford (1989). All recordings meeting the above criterion (single pod recording) were used to describe the call repertoire of a pod. Table 2.1 shows the number of single pod recordings analysed.

Table 2.1: Number of pod encounters with recordings analysed for six pods (AB through AK) for each year and the number of biopsy samples collected from these pods. Actual recording duration differed among encounters, as did vocal activity.

Year/Pod	AB	AI	AJ	AN	AD	AE	AK	# of recs./ year
1984	9	3	1	4	4	3	2	26
1985	4	0	0	4	2	4	1	15
1986	0	0	0	1	1	1	0	3
1988	0	0	0	0	0	0	1	1
1989	2	0	0	1	0	0	3	6
1990	1	3	4	2	1	2	2	15
1991	0	3	1	2	1	3	4	14
1992	3	2	0	1	0	2	1	9
1993	0	0	0	0	1	1	0	2
1994	0	1	1	0	0	0	0	2
1996	1	2	1	0	0	3	0	7
1997	0	2	2	5	4	3	2	18
1998	1	0	0	0	1	0	1	3
1999	0	0	0	0	1	0	0	1
total # of recordings	21	16	10	20	16	22	17	122
total # of biopsies	14	6	12	8	15	12	8	

We inspected recordings for the presence of calls by listening to tapes while monitoring real-time spectrograms of the acoustic signals using a Kay Elemetrics DSP Sona-Graph, Model 5500. A sample of recognized calls (minimum of 100 per pod) was digitised and further analysed spectrographically using Canary 1.2.4 sound analysis software (Cornell Laboratory of Ornithology, Ithaca, NY, USA, 1998). The calls used for spectrographic analysis were digitised at a 44.1 kHz sampling rate with a 16 bit sample size. The spectrographic analysis was done using Fast-Fourier Transformations (FFT) with sizes of 1024 points for each analysed time series. Spectrograms were produced using an 87.5% overlap of analysed time series. Resulting spectrograms had a time resolution of 2.9 milliseconds and frequency resolution of 43 Hz.

Calls are stereotyped vocalizations of 0.25 to 2.5 seconds in duration (Schevill & Watkins 1966) that are often composed of two components (Fig. 2.2). Following Miller & Bain (2000), components with lower sound frequency (lowest band in spectrogram at 0.5 kHz to 3.5 kHz) were called lower frequency components (LFC, see Fig. 2.2), and components with higher sound frequency (lowest band always above 3.5 kHz) were called upper frequency components (UFC, see Fig. 2.2).

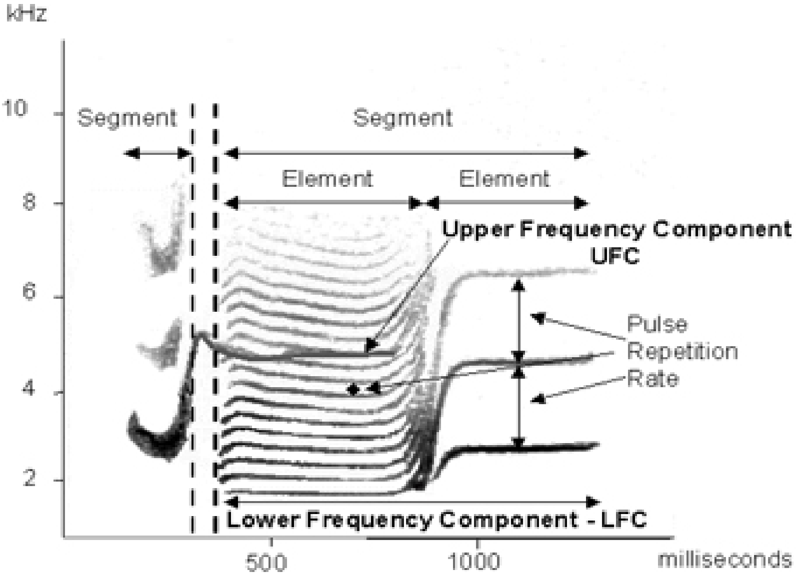

Figure 2.2: Spectrographic examples of a discrete call (AKS 02). Calls often consist of two components, a) a lower frequency component – LFC (duration : 0.5 to 2 sec/ pulse repetition rate: 0.2 to 2.5 kHz), and b) an upper frequency component – UFC (duration: 0.5 –2.5 sec/ frequency range: 4 to 8 kHz) . Abrupt shifts of the pulse frequency in the lower frequency component distinguish elements. Elements differ from call segments that are characterized by silent intervals between them.

LFCs consist of rapidly produced broadband pulses that overlap to produce the equivalent of sine wave tones. The distance between spectrogram bands reflects pulse repetition rate (Watkins 1967), although intensity differences due to super-positioning of pulse tones may reduce the number of bands in the spectrogram. For example, when the pulse rate is a 2n multiple of the pulse frequency, the harmonics of the pulse frequency will show up as stronger bands in the spectrogram, and bands in between may disappear completely. Both the pulse repetition rate and pulse frequency are usually modulated over the duration of the call (Fig. 2.2). UFCs often have no sidebands but have true harmonic bands and can then be better described as narrow band signals, such as whistles, produced simultaneously to LFCs (Fig. 2.2, see also call-type AKS 05 in Fig. 2.5). Furthermore, many LFCs of calls can be divided into elements separated by rapid shifts in pulse repetition rates (Fig. 2.2, see also AKS11 in Fig. 2.5). Some calls may also be segmented with segments separated from each other by silent intervals (Fig. 2.2; see also call-type AKS 21 in Fig. 2.5).

Call-type categorization

We categorised call-types by ear and by visual inspection of the sound spectrogram. Categorisation was based on the distinctive audible characteristics of the calls, which appeared as distinguishing structural differences in the frequency/time contours of a call's spectrogram. Particular attention was given to call duration, segmentation, element structure of LFCs, and the existence of UFCs (Fig. 2.2). A similar method was described by Ford & Fisher (1983) and Ford (1984). Ford (1984) found no significant difference between the categorisation of killer whale calls based on a statistical comparison of certain sound parameters and the categorisation using aural and spectrographic comparison. Bain (1986), comparing sound and visual appearance of calls, obtained similar call categories from two captive killer whales of the same population that Ford (1984) described. Deecke et al. (2000) compared the results of call similarity analyses from neural networks with those made by humans that have been trained to distinguish between calls and found no significant difference in the results of the types of analyses.

Our categorization method differed slightly from the one Ford (1984) used to define stable call variants. Our definition of a call variant was based on contour variations within elements and not on occurrence of elements within a call. Calls that had different numbers of elements but were otherwise similar were categorized as two distinct call-types. This allowed for a greater structural resolution of call-types in the categorization process.

Call-types can be described by their gestalt (Katz 1950; Deecke et al. 2000), where gestalt means that acoustic similarities and differences of calls can be distinguished by humans without previous experience in categorizing calls. Furthermore, gestalt differences and similarities can be more effectively described by humans that are trained to distinguish between call-types by listening to a great number of different calls (Deecke et al. 2000). To test whether our call-type categorizations could be reproduced by others, we gave samples of categorized calls to two groups of human observers.

Group A consisted of 17 individuals unfamiliar with either killer whale or other cetacean vocalizations, and group B consisted of 7 individuals who had experience in categorising killer whale and/or other cetacean vocalizations. Each individual was asked to find the most similar call to a sample call among four similar sounding calls (Fig. 2.3). Aside from detecting similar sounding calls, observers were asked to find similarity based on a) similar call duration, b) the existence of the same number of components (if possible), c) an equal number of segments and elements, and d) similar contour modulations within elements (Fig. 2.3).

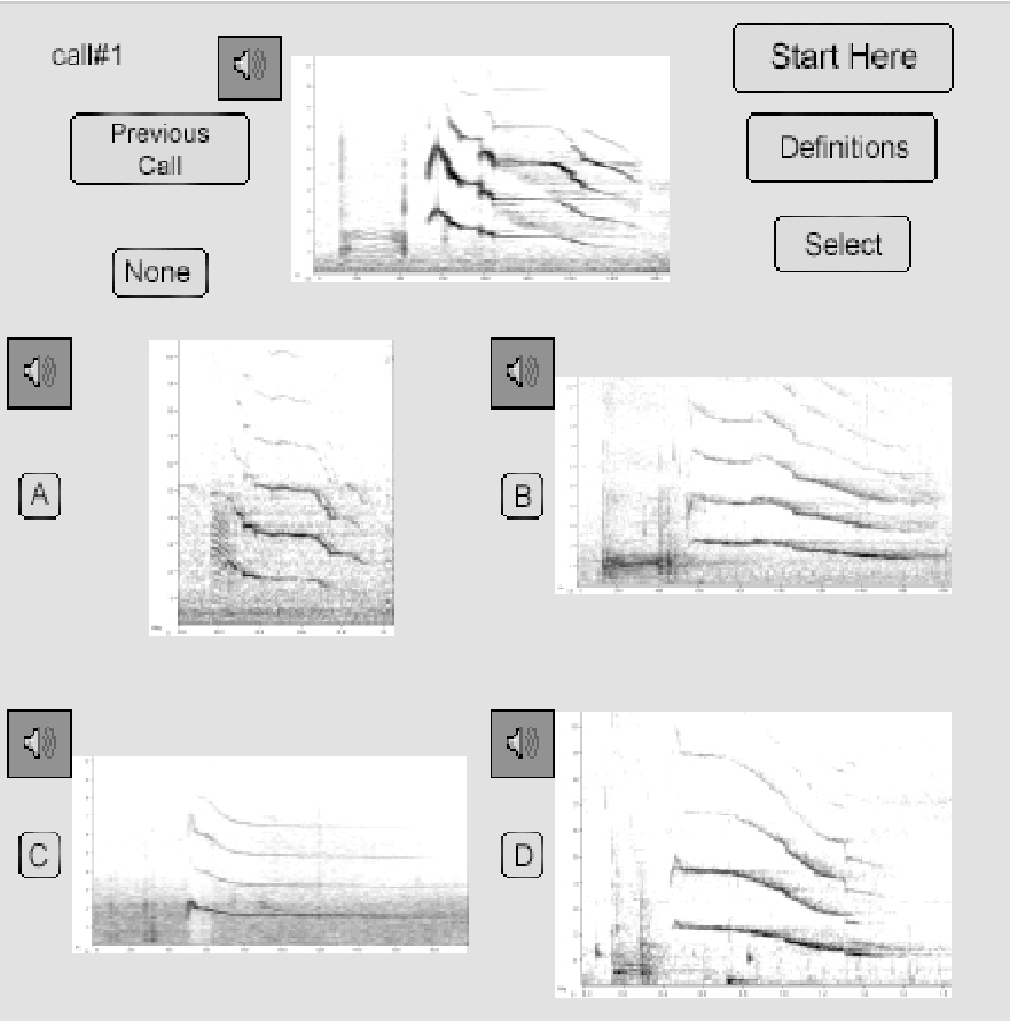

Figure 2.3: Example frame of the call-type re-evaluations conducted by 17 inexperienced and 8 experienced observers. The observers were asked to determine which sound and spectrogram of the four call samples in the lower part of the frame is most similar to the one at the top of the frame.

Calls were presented in two test sequences consisting of 10 calls each. First, individuals from groups A and B both evaluated the same test sequence. In the second test sequence, group A individuals evaluated calls with equal degrees of similarity to the first sequence, while group B individuals were given call samples with higher degrees of similarity (e.g. different call-type variants of the sample call were presented together with different call-types among the four choices). In total, 12 call-types were evaluated by both groups to identify possible effects of experience on call-type categorisation. Different examples of the same call-types were used in more than one evaluation to minimize influences of variation in different recordings of calls. Results were arcsine square root transformed and mean differences between observer groups tested using a paired Student t-test.

Discrete call-types were named alphanumerically using the prefix AKS to designate that the calls were from southern Alaskan resident killer whales. Numbers reflect the order in which the calls were identified and are otherwise arbitrary. The subscripts (e.g. i, ii, iii etc.) that are used in combination with the AKS, and number denomination of some call-types indicate the existence of call-type variants (Table 2.2). We considered maximum repertoire size to be reached when no new call-types appeared after new recordings of a pod made in 2 consecutive years were added to the analysis. Based on this re-evaluation of our call categories we placed all calls in a particular call-type category.

Call-type sharing

We obtained a measure of the similarity of call-type repertoires or dialects for each pair of pods from an index based on the degree of call-type sharing. This index was derived from Dice's coefficient of association (Ford 1991), which normalizes the data to account for differences in repertoire size:

$$\text{Index of Similarity} = \frac{2N_C}{R_1 + R_2}$$

where N_C is the total number of call-types and sub-types shared, and R_1 and R_2 are the repertoire sizes (call-types plus subtypes) of the two pods. We used the index values, which ranged between 0 – 1, to calculate a hierarchical structure of acoustic similarity, which we displayed in the form of a dendrogram by means of average-link cluster analysis.

Genetic analysis

Skin biopsies were collected for DNA analysis by L.B.-L. and C.M. using lightweight darts projected with a pneumatic rifle (Barrett-Lennard et al. 1996b). We approached whales slowly on a gradually converging course and then travelled parallel to them at a distance of 10 - 15-m. After taking identification photographs of the entire group, we selected a whale to biopsy that we could identify visually and that had not been biopsied previously. We fired the darts at a region of the back approximately 1 m behind the dorsal fin and 50 cm below the dorsal ridge. The darts were designed to excise and retain a 0.5 g plug of skin and blubber, and to bounce off the whale and float. We re-photographed the darted whale if possible to confirm its identity and retrieved the darts from the water. We attempted to sample at least one member of each matriline. The collection of skin samples was covered under National Marine Fisheries Service permits No. 840 and No. 875-1401. The number of biopsies that were collected from different pods is also presented in Table 2.1.

Table 2.2: List of all identified call-types of southern Alaskan residents and their variants in alphanumerical order. An X in the appropriate column indicates call-types produced by an individual pod. Pods that share call- types are grouped together. Number of whales per pod is based on a 1998 census.

	Pod Names (# of matrilines, # of whales)						
Call Type	AB (11,25)	AI (1,7)	AJ (8,38)	AN (13,51)	AD (6,24)	AE (5,16)	AK (2,11)
AKS 01 i					X		X
ii					X		X
iii					X		
AKS 02 i						X	
ii						X	
AKS 03					X	X	X
AKS 04 i					X	X	
ii					X	X	X
AKS 05					X	X	X
AKS 06						X	
AKS 07					X		
AKS 08					X		
AKS 09 i					X	X	X
ii					X		X
AKS 10 i	X			X			
ii	X	X	X	X			
AKS 11 i	X	X	X				
ii	X	X	X	X			
AKS 12	X						
AKS 13	X	X		X			
AKS 14	X	X		X			
AKS 15 i	X	X	X	X			
ii	X	X	X	X			
AKS 17 i	X	X		X			
ii	X	X					
iii	X	X		X			
iv				X			
v				X			
AKS 18	X	X	X	X			
AKS 20				X			
AKS 21	X	X		X			
AKS 22	X	X		X			
AKS 23			X				
AKS 24 i			X				
ii			X				
AKS 25	X	X	X				
AKS 27			X				
AKS 28			X				
AKS 29			X				
TOTAL	17	14	13	15	11	8	7

Skin tissue from the biopsy samples was ground finely in a ground-glass tissue grinder and digested with Proteinase K for 24 hrs at 54 degree Celsius. DNA was than purified using phenol and chloroform and precipitated with ethanol, using the procedure of Sambrook et al. (1989). The entire mitochondrial D-loop of each sample was amplified using the polymerase chain reaction and sequenced using an Applied Biosystems 377 automated DNA sequencer. The sequences were aligned using the program Clustal-W (Thompson et al. 1994), and differences between sequences detected manually by comparing their output graphs from the automated sequencer. Further details of this procedure can be found in Barrett-Lennard (2000).

2.3 Results

Call-type repertoire analysis

Different observers made 848 recordings concurrent with photo-identification of killer whales between 1984 and 1999 (Table 2.1). We analysed 112 single pod recordings that were distributed over the whole recording period (Table 2.1). The number of recording sessions per pod ranged from 16 to 22 with durations of sessions ranging from 5 to 135 minutes. A minimum of 5 hours of recording was inspected for each pod. In total, 9000 calls were categorized by ear and visual inspection of spectrograms.

The energy distribution within the call spectrum usually allowed good spectrographic representation of frequencies from 0.5 kHz to 12-14 kHz. The lower frequency components (LFCs) ranged in frequency from 0.5 to 3.5 kHz, while the lowest band or fundamental frequency of the upper frequency components (UFCs) ranged from 4 to 11 kHz (Fig. 2.2). However, UFCs appeared to be more directional than LFCs. Occasionally, we observed the appearance or disappearance of the upper frequency components in calls made by whales that suddenly changed direction in front of the hydrophone. A call that showed UFCs in the majority of samples was labelled as always containing the component.

Call-type categorization

Most call-types could easily be distinguished and categorized by ear. For those that appeared to be aurally similar, differences existed in most of the following acoustic variables taken from the spectrogram: duration of calls, number and duration of segments and elements, existence of UFCs, as well as pulse repetition rates of LFCs (Fig. 2.2).

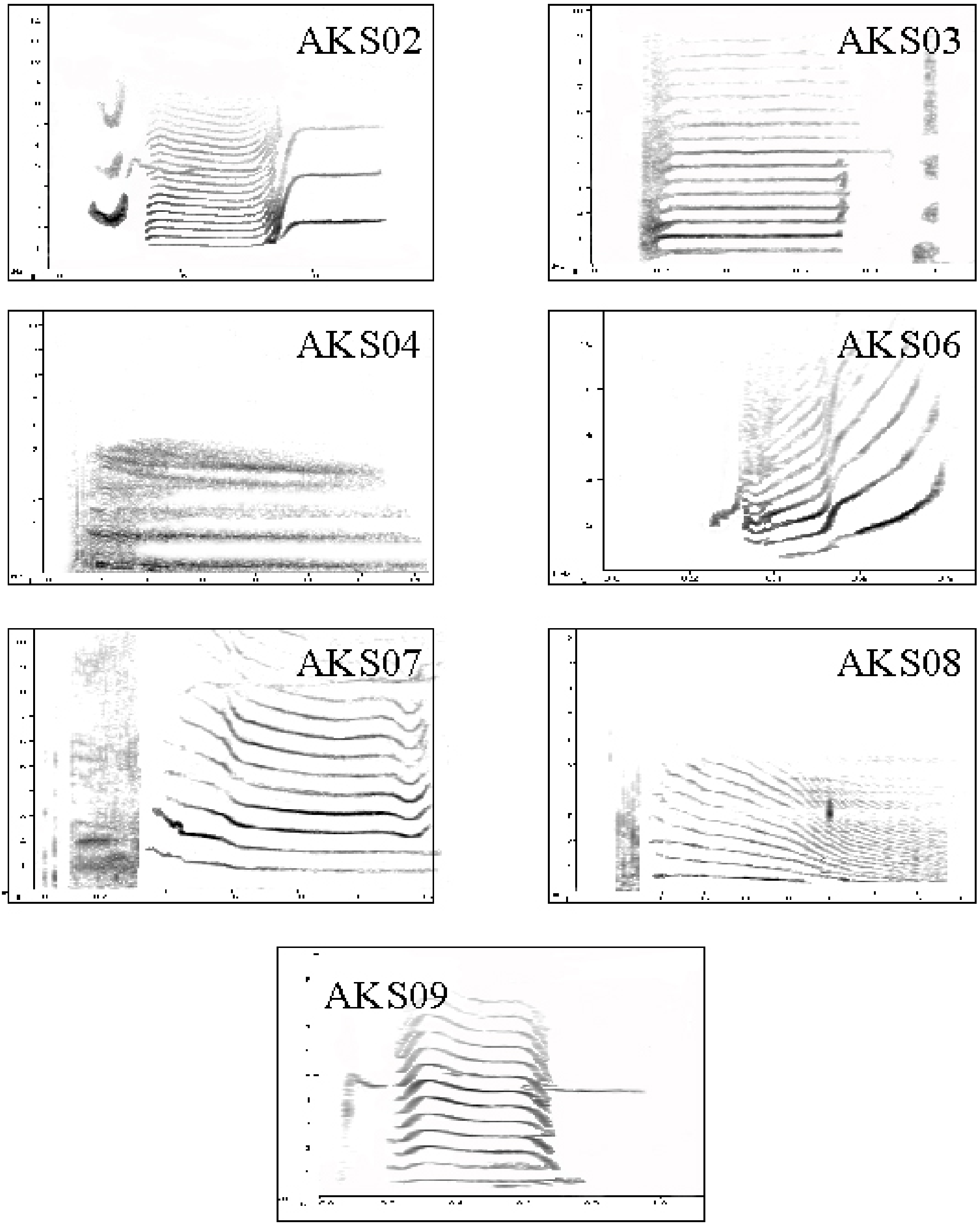

Figure 2.4a: Spectrographic examples of call-types that were used by the AD, AK, and AE pods of AD-clan with the exception of AKS01 and AKS05 that are displayed in figure 5. Please, view Table 2.2 to find out which call-types were shared between AD-clan pods.

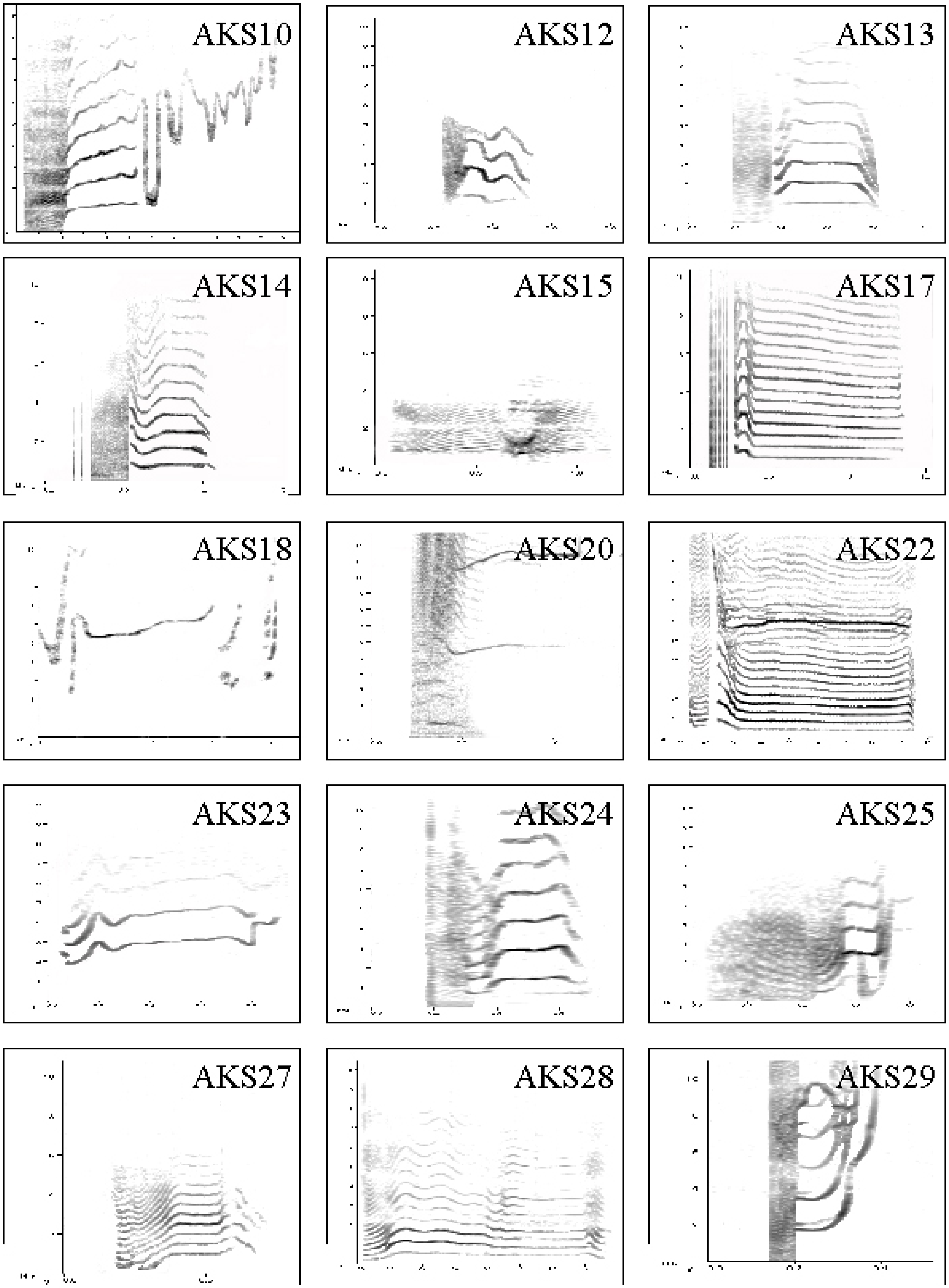

Figure 2.4b: Spectrographic examples of call-types produced by the AB, AI, AJ, and AN pods of the AB-clan with the exception of AKS 11 and AKS 21, which are displayed in figure 2.5. Please, view Table 2.2 to find out which call-types were shared between AB-clan pods.

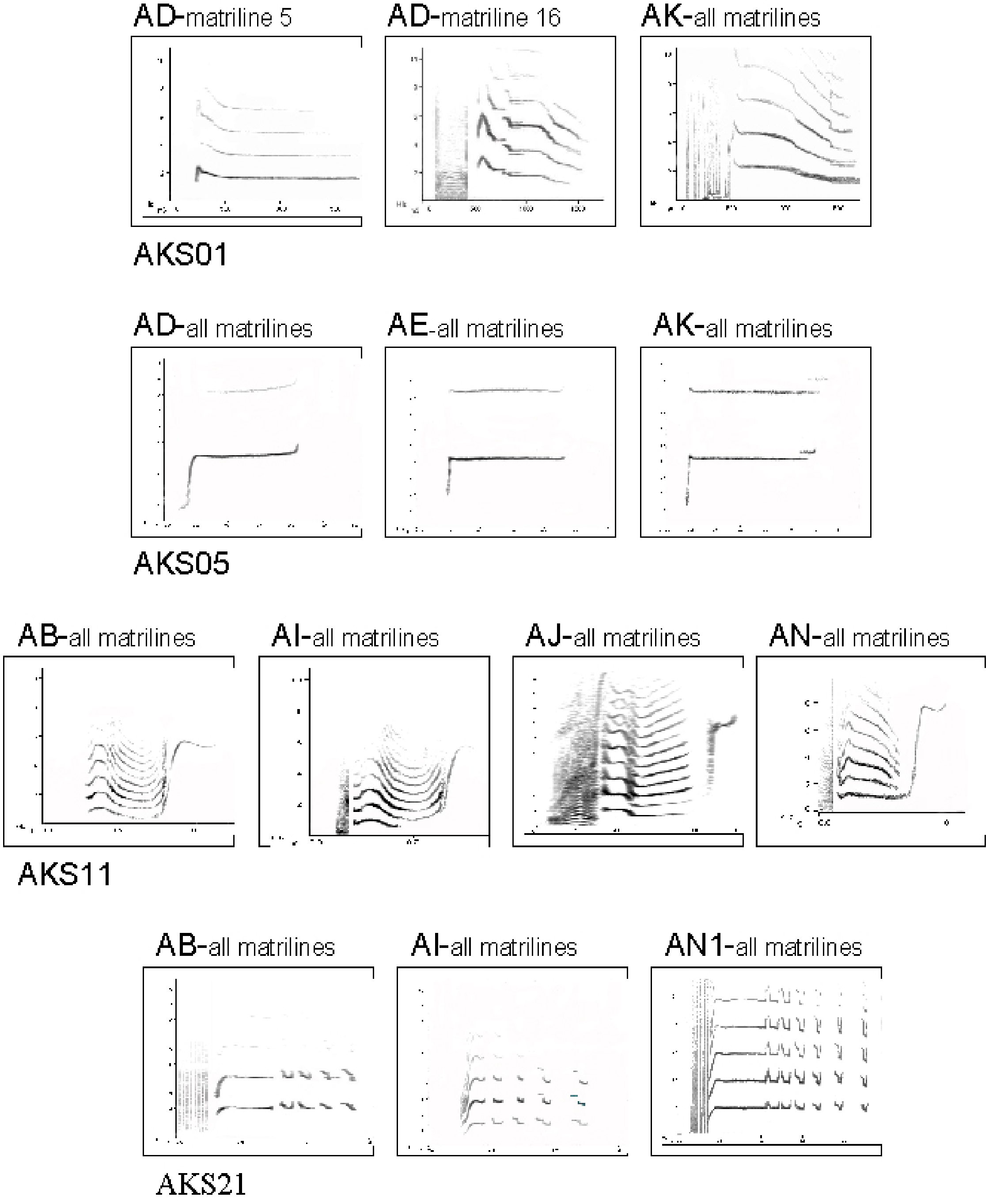

Figure 2.5: Spectrographic examples of call-types AKS01, AKS05, AKS11, AKS21 shared by members of AB-and AD-clan.

The seven pods AB, AD, AE, AI, AJ AK, and AN produced 26 distinct call-types (Fig. 2.4 and 2.5). Three types (AKS 16, 19, and 26) that were aurally considered call-types could not be differentiated from other call-types based on the spectrograms. These three types also occurred in only one or two of the recording sessions and were eliminated from further analysis. Nine of the 26 distinct types exhibited more than one stable variant. One had five stable variants, one three variants, and seven had two variants making a total of 39 discrete calls. Table 2.2 lists all discrete calls and the pods that produced them. AN pod and AD pod have recently split into four pods called AN10, AN20, AD5 and AD16, respectively (Matkin et al. 1999). However, the majority of recordings were made when these pods were still travelling in close association with each other. Therefore, we used the original pods in our analysis.

The inter-observer consistency of call-type categorization is usually very high (Bain 1986; Deecke et al. 2000). The evaluations done here showed that on average 71% (geometric mean = 68%, sd = 20) of the inexperienced evaluators agreed with our call-type definitions and 88% (geometric mean = 85%, sd = 20) of the experienced evaluators did (Fig. 2.6). The mean difference of 17% between the two groups was significant (paired t-test: $t_{11} = 2.84$, $p = 0.02$). The discrepancies between our call-type classifications and those of the experienced evaluators always involved the same three call-types (AKS 02, 04, and 05), while agreement was 100% for most other types. Given the number of choices presented to the observers, the probability that a call-type was considered similar by chance was 25%. The lowest value of agreement was 46% for AKS 02, while agreement for AKS 04 and 05 was 72% and 57%, respectively (Fig. 2.6).

All three values were considerably higher than expected by chance. Furthermore, two of the choices for similar call-types to the reference AKS 02 call were not produced by Alaskan residents, but were included in the experiment because they appeared to be close matches because of their similar frequency contour to the tested call type. Therefore, while the probability of erroneous categorisation may be considerable for call-types that exist in different sub-populations, it appears to be low for call-types produced within the same sub-population.

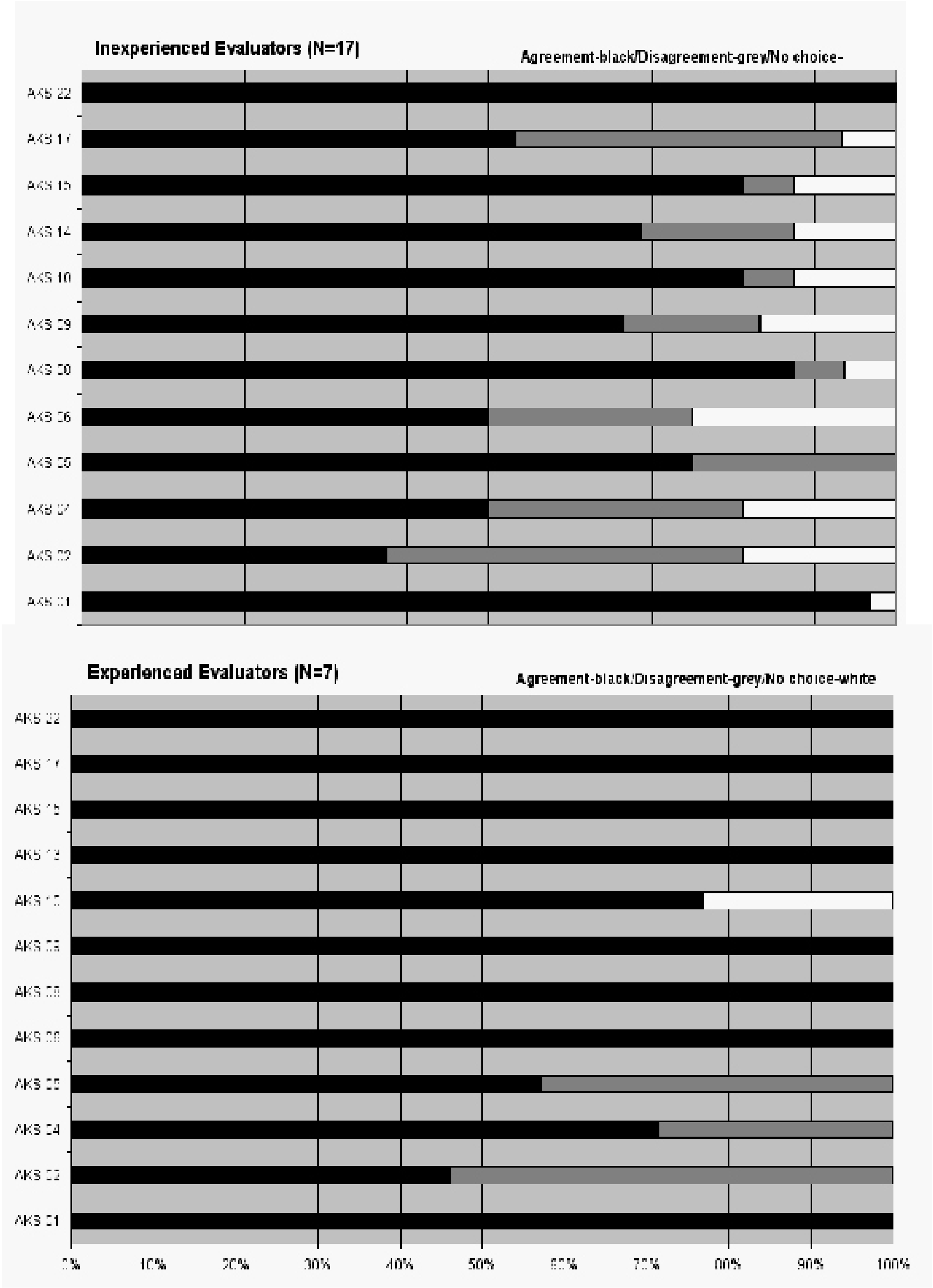

Figure 2.6: Results of the call-type evaluations by 17 observers without previous experience and 7 observers with previous experience with cetacean vocalizations

Call-type description

More than one segment was found in 9 call-types: AKS01, -02, -03, -11,. -14, -17, - 18, -21, -22 (Figs. 2.2, 2.4 and 2.5). In all cases except one (AKS 02), the initial segment was characterized by low pulse repetition rates that sounded like a buzz and therefore could have been confused with strings of echolocation clicks. However, unlike echolocation clicks these buzzes always preceded another sound segment by less than 0.1 seconds. The initial segment of AKS02 was a tonal segment that appeared to be part of the low frequency component of the call (Fig. 2.2). However, the spectrographic representations in no case revealed a connection between this segment and the rest of the LFC (Fig. 2). In five of the nine call-types (AKS01, -03, -11, -17, and -22), the number of elements of the second segment and/or the pulse repetition rates slightly varied among pods (Fig. 2.4 and 2.5). Call-types 13 and 14 did not vary greatly in either element structure or contour modulation between pods AB and AI, but these call-types of AB and AI pods did differ from AKS 13 and 14 produced by the AN pod (Fig. 2.4b).

Call-types AKS10 and AKS21 were characterized by a high number of elements (AKS10, Fig. 2.4b) or segments (AKS21, Fig. 2.5), relative to other calls. AKS10 was the longest call (> 2.5 sec.) with the highest number of elements (up to six) and had the most contour variations per element among pods of all call-types. AKS21 was characterized by two to six segments with almost identical contours (Fig. 2.5).

Four call-types (AKS03, -09, -11, and –22) had distinct pairs of LFC- and UFCs (Fig. 2.4 and 2.5). Others, such as AKS05 (Fig. 2.5) and AKS18 (Fig. 2.4b), consisted mainly of single UFCs, and therefore appeared acoustically more similar to whistles than to any pulsed call. Temporal spacing of contour modulations of the lowest band of AKS18 was distinctly different among pods (Fig. 2.4b).

Call-types AKS04 and AKS15 were characterized by small degrees of variation in pulse repetition rates (AKS 04: 900-1200 Hz; AKS 15: 300-700 Hz) and low peak frequency ranges (AKS 04:300-500Hz; AKS 15: 500–700 Hz) among pods. These two call-types were recorded predominantly in situations when the majority of the whales in a group were resting.

AKS02 (Fig. 2.2) produced by AE pod is one of the 9 call-types that were not shared by whales from more than one pod. The other 8 call-types were AKS06, also of AE pod, AKS07 and AKS08 of AD pod, AKS20 -23, -24, -27, 28 and –29, all of AJ pod . All of these calls showed a distinct number of elements and distinct contour variations, which made it easy to distinguish between them, at least among call types produced by Alaskan residents.

Call-type variants

Call-types varied predominantly in the number of segments and elements and/or showed consistent differences in the contour variation of call elements among pods (Fig 2.5).

Calls that were characterized by simple contour modulations, usually down-sweeping contours (e.g. AKS17 and AKS01, Fig. 2.4b and 2.5), produced more variants than calls that were structurally more complex (e.g. AKS22 or AKS03, Fig. 2.4a and b) or consisted of single UFCs (AKS05 and AKS18, Figs. 2.4a and b). Generally, a pod only used one call variant. Therefore, call variants could often be used to distinguish pods. However, in three cases, more than one call variant was used by a single pod: AKS01 in AD pod, AKS02 in AE pod, and AKS24 in AJ pod. These pods were characterized by matrilines that often swim alone (AD5 and AD16) and/or that shared few calls with other pods (AE and AJ). Differences between call-type variants are highly distinguishable based on their gestalt, because 70% of all experienced observers agreed with our choices of 7 call-type variants. Furthermore, this number increased to over 85% for those observers with previous experience in killer whale call-type categorization (n=3).

Relationship between repertoire sizes and group sizes

The mean number of call-types given by each pod was 12 (mean ± se = 12.14 ± 3.67, n = 7), and the median 13 (Table 2.2). AK pod used the least (seven) while AB pod used the most (17) number of call types. We did not detect any differences in the numbers of call-types produced by different matrilines of the same pod. The number of call-types produced per pod was not closely correlated with the numbers of whales in that pod (r6 = 0.438, p = 0.33). Similarly, the number of matrilines within a pod was not correlated with repertoire size, although there was a non-significant trend (Fig. 2.7; $r_6 = 0.618$, $p = 0.14$). Regression residuals were approximately normally distributed. If the AI pod, which started splitting from the AB pod during the early 1980s was combined with the AB pod, the correlation between matriline number per pod and repertoire size increased ($r_5 = 0.932$, $p = 0.007$).

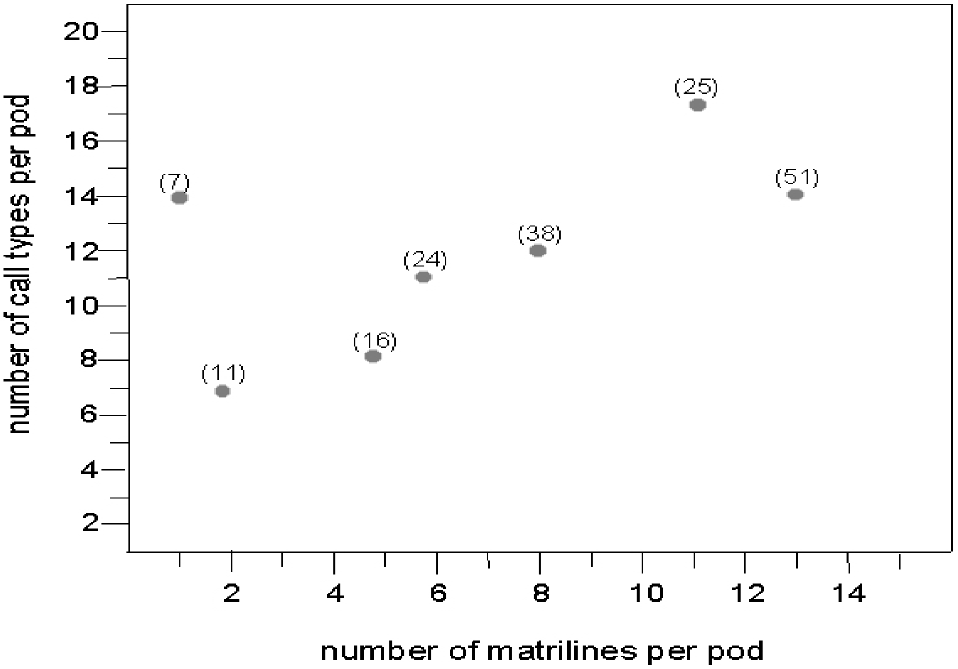

Figure 2.7: Comparison between pod repertoire size and number of matrilines per pod. The numbers in parentheses represent the number of whales per pod based on the 1998 census.

Call sharing

Forty-eight percent of the discrete calls identified (n=8000) were shared by more than one resident pod, and pods shared between 53 and 100% of their call-type repertoires with other pods (Table 2.2). Although all seven pods shared calls with at least two other pods, the pattern of sharing revealed two distinct clusters of pods. AB, AI, AJ and AN pods shared calls, as did AD, AE, and AK pods, but no calls were shared between these two groups of pods. Similar to Ford (1991), we defined pods that shared calls as a vocal clan. Therefore, we defined two vocal clans among southern Alaskan resident killer whales. AB, AI, AJ, and AN pods belong to the AB-clan, and AD, AE, and AK pods belong to the AD-clan.

We calculated the degree of repertoire similarity between pairs of pods of each clan using the index of similarity (Ford 1991). Because pods from different clans did not share any calls, the similarity between them was 0 (Table 2.3).

The repertoires of AB, AI, and AN pods within AB-clan were more similar to each other than they were to the repertoire of the AJ pod. Similarly, AD and AK pods within the AD-clan had more shared calls than either had with the AE pod. The results of the repertoire analysis are displayed in the form of a dendrogram by means of average-link cluster analysis (Fig. 2.8).

Table 2.3: Acoustic similarity between pod repertoires based on the index of similarity (Ford 1991) where 1 means the repertoire of two pods are identical and 0 means the two pods do not share any call.

Pod	AB	AI	AJ	AN	AD	AE
AI	0.903					
AJ	0.533	0.519				
AN	0.75	0.759	0.429			
AD	0	0	0	0		
AE	0	0	0	0	0.444	
AK	0	0	0	0	0.824	0.533

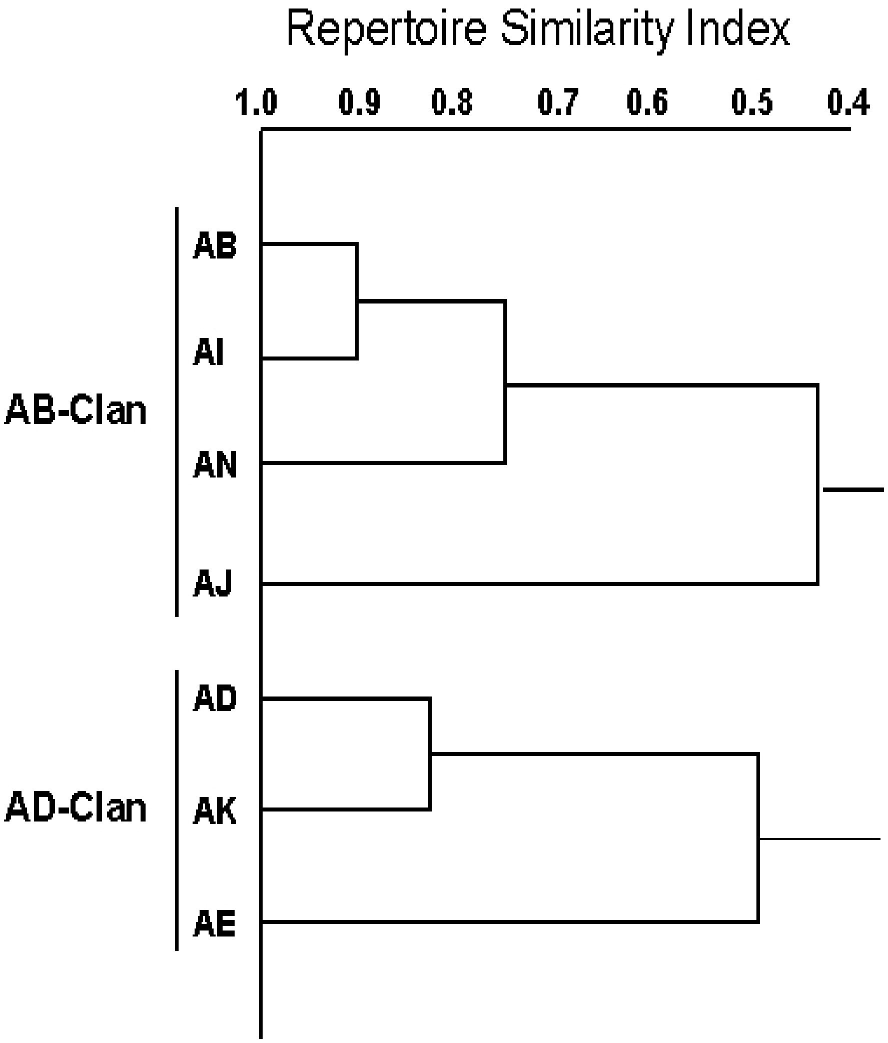

Figure 2.8: Degree of repertoire similarity between pods based on a single-cluster dendrogram of acoustic similarity.

Table 2.4: Mitochondrial D-loop haplotype distinctions of AB- and AD-clans in comparison to other resident killer whale clans in the Northeastern Pacific. NR stands for Northern Resident type and SR for Southern Resident type.

Clan	# of biopsied whales	Community	D-loop haplotype
AB	44	Southern Alaska	NR
AD	38	Southern Alaska	SR
A	75	Northern Brit. Columbia	NR
G	34	Northern Brit. Columbia	NR
R	17	Northern Brit. Columbia	NR
J	8	Southern Brit. Columbia	SR

Genetic analysis

Eighty-two photo-identified resident whales from southern Alaska were biopsied. The complete mitochondrial D-loop sequence was determined for 40 of these whales, including one individual from each set of mothers and known offspring. All of the sequenced whales in the four pods that belong to the AB-clan had the same mitochondrial D-loop haplotype (Table 2.4). This haplotype has also been found in all biopsied killer whales (n=126) of the Northern Resident (NR) community, which inhabits most of British Columbia and the southern tip of Alaska (Fig. 2.1). In contrast, all whales in the three pods of the AD-clan showed a mitochondrial haplotype that has also been found in all biopsied whales (n=8) of the Southern Resident (SR) community (Table 2.4), which is usually sighted in southern British Columbia, Washington State, and occasionally further south (Fig. 2.1).

2.4 Discussion

This study is the first to provide direct evidence that the vocal clans of resident killer whales, which Ford (1991) described as clans, are maternal lineages. One could argue that the call-type categorization method that I used to define clans is less objective than one that uses statistically significant differences among sound variables to make discriminations. However, the ability of my discrimination method to detect acoustic differences between maternal lineages is proof that it provides biologically meaningful categorizations. This discrimination method has also been used in the categorization of discrete acoustic structures in bird and humpback whale songs, such as notes, phrases and themes, and has proven to be highly reliable in detecting overall similarities and differences among these structural parts within and between songs (Marler & Tamura 1962); (Payne & McVay 1971).

Evolution of clans

My results and those of Barrett-Lennard (2000) show that maternal relatedness is reflected in call sharing among resident killer whales. Ford (1991) proposed such a system of call sharing but had no access to genetic data.

Call-type transmission and learning

Call-types could be inherited vertically from their parents (genetically or culturally) or learned from all members of the group, which implies at least some form of horizontal/oblique transmission (Deecke et al. 2000). Furthermore, call-types could be culturally selected to identify the group.

All members of the matriline use the same set of calls (Ford 1991; Miller & Bain 2000), and mating usually takes place between pods (Barrett-Lennard 2000). Paternal genetic inheritance can be ruled out, because it would produce different repertoires for individuals of the same pod. Maternal genetic inheritance of call-types either through mitochondrial DNA, maternal sex chromosomes, or through genomic imprinting is also unlikely, because many call-types are highly complex. Genomic imprinting has been reported to influence the transmission of certain social behaviours (Spencer et al. 1999). However, I could not find any evidence in the literature that structural modifications that enable organisms to produce complex behaviours have been encoded by mtDNA or have been imprinted.

Although call learning in killer whales has not yet been demonstrated in a controlled experiment (Janik & Slater 1997), observations of captive killer whales with different regional ancestry (Bain 1988; Ford 1991) have shown that whales regularly imitate calls of their tank mates, and young whales copy calls preferentially from close relatives (Bowles et al. 1988). Learning is also the most likely mechanism for true vocal mimicry (Ford 1991), and horizontal or oblique transmission of calls among wild killer whales (Deecke et al. 2000). Therefore, the most parsimonious explanation for the existence of vocal clans is that killer whale calls are socially learned from maternally related individuals.

The genetic differentiation of clans is best explained by a lack of dispersal of females (Barrett-Lennard 2000). Consequently, the differences in repertoires among dialect groups within each clan could either be the passive result of gradual pod splitting and call divergence over time (genetic separation followed by genetic or cultural drift (Bigg et al. 1990)), the result of cultural selection on repertoires after separation, or both.

Ford (1991) proposed a number of potential mechanisms for repertoire divergence such as cultural drift, vertical cultural transmission from mother to offspring, cultural diffusion and innovation. Cultural drift is the passive result of pod fission, and call divergence would be caused by copying errors during the transmission process. New calls should form and old ones lost at a somewhat constant rate that would correspond to the change in number of matrilines per pod. Repertoire size would tend to increase very gradually with the increase in number of matrilines of the pod. For example, AI03 matriline of AI pod (7 whales: 4 males, two females, one juvenile), which is believed to have split from AB pod during the first half of the 1980s (Matkin et al. 1999), consistently shared 14 of the 17 calls from the AB pod repertoire. Therefore, AI03 differs in 18% of its repertoire from AB pod, a number that is consistent with drift. However, this 18% difference is based solely on call losses. No new call-type or variant has yet been invented. Concurrently, the 12 matrilines that comprised AB pod in 1984 declined from around 50 members to 25 members and 8 matrilines in 1998 (Matkin et al. 1999). A change in repertoire size, however, was not detected in recordings of the remaining 8 matrilines. Drift should produce slightly different repertoires between matrilines, if call use varies between matrilines, as has been shown for some matrilines in the Northern Residents (Deecke et al. 2000; Miller & Bain 2000). If cultural drift is the only cause for vocal change there should have been at least some repertoire change in the AB pod, which lost four complete matrilines or 33% of its original number of matrilines. Furthermore, it appears that certain call-types change more quickly than others (Deecke et al. 2000). Therefore, cultural drift alone cannot explain all the observed differences in repertoires.

If vertical cultural transmission from mother to offspring were the only mechanism responsible for the transmission of call-types, one should also see minor variations among calls produced by different matrilines. However, as Deecke et al. (2000) showed, such variation only occurs in structurally simpler call-types, while complex call-types remain highly similar among matrilines of the same pod. Therefore, vertical cultural transmission also cannot be the only mechanism for the observed repertoire differences.

Cultural diffusion results either from dispersal of whales between matrilines or the sharing of calls between matrilines that are not closely related. Dispersal has not been observed in over 25 years of study on resident killer whales in British Columbia (Ford et al. 2000). Call mimicry between not closely related matrilines has been observed (Ford 1991). Mimicked calls, however, can always be distinguished from the calls produced by the matriline that commonly uses the mimicked type. No call type transfer has been observed for either resident killer whale clans in British Columbia or Alaska. Call innovation, though the most plausible cause for major divergence in resident killer whale repertoires, also has yet to be observed.

Considering reports of variation in call frequency among matrilines of the same dialect group (Ford 1991; Miller & Bain 2000), my findings are in support of a transmission process based on both cultural drift in call structure and selection on repertoire difference and similarity. Repertoire difference could be readily achieved by selectively dropping calls and changing the frequency of others during matriline fission, while similarity is maintained by keeping the majority of calls stable, while only allowing certain call structures to change gradually over time. Such gradual processes have been detected in call-types of the Northern Residents (Ford 1991; Deecke et al. 2000; Miller & Bain 2000). Deecke et al. (2000) proposed a cultural drift model for the change they observed. However, they could not determine whether this change was neutral with regard to loss or invention of call structure, and also failed to detect a similar gradual change for another call-type. Barrett-Lennard (2000) provided support for cultural selection of call repertoires by showing that an inbreeding avoidance function of group-specific dialects is the most parsimonious explanation for the observed mating patterns in the Northern Residents. Mating is virtually absent within pods, rare within clans, and common between clans. Acoustic differences between clans could therefore be the result of both types of cultural evolution, A) call-type selection for parts of the repertoire, presumably calls that are complex in structure and difficult to produce and learn, and B) drift for those calls that are easier to produce and learn.

Possible functions of clans

If calls are learned selectively from their mothers within the matriline, females could determine their degree of relatedness to prospective mates. Any males that attempted to cheat by using different calls could easily be unveiled, because females could determine the relatedness of a male based not only on his own calls, but on those used by his matriline (Barrett-Lennard 2000). Since male killer whales have not been observed to form male coalitions that coerce females into mating (Connor et al. 2000), males likely depend on female choice for their mating success. Cultural lineages based on calls learned in the matriline serve to associate males strongly with their mothers. Mating success of males therefore could depend on the status of the matriline within a clan or community. Males of matrilines that are highly successful in matters of survival and reproduction might be chosen preferably as mating partners (Barrett-Lennard 2000).

A similar example of gene/culture lineages is found among certain human populations. The Tsimshian of the coast of British Columbia and Alaska were historically organized in four named clans. The names were shared with two other societies, the Haida and the Tlingit (Garfield 1939). Before the Tsimishian came in contact with Europeans, each clan had several names that were the sole property of that clan. Children of marriages between members of different clans carried a maternal clan name with an addition that indicated the clan of the father. Clan names thereby always reflected degrees of relatedness and were used to avoid marriage between close relatives (Garfield 1939).

With the exception of a Southern Alaskan Resident call-type (AKS 02) from the AD clan that was very similar to a Northern Resident R-clan call-type (N 32ii), all other call-types were used only within their respective clans. The two clans (AD and R) that used similar call-types have adjacent ranges but have not been observed associating with each other. Therefore, call-type transmission appears to take place solely within clans, and call-type exchange between clans is negligible if it occurs at all. The two vocal clans within the Southern Alaskan Residents have different mitochondrial DNA haplotypes, while the three clans of the Northern Residents share the same haplotype. This indicates that call repertoires evolve faster than mitochondrial DNA, because female exchange between matrilines, pods, or clans is very rare or non-existent (Barrett-Lennard 2000), thereby pointing towards the same maternal ancestor of the three vocal clans among Northern Residents. Furthermore, the two vocal clans of the southern Alaskan sub-population, which clearly are distinct cultural and genetic lineages, may have joined to form a breeding population after both clans had migrated into the area.

Another possible function of clans could be to help kin survive. One of the main food sources of resident killer whales is salmon, particularly chinook (*Oryhnchus tshawytsch;* (Ford et al. 1998)) and coho (*O. kisutch*; (Saulitis et al. 2000)). Large brained animals, such as killer whales, potentially have the ability to store temporal and spatial information in their memory. Long-lived females can positively affect the survival of their relatives by using such an ability to store information on the seasonal distribution of salmon.

The evolution of parallel cultural and genetic lineages in resident killer whales shows similarities to the development of parallel lineages in humans. In humans and in resident killer whales the similarities of vocalizations within genetically distinct lineages is in sharp contrast to distinct vocal differences among lineages (Barbujani 1991). Human languages, which might have evolved through a process of dialect divergences (Hill 1978), also show geographical distinctiveness. However, different dialects can also co-exist in the same area, as seen by the African American vernacular versus standard American English.

Killer whale dialects identify maternal relatedness. Because resident killer whales do not appear to leave their natal group this lowers the rate by which dialects change over time. The change of dialects is probably a result of cultural drift. However, cultural selection on a group level that would regulate how dialects change over time cannot be ruled out as an alternative explanation.

2.5 Summary and conclusions

Resident killer whales in the Northeastern Pacific are characterized by cultural lineages based on shared vocal repertoires. Cultural lineages are the result of learned social traditions that are stable for several generations. When cultural lineages also reflect common ancestry and/or are shared by individuals that live together they are called clans. Most human societies were at some point characterized by the existence of clans. Clans also exist among other mostly cooperatively breeding mammals and cooperatively breeding birds. The existence of clans among killer whales has been previously proposed but has not been confirmed. By comparing my analysis of vocal repertoires to a pre-existing study on genetic relatedness, I could show that clans exist among the resident type killer whales, *Orcinus orca*, in Southern Alaska. Resident killer whales live in stable matrilines from which emigration of either sex has not been observed. Matrilines that associate regularly (≥ 50% observation time) were called pods. Pods are believed to consist of closely related matrilines and share a unique repertoire of discrete call-types. Pods that share parts of their repertoire form what has been proposed to be a clan. I identified discrete call-types of seven pods from southern Alaska, using a method based on human discrimination of distinct aural and visual (spectrogram) differences. The repertoires and genetic relatedness of the seven pods that belonged to two acoustically distinct groups were compared. Each group was monomorphic for a different mitochondrial D-loop haplotype. Nevertheless, pods from different clans associated frequently. It thus appeared that the acoustic similarities within groups, which I presumed to be cultural, reflected common ancestry, and that these groups therefore meet the above definition of clans. I also argued that a combination of cultural drift and selection were the main mechanisms for the maintenance of clans.

3. CULTURAL MARKERS OF KILLER WHALE CLANS, COMMUNITIES AND POPULATIONS

3.1 Introduction

Most animals use signals to communicate their membership in a particular group, population, or species to others (Bradbury & Vehrencamp 1998). The most common markers are chemical signals, such as scent markers, and visual signals, such as ornaments and colourations, or specialized sounds and vocalizations (Bradbury & Vehrencamp 1998). In many cases these marker signals are used to acquire and defend resources (Krebs & Davies 1993). However, markers can also help to solicit cooperation, especially when the signals reflect relatedness and the intended receivers of the signals are close relatives (Hauser 1996). Markers that reflect relatedness can also function in mate choice to reduce costs of inbreeding or excessive outbreeding (Pusey & Wolf 1996).

The structure of chemical signals, many visual signals and a number of acoustic signals are genetically determined (Bradbury & Vehrencamp 1998), which means they reflect the genotype of the sender. However, the process of distinguishing between signals can still be a learned behaviour by the receiver (Hauser 1996). Other group markers, such as song dialects of birds, call dialects of bats and cetaceans, and languages of humans have to be learned through imitation (Janik & Slater 2000). In these species the function of the markers are often socially learned and therefore cultural traits.

Vocal markers are either specific vocalizations, e.g. flock-specific calls of black-capped chickadees (*Parus capillus*) (Nowicki 1983), or are parts of complex signals, such as element variations of songs (Marler & Tamura 1962). The structural complexity of signals can be linked to their function as group markers, if sounding similar increases fitness. Song repertoires of birds that defend territories as a group may increase fitness if the songs elicit cooperation from neighbours (Lachlan et al. 2004). The same can be said for human dialects and languages (Aiello 1998). However, Aiello (1998) also suggested that large group-specific signal repertoires of humans may be the result of the need to cooperate efficiently. Increasing group sizes may have resulted from greater predator pressures after changing habitats from forested areas to the open savannah. To cooperate in these larger groups and to keep track of close relatives and potential mates, complex signals may have become beneficial.

In animal communities that consist of individuals with varying degrees of relatedness, the structural complexity of signals is often associated with the social organization. For example, birds combine notes and syllables to form songs, which can reflect genetic and cultural relatedness of communities (e.g. Baker 1974; MacDougall-Shackleton & MacDougall-Shackleton 2001). In humans, language is based on sentences, which are structured strings of words. Words themselves are combinations of syllables, whose distribution patterns reflect social, genetic and cultural relatedness (Cavalli-Sforza 2000). In birds and humans, signal structure can be associated with both individual fitness and group recognition. The common feature of these markers is that they are learned and often receive little change between generations. This leads to cultural stability and can make learned vocal markers even more effective than their genetically pre-determined counterparts.

Aside from birds and humans, learned vocal signals are only known to occur in a few other species, such as greater spear-nosed bats (Boughman 1998) and some marine mammals (Janik & Slater 1997; Slater et al. 2000). For example, female greater spear-nosed bats learn the calls of the group that the female immigrates to after reaching maturity (Boughman 1997). The learned signature whistles of male bottlenose dolphins appear to reflect maternal relatedness (Sayigh et al. 1995). Associations between signal structure and social and genetic structure of populations occurs in song birds (e.g. song sparrows, Reid et al. 2005b), cetaceans (e.g. killer whales, Bigg et al. 1990; Barrett-Lennard 2000) and humans (Cavalli-Sforza 2000). Killer whales live in stable groups of closely related individuals in which they learn their calls. Call or dialect divergence is associated with the social divergence of these groups (Ford 1991; Deecke et al. 2000; Miller & Bain 2000). As a result, dialects are likely culturally transmitted vocal markers of social and genetic relatedness. Therefore, killer whales are excellent models to study associations between signal structure and genetic and cultural relatedness.

Cultural markers and gene-culture coevolution

If calls are used as vocal markers of social and genetic relatedness, adaptive culture or culture-gene co-evolution could exist in killer whales (Whitehead 1998; Whitehead 2005). According to the gene-culture co-evolution theory, a culturally selected trait can influence the fitness of individuals if it influences behaviours, such as who to associate, mate, and cooperate with. Ultimately, the vocal marker would then affect both the social and genetic history of a population or sub-population (Feldman & Laland 1996). To do so, a cultural marker needs to be stable enough to reliably identify members of a cultural group or population. At the same time the marker must vary enough to allow for reliable discrimination of individuals or groups. In the case of a vocal marker, information about social and genetic history could be encoded in the structure of complex vocalizations, such as compound signals (Bradbury & Vehrencamp 1998). These types of signals can transmit more than one type of information at the same time. There is evidence that some killer whale calls are compound signals because they consist of structural components that are produced at the same time but are often modulated independently (see below).

The production mechanisms and structures of killer whale calls

Killer whale calls are complex structured vocalizations (Fig. 2.2 in Chapter 2) that often consist of both upper frequency (UF) and lower frequency (LF) components (Fig. 2.2 in Chapter 2). The components have different acoustic properties and might have different functions (Miller 2002). They are most likely produced by bi-phonation (Tyack & Miller 2002). Bi-phonation in odontocetes is the result of contractions of two nasal plugs causing air movement through two pairs of phonic lips at the bottom of the upper nasal passage (Cranford 2000). The two plugs can be contracted independently (Dormer 1979), which causes air to move past different parts of the phonic lips (Cranford et al. 1996). The actual sound production seems to take place when the phonic lips part (Cranford 2000). Clicks and pulses appear to be generated with either of the two pairs of lips or with both pairs working in unison (Cranford et al. 2001). Whistles are generated with only the left pair and contraction of the left nasal plug (Dormer 1979; Cranford et al. 2001). The longer the lips remain closed during contraction of the nasal plugs, the greater is the air pressure difference between the lower and the upper nasal passages. The sound energy of the emitted vocalization increases linearly with the pressure difference (D. Bain, pers. comm.). The movements of the two nasal plugs can vary in how strongly their contractions are coupled, which possibly leads to differences in loudness of call components. How strongly the opening of the phonic lips are coupled may be responsible for the similarity of the frequency modulations of the two components.

UFCs of killer whale calls are transmitted directionally with most of the sound energy emitting to the front of the whale, while LFCs are omnidirectional (Miller 2002). The potentially different functions of the two components could have caused separate evolution of the two components. A whale can lower the sound amplitude of its directional signals when addressing an intended receiver to make eavesdropping by others more difficult (McGregor & Dabelsteen 1996). Non-directional signals, such as LFCs, can be used to detect distances of a sender through linear degradation of sound intensity (Naguib & Wiley 2001). UFCs are probably good indicators of travel directions of killer whale groups along narrow fjords and channels. LFCs, on the other hand, may be good indicators of group distances in open water. Interestingly, the LFCs of many calls can be further divided into smaller elements based on abrupt frequency shifts (Ford 1984; Hoelzel & Osborne 1986; Strager 1995 and Chapter 2). Abrupt frequency shifts tend to increase signal distinctiveness against background noise (Ford, pers. comm.).

The occurrence of UF and LF components and elements within LFC of calls is a stable call type characteristic (Ford, pers. comm.) that can be called the syllabic call structure.

Divergence of syllabic call structure and possible function

Previous researchers have examined structural divergences of calls among closely related and frequently socializing resident killer whale groups (Ford 1984; Deecke et al. 2000; Miller & Bain 2000). They found that call structure diverges proportionally to the decrease in social contact and relatedness among matrilines of the same clans (Ford 1991 and Chapter 2). Consequently, they concluded that call divergence could be the result of cultural drift due to social divergence. At the clan level however, acoustic similarity of call types is so reduced that call type similarity disappears (Ford 1991). Because many clans still socialize, distinct repertoires of clans may not merely be the result of drift, but may result from divergent selection acting to produce distinct repertoires. Call repertoires or dialects would then function more reliably in mate choice because clan identity can be better recognized. Community membership appears to be stable in resident killer whales (Ford et al. 2000). Matrilines from different communities do not associate and may avoid each other. Furthermore, matrilines that are not always in acoustical contact could still use call structures as reliable markers of community membership. Community markers can be beneficial not only in mating but also in spacing to avoid conflict over other resources.

Mating among resident killer whales takes place within communities (Barrett-Lennard 2000). In the northern resident community, mating takes place preferentially between members of different clans (Barrett-Lennard 2000). For small populations, it is particularly advantageous to have a mechanism for avoiding close inbreeding and extreme outbreeding (Keller et al. 1994; Pusey & Wolf 1996). All resident communities have small effective population sizes (< 100 whales) (Barrett-Lennard 2000), therefore dialect differences could have adaptive significance by reducing inbreeding through mate choice. Selection on repertoires to diverge would cause an increase in distinct calls. To distinguish between members of the same and different communities, killer whales need to regularly update their repertoire of known calls or use other vocal features to make that distinction. Call repertoire similarity appears to be associated with the degrees of social contact between matrilines (Ford 1991; Deecke et al. 2000). Without markers identifying community membership, a reduction in social contact after matriarchs die could cause communities to diverge. This would then result in a loss of potential mates and is likely selected against. For a species living in an environment that does not favour the transmission of chemical or visual signals, such a marker would be best embedded in the structure of vocalizations. Because vocal learning is present in killer whales (Bain 1988; Ford

1991; Barrett-Lennard 2000) there might be positive selection for some aspect of the call structure.

Transient communities also appear to be stable, although temporary crossover of individuals between geographical regions occurs (Ford & Ellis 1999). Transients use fewer call types than residents (Ford & Morton 1991; Deecke 2003). Regional vocal dialects are also present within transient communities, but they involve structural variations of shared call types rather than distinct call repertoires (Ford & Ellis 1999; Deecke 2003). All transients of the same community appear to mix socially and genetically (Ford & Ellis 1999; Barrett-Lennard 2000). Clan structure appears to be absent. Vocal repertoires of transients may therefore be less structurally diverse than repertoires of residents because they do not need to reflect clan memberships. Because of their differences in social structure, transients and residents are good candidates to examine differences in associations between vocal repertoires and social structure.

In this chapter, I examine the stable structure of killer whale calls by comparing syllable distributions among clans, communities and between two populations. The main focus here is to test whether selection acts on syllable structure, which would allow syllables to be used as community and population markers. Based on the results I discuss syllable evolution and function.

I start by describing the extraction of syllables from identified call types. I then categorize syllables and test how reliably human observers can recognize syllable categories in a blind procedure. Finally, I examine and test mechanisms leading to syllable divergence (drift versus selection) with a method designed to test for adaptive changes in nucleotide sequences (McDonald & Kreitman 1991). I modified this method to test whether variation in the occurrence of syllable types in clans, communities and populations evolved through neutral drift or whether selection acted on syllable divergence. If neutral evolution was responsible for syllable type differences among groups, ratios of syllable variation within groups versus fixed syllable types between groups should be equal. If variant and fixed type ratios differ across groups however, I can infer that selection has acted on the variation in syllabic call structure within and between groups.

3.2 Methods

Before I could categorize syllables and analyze how types are distributed among different groups of killer whales, I had to recognize syllable boundaries and extract syllables from calls. To do this, I used the fact that many calls are separated into two frequency components that are often modulated independently of each other. Upper frequency components, or UFCs, have pulse repetition rates or tone frequencies above 3.5 kHz. Lower frequency components, or LFCs, have pulse repetition rates below 3.5 kHz; Fig. 2.1 in Chapter 2 and Fig. 3.1) (Ford 1987; Miller & Bain 2000). Both components can extend over the full length of a call, but one is often longer than the other (Ford 1987 and Chapter 2). LFCs of many calls can be divided further into smaller units based on distinct (abrupt) changes in the frequency contour and sound pitch. Most UFCs are single units that only occur once in a call.

To distinguish syllables, spectrograms were examined for the occurrence of independently modulated frequency contours and abrupt shifts in frequency. Spectrograms were produced using Canary Sound Analysis Software (Cornell Laboratory of Ornithology, Ithaca, NY, USA, 1998). The sounds were sampled at 44.1 kHz. The spectrographic analysis was set to use a 1024-point Fast Fourier Transformation (FFT) and an overlap of analysed time series of 87.5%. The resulting spectrograms had a time grid resolution of 2.902 milliseconds and frequency grid resolution of 43 Hertz. Spectrograms are optical representations of sounds in three dimensions, the time (x-Axis), the sound frequency (y-axis), and the relative power spectrum density (darkness or gray scale of contour bands).

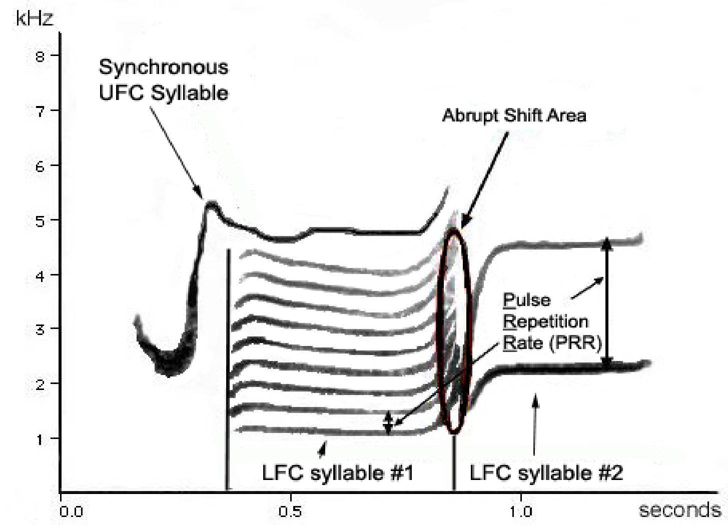

Figure 3.1: Example of a discrete call with upper and lower frequency components. Ellipse marks area of abrupt pulse repetition rate shift (sound pitch change) that divides lower frequency component into two elements (syllables)

Separating syllables from calls

I examined calls from several recordings with high signal-to-noise ratios. Where no appropriate sound recordings were available, I used spectrograms from a reference catalogue (Ford 1987). Depending on the frequency with which calls occurred in recordings, I examined between 10 and 30 spectrograms of most of the 147 categorized calls of resident killer whales (Ford 1987; Matkin et al. 2002, Chapter 2). Calls include both distinct call types and distinct variants of types (Ford 1987 and Chapter 2). I also included 16 calls of transient killer whales (Ford 1987; Deecke 2003).

Some calls contained UFCs that were produced sequentially with syllables in LFCs (Fig. 3.2), while other UFCs were produced in parallel or synchronously with LFCs (Fig. 3.1). Synchronous UFC syllables were modulated differently than the corresponding LFC syllables and were probably produced by different parts of the vocal system of killer whales (Miller 2002). This result has been demonstrated for high frequency components of signals of other cetaceans (Amundin 1991). Here, I distinguished between parallel or synchronous UFC (P-UFC) syllables (Fig. 3.1), and those that occurred sequentially (S-UFC) with LFC syllables (Fig. 3.2). Aside from UFCs and LFCs, killer whale calls also include buzzes (Fig. 3.2) and unstructured elements (Ford 1987; Miller & Bain 2000; Tyack & Miller 2002). These are difficult to categorize and were not considered in this analysis. Whistles and echolocation clicks were also excluded (Ford 1989). Echolocation clicks are strongly directional signals and whistles appear to be associated with close proximity of whales (Ford 1989; Thomsen et al. 2002). They are probably less reliable for group recognition over greater distances and in every direction.

UFC and LFC syllables were extracted from call spectrograms based on the procedure shown in Figure 3.3. LFC- and UFC syllables were included in the analysis if the frequency contour differences were considered discrete and not gradual, i.e. if they showed discrete differences in number and locations of frequency modulations (Fig. 3.4). This means that sometimes more than one syllable was extracted from the same within-call position of the same call type (Fig. 3.4).

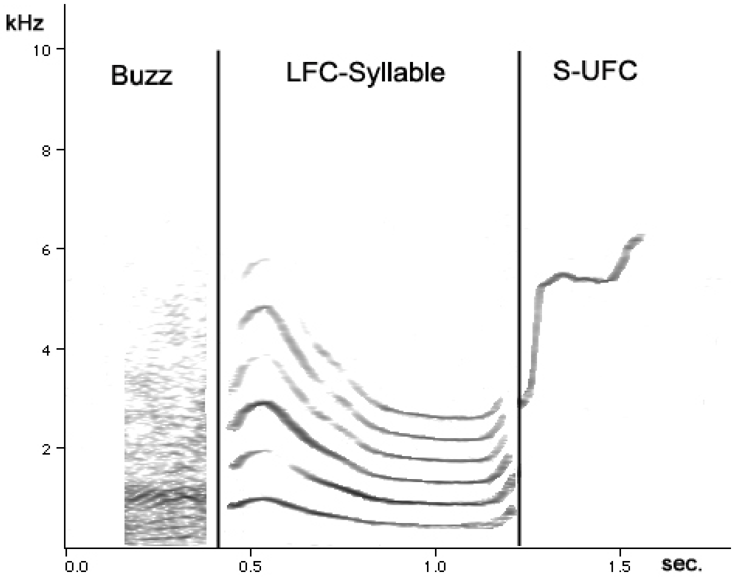

Figure 3.2: Spectrogram of a discrete call separated into buzz note, LFC syllable, and sequential UFC (S-UFC). The LFC syllable and the S-UFC belong to two different frequency component categories based on their transmission patterns. While the LFC-syllable is transmitted omnidirectionally, the S-UFC is usually transmitted in front of the whales' head (see description of UFC and LFC differences in chapter 2 and in (Miller 2002).

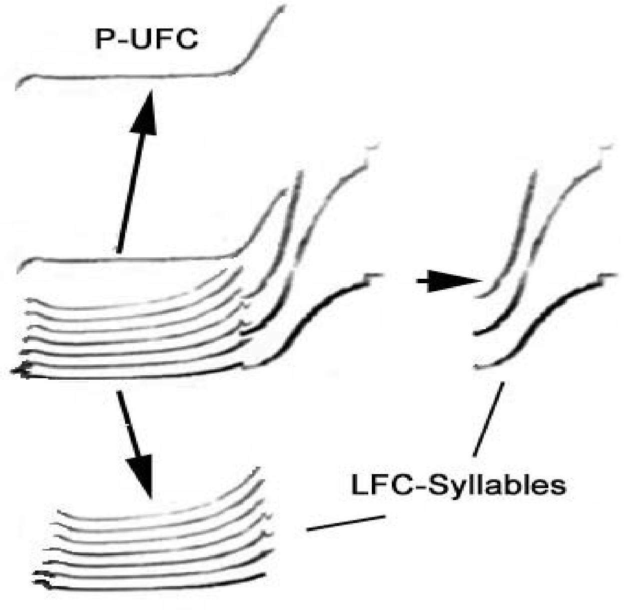

Figure 3.3: Separation of a discrete call into one parallel UFC and two LFC-syllables.

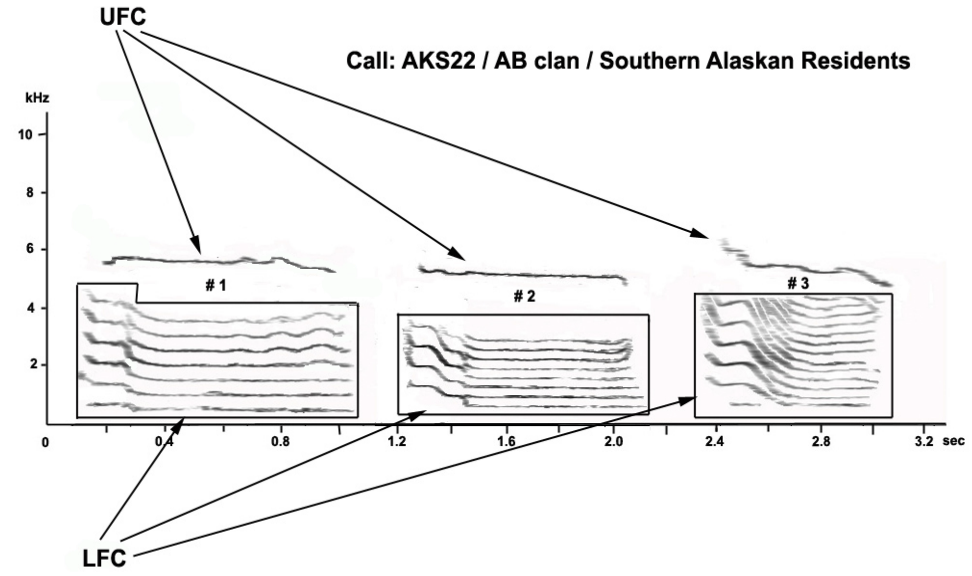

Figure 3.4: Three examples of syllable variations of the UFC and LFC syllables of the same call type. Only the UFC syllable of call # 3 and the LFC syllable(s) of call # 2 were considered different. The UFC of # 3 has two distinct frequency modulations, while # 1 and # 2 show no distinct frequency modulations. The LFC of # 2 has three distinct frequency contour modulations, while #1 and # 3 have only two.

Some call types included two or more discrete variations of the stereotypic form, which allowed the classification of sub-types (Ford 1987 and Chapter 2). Syllabic structure of the sub-types was identical with the exception of syllable additions and deletions (Ford 1987). Matching syllables among sub-types were only extracted once from a particular call type. All syllables were extracted graphically using Photoshop Version 5.5 (Adobe Systems) (Fig. 3.3).

Selected syllables were placed into a database (FileMaker Pro, FileMaker Inc., Santa Clara, CA, USA, 2001) that allowed visual comparison of spectrograms. The database was then copied and call type names and information of syllable position within calls were removed from the copy. I then used this copy of the database to categorize syllables.

Syllable categorization

Spectrographic representation was used here because it simulates how sound is perceived by structures of the mammalian inner ear (cochlea). It accurately displays areas of perceived abrupt and gradual frequency changes in calls of mammals (Bradbury & Vehrencamp 1998). Syllable similarity was determined through visual inspection of spectrograms (Ford 1984; Bain 1986 and Chapter 2) using the following rules:

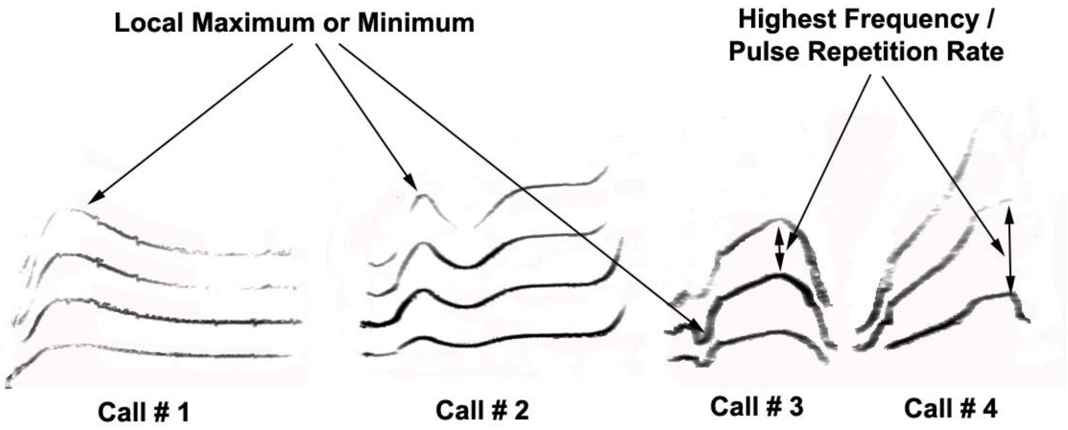

Figure 3.5: Examples for categorization rules: Local maxima or minima are locations of contour direction change. In LFCs, the highest frequency is represented by the largest pulse repetition rate. In UFCs, the highest frequency is the highest point of the contour.

Syllables were considered different if,

1. the variation in contour shape or *gestalt* (e.g. no frequency modulation; mainly rising in frequency; mainly descending in frequency; chevron shape contour, etc.) was distinctly different (Fig. 3.5). Gradual changes in continuous contours were not used to differentiate types (Fig. 3.4). If abrupt changes occurred this was considered a syllable type boundary.
2. the location of a local maximum or minimum (contour peak or valley) or the location of the highest or lowest frequency was distinctly different (Fig. 3.5). I assessed whether the peak or valley or the lowest or highest frequency was within the first third of a contour, in the centre of a contour, or in the last third of contour.

Frequency modulation is used by many mammals and birds to distinguish between signal categories (Horn & Falls 1996). Differences in contour shape are appropriate here because they can be applied to large data sets (~51000 spectrogram comparisons). Frequency contour variation is often used to categorize signals of killer whales and other species (Payne & McVay 1971; Caro et al. 1979; Ford 1984; Janik 1999). The categories reflect similarity well but are poor indicators of differences in the fine structure of vocalizations (Nowicki & Nelson 1990).

Proposed syllable types were labeled alphanumerically starting with the element or component type, LF or UF, followed by a number identifying the primary category followed by a dash and another number for a distinct sub-category if such was present, e.g. LF03_01. I examined the reliability of syllable categorizations by testing how well other human observers distinguish between the visually categorized syllable types.

The reliability of syllable categorizations

Recognition of syllable type differences by human observers

I used a web-based evaluation procedure (web test) to assess the repeatability in category recognition by human observers. I then tested agreement between similarity ratings of web testers and my categorizations.

A custom web program (McKenzie Software, Burnaby, Canada, 2003) randomly chose UFC and LFC syllable combinations without replacement from different pre-determined groups and displayed them on a computer screen. Observers were asked to rate similarity on a seven-point scale: from no; very low; low; medium; high; to very high similarity, and identical. Medium similarity was considered to be an indifferent choice and all medium ratings were omitted from the analysis. Because my goal was to test reliability of categorizations, evaluators were given instructions on how to perform the evaluations and how to rate similarity. The complete evaluation instructions can be found in the Appendix or at http://www.blackfish-acoustics.org/.

First, the rating behaviour of raters was assessed on the basis of how consistently different raters rated the same spectrogram combinations. This procedure was necessary because I was not able to assess rater behaviour or attitude toward the test a priori. Any individual who browsed the web-site was allowed to rate the spectrograms, but this left the procedure open to respondents who willfully answered incorrectly or randomly. Because raters were not asked to assess the same combination twice, I could not assess the degree of repeatability for individual raters. To assess rater consistency, I compared the ratings of the same spectrogram combinations by different raters and excluded raters whose scores were inconsistent with the majority of raters. The procedure minimized the effects of erratic rating on the results of the web test by selecting a group of raters with a more consistent rating behaviour. The loss of rating variability due to this homogenizing procedure is offset by the high power of the web test, i.e. a large number of ratings that were collected.

To determine observer rating behaviour, evaluators had to perform at least 60 evaluations of which 20 had to be spectrogram combinations that were also evaluated by others. The difference between any pair of raters in rating the same combination can take a value between 0 and 6 with 0 = no difference and 6 = maximum possible difference. I determined the rating differences for each rater and calculated a rater concurrence coefficient (Table 3.1).

Table 3.1: Sample calculation for the concurrence coefficient of one rater in comparison to all other raters that rated the same syllable combinations. The proportion of 0 or 1 difference between ratings minus the proportion of 2 – 6 differences was used as the concurrence coefficient.

Rater			
Rating Difference	Observed	Observed/total	Reliability coefficient = Proportion (0-1) – proportion (>1)
0 -1	282	0.647	= 0.647 – 0.353 = 0.294
>1	154	0.353	
0	154	0.353	
1	128	0.294	
2	87	0.199	
3	40	0.092	
4	18	0.041	
5	7	0.016	
6	2	0.005	
Total	436		

The coefficient is the difference between the sum of the proportional values for rating differences 0 to 1 and the sum of the proportional values for rating differences 2 to 6. Rating differences equal to 1 were considered minor agreement differences and not the result of differences in rater attitude toward the test. Evaluators who scored higher than 0.25 for this concurrence coefficient were chosen as a test population for determining the reliability of syllable categorizations.

By eliminating evaluators who typically disagreed with other raters, the variability among raters was reduced. Nevertheless, because 41 out of 55 raters had concurrence coefficients equal to or greater than 0.25, these consistent raters provided a good test population for determining which syllables should be classified as the same versus different.

Next, I tested whether the raters agreed with my categorization of syllables into syllable types using Kappa Statistics (Cohen 1960; Siegel & Castellan 1988). If the raters agreed with my categorization, syllables that I had assigned to different syllable types should be consistently associated with low similarity scores by the raters, and conversely syllables within the same syllable category should receive high similarity scores. The Kappa or *K* coefficient describes agreement among raters performing the same ratings and is used to test inter-observer reliability. The coefficient can vary between 0 and 1 with higher values referring to greater agreement among ratings (Siegel & Castellan 1988). I tested for agreement twice. First, to see whether raters agreed with the way I split syllables into different categories, and second, whether raters agreed with me on the placement of particular syllables.

Structural variation of syllables among categories

To further corroborate categorizations, I examined the structural variation of two acoustic variables, maximum sound pitch and duration, among syllable types. I assessed structural variation by testing sound pitch and duration differences of 178 LFC and 65 UFC syllables. This choice represented about 50% of the repertoire of known call types (Table 3.2) and reflected the differences in repertoire sizes of clans, communities and populations. I recorded frequencies of measurements in intervals of 1 kHz for sound pitches and 0.4 seconds for durations. Interval size was based on observed distributions of sound pitch and durations. Smaller interval sizes would have produced a number of empty intervals, while larger ones would have reduced the power of the statistical tests. I tested for differences in pulse repetition rate and duration between syllable types with Kruskal Wallis non-parametric ANOVA procedures (Siegel & Castellan 1988). All tests were done using statistical software SPSS, Version 11.0 (SPSS Inc., Chicago, IL, USA, 2001). All syllables that were considered different by human observers, and showed more variation in maximum sound pitch and duration between than within categories, were considered distinct types.

Variation in syllable type occurrence and structure among clans and communities

First, I examined whether maximum sound pitch and duration varied among clans, communities, and between residents and transients. I used the same data as above for this analysis and tested for significant differences among population levels with Kruskal Wallis non-parametric ANOVA procedures. I also tested whether differences between population levels were associated with one or both types of syllables, LFC-syllables or UFC-syllables. Because of the potentially different functions of the two call components (Miller 2002), distribution patterns of maximum frequency and duration could indicate whether selection acts on syllable and call structure.

I then examined the frequency of occurrence of syllable types for all described calls to determine differences in the distribution of particular types among clans, communities and populations. Next, I used modified Dice's or half-weight coefficients of association (Ford 1991, see Chapter 2 for formula) to calculate the acoustic similarities between population levels. Dice's coefficients account for differences in repertoire size and are appropriate for displaying associations among distributions of known sizes (Cairns & Schwager 1987). These indices reflect relative differences in occurrences of syllables of the same type between two clans or communities. The indices were then used in average linkage association diagrams to display relative acoustic similarity of clans and communities. Syllable types that only appeared in one call type within any of the groups were ignored because differences in the frequency of occurrence could not be tested.

Test for selection on syllable type usage among clans, communities and populations

I tested whether selection was acting on syllable variation by adopting a method developed for the investigation of adaptive evolution in genetic sequences (McDonald & Kreitman 1991). The concept behind this test is that drift affects call structure randomly and over time will create equal amounts of variation (mutations) in different call components.

When call elements are separated and variation in element structure among different population levels is examined, the ratio of fixed and variable mutations should be equal for all call elements. If neutral evolution is the sole cause for divergence in call structure the ratio of the proportions of UFC and LFC types (amount of fixed syllables) within versus between population should be the same. Whether the occurrence of LFC- and UFC- syllable types was fixed or differed more than expected at different population levels was tested using the McDonald-Kreitman test. If syllable divergence evolved neutrally by social drift, the ratio of distinct versus variable UFC and LFC types should be equal at the clan, community, and population levels. Significant deviation from that equality would indicate selection on one or both of the syllable types. I compared the number of distinct syllables that occurred within each population level with the number of shared types between population levels. Differences were tested for independence using Fisher exact tests.

3.3 Results

Separation of syllables from calls

In total, 312 LF-syllables were extracted from 160 LFCs, which were part of 163 call types (Fig. 3.2C). Three resident call types consisted of only UFCs. Seventeen UFCs of resident calls were produced in series with LFC-syllables, which came from 8 call types. In addition, 74 UFCs (68 in resident calls, 6 in transient calls) were produced synchronously with LFCs in 43 call types. Table 3.2 summarizes the number of UFC and LFC-syllables that were extracted from the different call types and resident and transient communities.

Table 3.2: Components and syllables extracted from discrete calls of (A) resident killer whales and (B) transient killer whales, and (C) residents and transients combined.

A. Residents: P-UFCs and LFCs appear synchronously in calls, while S-UFCs and LFC-syllables appear sequentially.

Resident Communities	**Clans**	**Call types**	**Components**			
			UFC		LFC	
			#	Syllables	#	Syllables
Southern Alaska	AB	37	18	P-UFC: 10 S-UFC: 8	35	57
	AD	17	10	P-UFC: 10	16	25
Northern	A	38	33	P-UFC: 24 S-UFC: 9	38	79
	G	16	5	P-UFC: 5	16	34
	R	10	4	P-UFC: 4	10	23
Southern	J	29	15	P-UFC: 15	29	57
Total		147	85	P-UFC: 68 S-UFC: 17	144	275

B: Transients. Some uncertainty exists in the classification of transient call types in the literature. Given here are the numbers resulting from two assessments by Ford (1987) (generally fewer call types) and Deecke (2003). The greater repertoire size is displayed first and the smaller repertoire added in parentheses.

Transient Regions*	Call types [a](Ford 1987+ unpubl. data) & [b](Deecke 2003)	Components			
		UFC		LFC	
		#	Syllables	#	Syllables
Alaska	9 [b] (8) [a]	4	P-UFC: 4	9	18
BC	9 [a,b]	4	P-UFC: 4	9	17
California	12 [b] (10) [a]	3	P-UFC: 3	12	27
Total	16 [b] (14)[a]	6	P-UFC: 6	16	37

C: Combined numbers of resident and transient killer whales

Residents & Transients	Call types	UFC		LFC	
		#	Syllables	#	Syllables
Total	163	91	P-UFC: 74 S-UFC: 17	160	312

Transient killer whale calls show structural variation among different regions (Ford & Ellis 1999). However, regions are not characterized by completely distinct call type repertoires, such as the clans or communities of resident killer whales. Call types that are typically used by transients in Alaska, BC, and California are displayed separately in figure 3.2B. Because some sharing of call types occurs among those regions, the total number of transient call types (displayed at the bottom of figure 3.2B) is less than the sum of the numbers noted for each region. Transient calls do not have UFC-syllables that occur in series with LFC-syllables and generally have fewer call types with UFCs (37% or 43% depending on repertoire size) than resident call types (58%).

Syllable categorization

<u>*LFC Syllables*</u>

I divided the 312 LF-syllables into 11 categories (Figs. 3.6 and 3.7) based on contour shape and location of slope variation. Distinct sub–types were found in five of the ten categories based on distinct contour shape differences (e.g. contour steepness) before and after peaks or valleys (Fig. 3.5). Ten of the 11 categories contained syllables with uninterrupted contours (Fig. 3.6), while category 11 contained segmented syllables (Fig. 3.7).

While the majority of syllable types could be easily distinguished based on contour variations, some contour distinctions were less obvious. For example, LF07-2 resembled LF09 (Fig. 3.6). However, because LF09 always starts with a chevron shaped contour and LF07 never shows a chevron, I considered the two types distinct. Similarly, all three variants of LF06 start with an upside down chevron shape followed by a downward sloping contour. I considered them part of the same category, even though the peak frequency and the slope steepness differed among sub-types.

Some syllable types, such as LF03, 06, 07 had stable variants. Variants were characterized either by the location of the type-distinguishing contour modulation and/or the slope steepness of the contour before and/or after that modulation. Sub-categories carry numerical indices after the category name (Fig. 3.6).

Syllables that were characterized by discontinuous contours producing segments separated by contour breaks were placed into one category, LF11. Although there were differences in the spacing of segments, the pulse-repetition rates and the durations of segments appeared to be stable. However, the number of call types that contained discontinuous syllables was too low to accurately compare these differences (Fig. 3.7).

Nevertheless, differences in the contour shape of individual syllable elements (rising, constant, or descending contour) allowed me to split the syllable type into four sub-types (Fig. 3.7).

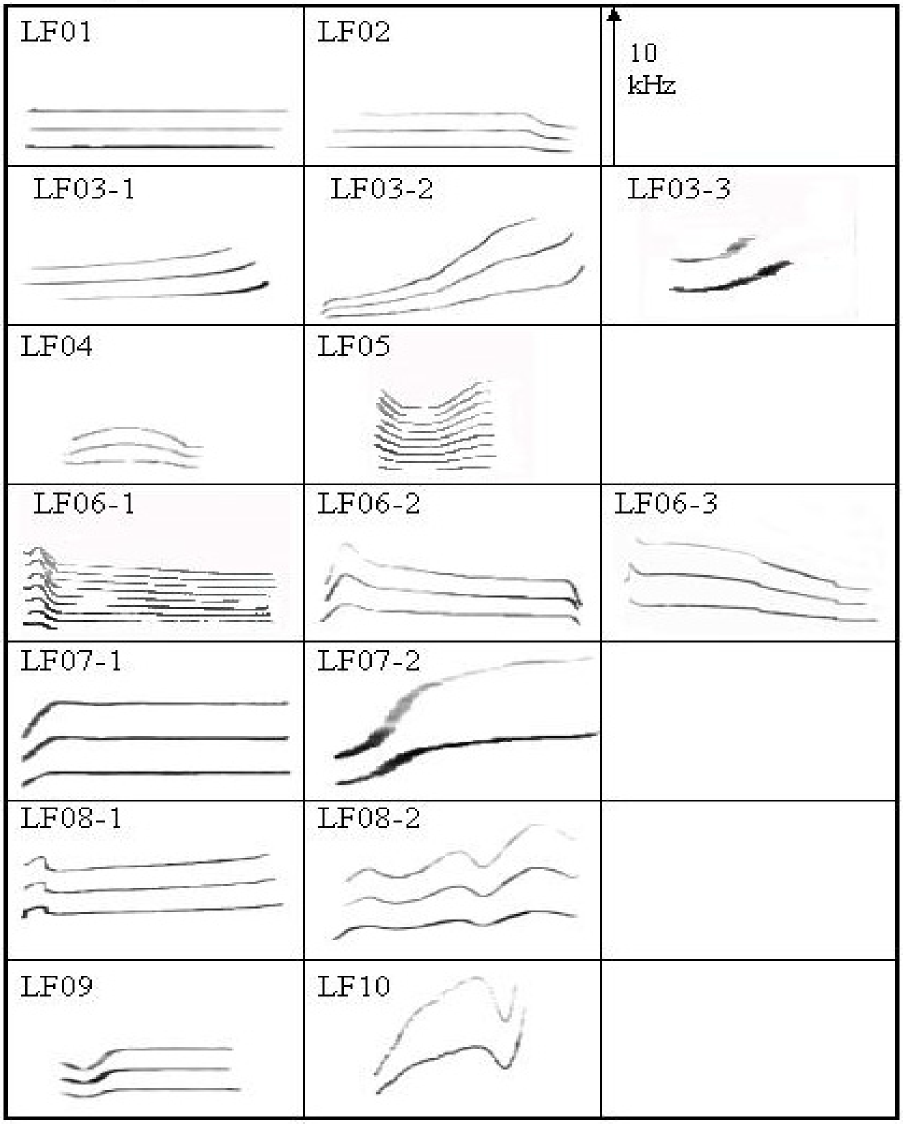

Figure 3.6: Examples of LF-syllable types with continuous contours. While the frequency range of each spectrogram was 10 kHz, the durations varied from 0.2 to 1.8 seconds. Durations were considered less important in syllable type recognition, because they are less stable in call types than frequency (Ford 1987; Foote et al. 2004)

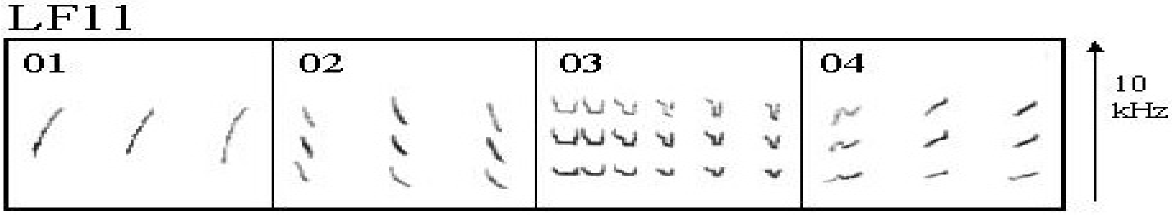

Figure 3.7: Examples of syllable sub-types with discontinuous contours

UFC Syllables

The 74 UFC syllables that were produced synchronously with LFCs (Figs. 3.1, 3.3, and 3.4) and the 17 UFC syllables that were produced sequentially with LFC-syllables (Fig. 3.2) were sorted into 7 categories (Fig. 3.8). Categorizations were made using the base frequency of UFCs. Harmonics of these sounds can have frequencies above 10 kHz and would not have been detectable in many recordings. The categorization procedure was based on the same criteria used in the categorization of LFC-syllables: differences in contour shape, the amount of frequency modulations, and the locations of peaks or valleys or the highest or lowest frequencies.

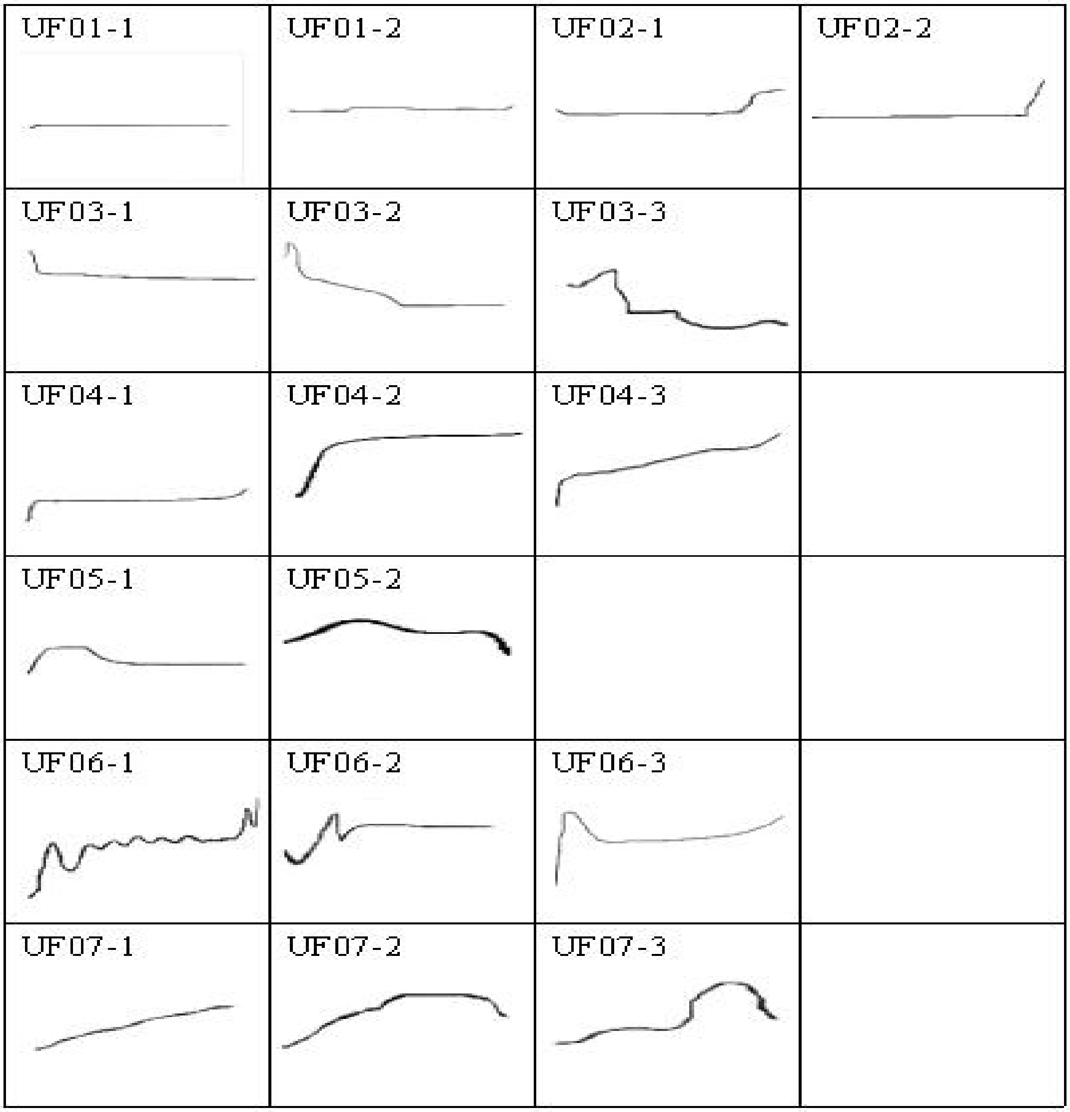

Figure 3.8: Examples of UFC syllable types. Most types showed variations that allowed further division into sub-categories. The frequency bandwidth of the spectrograms is equal to the one used in Figure 3.6 and 3.7 (10 kHz), Durations ranged from 0.4 to 2 seconds.

The reliability of syllable categorizations

Recognition of syllable type differences by human observers

I tested whether raters agreed with my syllable categories using Kappa coefficients to describe the reliability of category recognition. The 41 raters of the test population performed 3267 distinct evaluations. Of those, 976 evaluations resulted in “no similarity” ratings and 44 combinations were considered identical. Two tests were conducted, one to assess agreement for category splits, the other to test agreement for matches of web ratings with particular categories.

Of the 976 web ratings of no similarity among syllables, 920 agreed with the way I split categories and 56 were among syllables that I considered to be from the same category (Kappa Statistics*, $K = 0.945$, s.e. 0.009, $p < 0.01$*). Sub-categories were not tested because the numbers of web ratings for these were too low. Of the 56 evaluations for which the raters disagreed with me, 41 involved LFC syllables and 15 UFC syllables. The agreement was still high when LFC and UFC syllables were considered separately, $K_{LFCsyllables} = 0.875$ (*s.e. 0.01, $p < 0.01$*) and $K_{UFCsyllables} = 0.915$ (s.e. 0.027, $p = 0.027$).

Of the 44 combinations that were rated highly similar or identical by the web raters, 31 agreed with me on the same categories ($K = 0.664$, s.e. 0.082, $p<0.01$). UFC syllables were placed more often in the same predetermined categories than LFC syllables ($K_{UFCsyllables} = 0.806$, s.e. = 0.176, $p < 0.01$, and $K_{LFCsyllables} = 0.64$, s.e. = 0.099, $p < 0.01$). The most common disagreement between web ratings and my syllable categories involved LF08 and UF06 types (4 disagreements). Those types have similar contour modulations, but one is a lower frequency syllable and the other an upper frequency syllable. In addition to UF06, the web raters also considered LF08 to be similar to LF02, LF07, LF09, and LF10. Other disagreements included the combinations LF01-LF02, LF03-LF04, LF03-LF07, LF06-LF07, and UF06-UF07.

The results of the comparison of web ratings and my categorizations showed that syllable type boundaries were very reliably recognized. Agreement on particular categories was lower, especially for LFC syllables, but still considerably different from random.

Structural variation of syllables among categories

The visually categorized syllable types (Fig. 3.4) showed measurable structural variation in the form of differences in maximum pulse repetition rate (PRR) and duration (Table 3.3). Generally, maximum PRR and duration differed significantly among the 10 LFC syllable types (Kruskal-Wallis ANOVA $\aleph_9^2= 44.697$, $p<0.05$ for PRR; $\aleph_9^2= 39.777$, $p<0.05$ for Duration).

Table 3.3: Frequency distribution of maximum pulse repetition rate (PRR) and duration of the ten syllable types with continuous contours. The medians are displayed as group midpoints.

Type	PRRs (kHz)					Durations (seconds)					
	< 1	1-2	2-3	> 3	median	< 0.4	0.4-0.8	0.8-1.2	>1.2	median	Total
LF01	17	5	1	-	0.5	16	7	-	-	0.2	23
LF02	1	6	1	-	1.5	3	3	1	1	0.6	8
LF03	12	10	5	3	1.5	25	1	3	1	0.2	30
LF04	4	5	-	-	1.5	5	4	-	-	0.2	9
LF05	6	-	-	-	0.5	4	2	-	-	0.2	6
LF06	27	11	3	1	0.5	10	13	14	5	0.6	42
LF07	8	18	4	4	1.5	14	17	3	-	0.6	34
LF08	2	7	2	-	1.5	1	10	-	-	0.6	11
LF09	3	5	-	-	1.5	2	6	-	-	0.6	8
LF10	-	1	4	2	2.5	3	2	1	1	0.6	7
Total	80	68	20	10	1.5	83	65	22	8	0.6	178

The frequency distribution of the maximum tone frequencies of UFC syllables had two peaks. Tone frequency was either between 5 and 7 kHz (48%) or between 8 and 10 kHz (40%). The resulting median UFC tone frequency was 7.5 kHz. Most UFC syllables were between 0.4 and 1.2 seconds long (63%) (Table 3.4), and the median length was 0.6 seconds. While tone frequencies differed significantly among all 7 UFC syllable types (Kruskal-Wallis ANOVA $\aleph_6^2$= 25.052, p<0.001), durations did not.

Although not all syllable types were distinctly different from all other types based on maximum sound pitch and duration values alone, the results support the categorizations of the human observers. Because the categorizations were based on contour variations, sound pitch and duration differences are additional differences. Therefore, all LFC and UFC-syllable types will be included in the following analyses of clan, community and population differences. Reliable recognition of sub-categories could not be accurately tested and sub-categories are therefore not used in the following analyses.

Table 3.4: Frequency distribution of maximum pulse repetition rates and durations of seven UFC types. Median values are group midpoints.

Type	PRRs (kHz)						Durations (seconds)					
	<6	6-7	7-8	8-9	>9	Median	<0.4	0.4-0.8	0.8-1.2	>1.2	Median	Total
UF01	4	2	3	-	-	6.5	1	6	2	-	0.6	9
UF02	4	1	-	-	-	5	-	2	3	-	1	5
UF03	-	3	1	4	2	8.5	2	1	5	2	1.0	10
UF04	6	5	1	2	2	6.5	5	4	4	3	0.6	16
UF05	2	2	1	2	2	7.5	2	3	4	-	0.6	9
UF06	-	1	1	2	7	9.5	1	3	2	5	1.0	11
UF07	-	1	1	1	2	8.5	2	2	-	1	0.6	5
Total	16	15	8	11	15	7.5	13	21	20	11	0.6	65

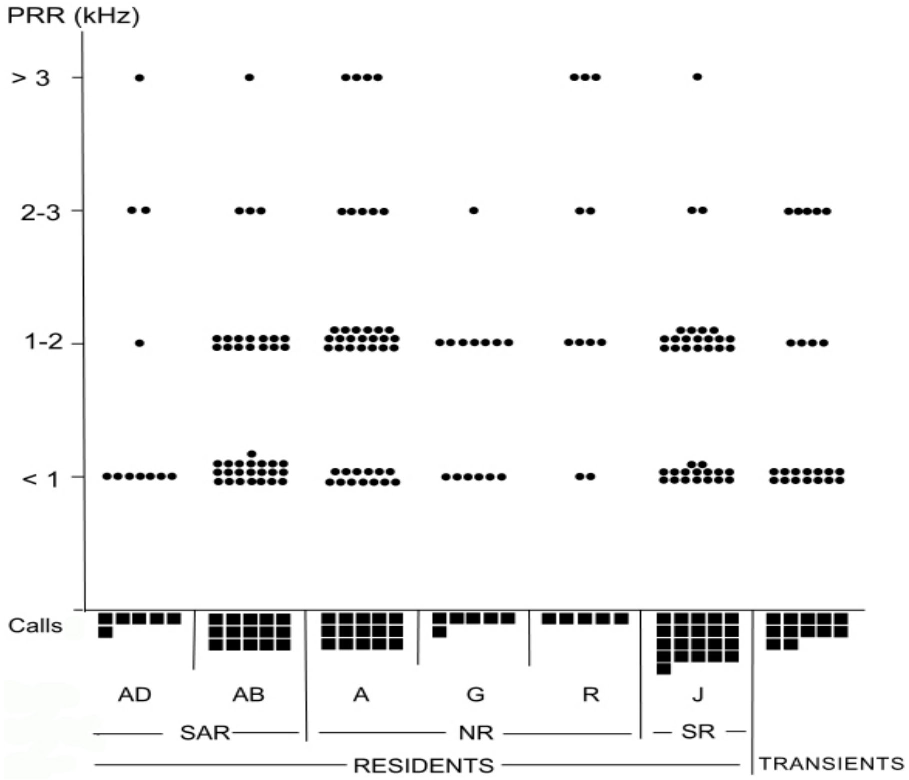

Figure 3.9: Differences in PRR of LFC syllables among clans, communities and populations relative to the number of discrete calls examined for each population level. Number of syllables (•) is not related to the number of calls (▪).

Variation in syllable type structure and occurrence among clans, communities, and between residents and transients

Structural variation of syllables among clans, communities and between residents and transients

The analysis of maximum sound pitch and duration differences included 178 LFC and 65 UFC syllables. These represented accurate proportions of call repertoires from all six clans of the three resident communities as well as the transient community. Frequency distributions of duration values of LFC syllables did not differ significantly among clans, communities, and between residents and transients.

Most of the variation in PRR could be explained by differences in number of syllables examined, which depended on the number of call types at each of the population levels. The proportion of syllables relative to the number of calls in each clan or community is negatively correlated with increasing PRR ($r = -0.773$, $p < 0.01$).

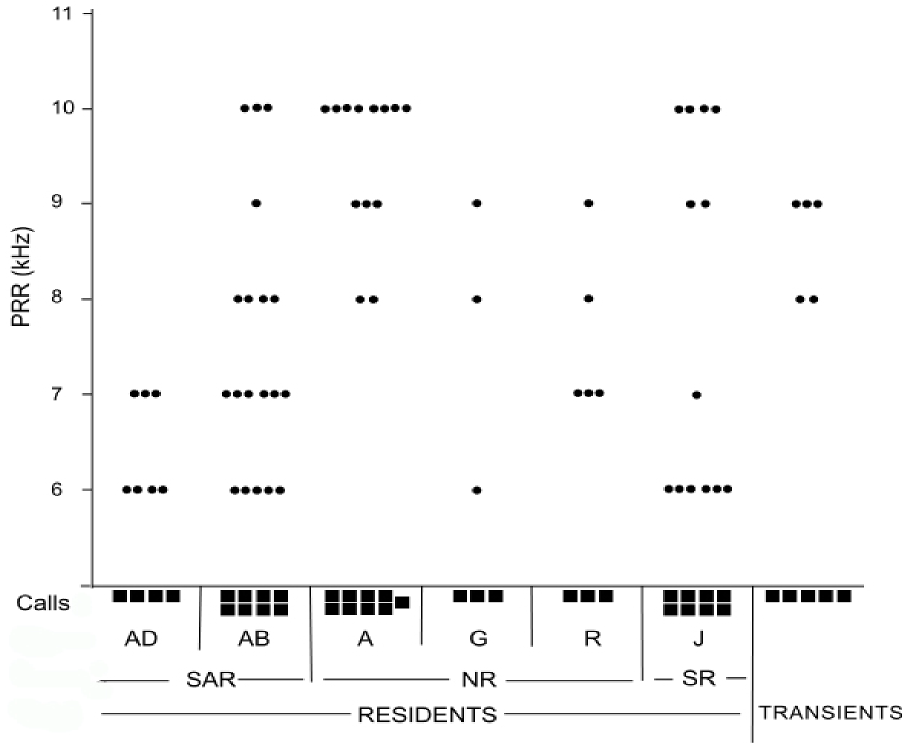

Figure 3.10: Differences in PRR of UFC syllables among clans, communities and populations relative to the number of discrete calls examined for each population level. Number of syllables (•) is linearly related to the number of calls (▪) within each clan ($R^2 = 0.345$, $F_1 = 33.215$, $p<0.05$), but PRR variation appears to be related to clan membership.

UFC syllables, on the other hand, showed distinct differences in the distribution of maximum tone frequencies among clans (Fig. 3.10). Differences between clans were significant (*Kruskal_Wallis* $\aleph_6^2 = 12.676$, $p<0.05$). In particular, the three clans with similar numbers of calls with UFC syllables (A, AB, and J-clan) showed distinct differences in maximum frequency. The A clan of the Northern Resident community had more high-pitched (> 9kHz) than low-pitched UFC syllables (< 9kHz), in comparison to AB and J clans (*Mann Whitney* U, $p< 0.05$). The A clan was therefore responsible for the second peak in the tone frequencies distribution of all syllable types (see previous section). J-clan had the fewest syllables with medium tone frequencies (7-8 kHz) of all clans, and AB clan had more syllables with frequencies below 8 kHz than A and J clans.

Because AB, A, and J clans are the largest clans within each community (or the only one in the case of J clan), maximum tone frequency differed among communities in similar ways than AB, A, and J-clan. Northern Residents had more syllables with high frequencies, while Southern Residents lacked syllables containing medium PRR, and Southern Alaskan Residents had the most syllables with low frequencies. UFC-syllable duration did not differ among any of the population levels.

Table 3.5: Differences in occurrence of syllable types in 163 call types, all of which contained LFC syllables and 90 contained also UFC syllables.

Occurrence in number of calls					
LFC Type	Count	Percent	UFC Type	Count	Percent
LF01	52	31.9	UF01	10	11.1
LF02	3	1.18	UF02	6	6.7
LF03	47	28.8	UF03	9	10
LF04	34	20.9	UF04	19	21.1
LF05	15	9.2	UF05	19	21.1
LF06	63	38.6	UF06	19	21.1
LF07	30	18.4	UF07	8	8.9
LF08	19	11.6			
LF09	10	6.1			
LF10	8	4.9			
LF11	4	2.4			

In summary, maximum sound pitch values of LFC syllables did not vary significantly among clans and communities or between populations. Maximum tone frequency of UFC syllables varied among population levels, particularly among clans. Durations of one LFC syllable type did differ from other types, but generally durations of LFC- and UFC-syllables did not differ between population levels.

Distribution of syllable types among calls, clans, and communities

Distribution among calls

The usage of LFC-syllable types differed considerably among the 163 calls (Table 3.6). LF02 and LF11 are rare types occurring in only three and four calls, respectively (Table 3.5). The other 9 types occurred more often, and their occurrences varied significantly among calls (Table 3.5; Goodness-of-fit to a uniform distribution $\chi^2_{10} = 167.081$, $p < 0.001$). Among those 9 syllable types, differences in usage allowed further division into three common types (LF01, LF03, and LF06), each comprising more than 28% of the examined calls, and four less common types (LF05, LF08, LF09, LF10), each comprising less than 12% of all calls. The usage frequency of LF04 and LF07 lay between the two groups at 18-20% each. UFC syllable distribution among calls was also uneven (Table 3.5; Goodness-of-fit to a uniform distribution $\chi^2_6 = 16.089$, $p < 0.02$). The three more commonly used UFC syllables were UF04, UF05, and UF06 (all 21% of all types), while the other four types occurred at frequencies of 11% and less.

Distribution among clans and communities

Usage of LFC syllable types varied significantly among resident clans (Kruskal Wallis $\chi^2_5 = 16.707$, $p < 0.01$) and communities (Kruskal Wallis $\chi^2_2 = 13.519$, $p < 0.01$) (Table 3.6).

Table 3.6: Distribution of LFC-syllable types of all described discrete calls among clans, communities, and populations. SAR = Southern Alaskan Residents; NR = Northern Residents; SR = Southern Residents; WCT = West Coast Transients

Populations		RESIDENTS							TRANSIENTS	Total
Communities		SAR		NR			SR		WCT	
Clans		AD	AB	A	G	R	J	All	N/A	
Calls		17	37	38	16	10	29	147	16	163
Syllable	LF01	3	3	14	6	3	13	42	11	53
Types	LF02	-	1	-	1	-	1	3	-	3
	LF03	2	8	19	2	6	11	48	6	54
	LF04	1	6	8	4	5	7	31	3	34
	LF05	1	2	4	5	-	3	15	-	15
	LF06	13	19	13	9	1	13	68	10	78
	LF07	2	6	10	5	5	1	29	1	30
	LF08	-	5	7	-	2	3	17	1	18
	LF09	-	3	-	1	-	1	5	5	10
	LF10	3	2	3	1	1	2	12	-	12
	LF11	-	2	1	-	-	2	5	-	5
Total		25	57	79	34	23	57	275	37	312

LF01, LF03, LF06, and LF09 occurred in more than one call of both residents and transients (Table 3.6). Syllable types LF02, LF05, LF10 and LF11 occurred only in resident calls. LF07 was a common type in Northern Resident and Southern Alaskan Resident calls, but it was rarely used by Southern Residents and West Coast Transients. LF08 was evenly used in all resident communities but was rare among West Coast Transients. LF09 was prominent in West Coast Transients and present in the AB clan of the Southern Alaskan Residents. However, it rarely occurred in the two resident communities NR and SR that live in sympatry with the West Coast Transients.

Table 3.7: Distribution of UFC-syllables of all described calls with UFCs among clans, communities, and populations. SAR = Southern Alaskan Residents; NR = Northern Residents; SR = Southern Residents; WCT = West Coast Transients

Populations		RESIDENTS							TRANSIENTS	Total
Communities		SAR		NR			SR		WCT	
Clans		AD	AB	A	G	R	J	All	N/A	
Calls		10	18	33	5	4	15	85	6	91
Syllable	UF01	3	2	1	4	-	-	10	-	10
Types	UF02	3	2	1	-	-	2	8	-	8
	UF03	-	3	2	1	1	-	7	2	9
	UF04	3	8	5	1	2	2	21	-	21
	UF05	1	2	10	-	1	1	15	2	17
	UF06	-	1	10	1	-	6	18	-	18
	UF07	-	-	4	-	-	1	5	2	7
	Total	10	18	33	7	4	12	84	6	90

Table 3.8: Repertoire similarity indices for pair wise comparisons of syllable type repertoires of resident clans. Transients are compared to each clan separately. Repertoire similarity is based on Dice's coefficients of association of either LFC or UFC syllables.

Communities	Clans		AD	AB	A	G	R	J
SAR	AD	LFC						
		UFC						
	AB	LFC	0.78					
		UFC	0.8					
NR	A	LFC	0.87	0.9				
		UFC	0.73	0.92				
	G	LFC	0.87	0.7	0.78			
		UFC	0.5	0.8	0.73			
	R	LFC	0.86	0.78	0.87	0.75		
		UFC	0.57	0.67	0.6	0.57		
SR	J	LFC	0.78	0.89	0.9	0.9	0.78	
		UFC	0.67	0.73	0.83	0.44	0.5	
TRA		LFC	0.71	0.77	0.75	0.75	0.86	0.78
		UFC	0.29	0.44	0.6	0.29	0.67	0.5

UFC syllable type usage also varied significantly among clans (*Kruskal Wallis* $\chi^2_5 = 16.758$, $p < 0.01$) (Table 3.7). This pattern however, did not show up when communities were compared. UFC-syllables were used only in six of 16 calls among transients, and transients used only three of the six syllable types (Table 3.7). This low number of syllable types corresponds to the low number of discrete transient calls (14-16, Table 3.2B) in comparison to resident calls (147, Table 3.2A). One syllable type, UF04, was shared by all resident communities, while three types, UF01, UF02, and UF06, occurred only in some clans.

Acoustic similarity of clans, communities and between residents and transients

The acoustic similarity among clans, communities, and between the two populations is best described by the similarity of syllable type repertoires (Table 3.8 and Fig. 3.11). Overall similarity of LFC syllable repertoires among clans appears higher than the similarity of UFC syllable repertoires (Fig. 3.11). Resident clans are on average acoustically more similar to each other than they are to the transient community. I tested for conditional independence between ecotype membership and repertoire similarity using the Mantel-Haenszel statistic, and found that differences in membership and variation in similarity are associated ($\chi^2_1 = 3.943$, $p < 0.05$). Furthermore, when the common-odds-ratios were calculated to estimate the influence that repertoire similarity has on detecting acoustic differences between residents and transients, the Mantel-Haenszel statistic rejected the hypothesis that variation in repertoire similarity among resident clans is equal to variation in similarity between residents and transients ($p<0.03$).

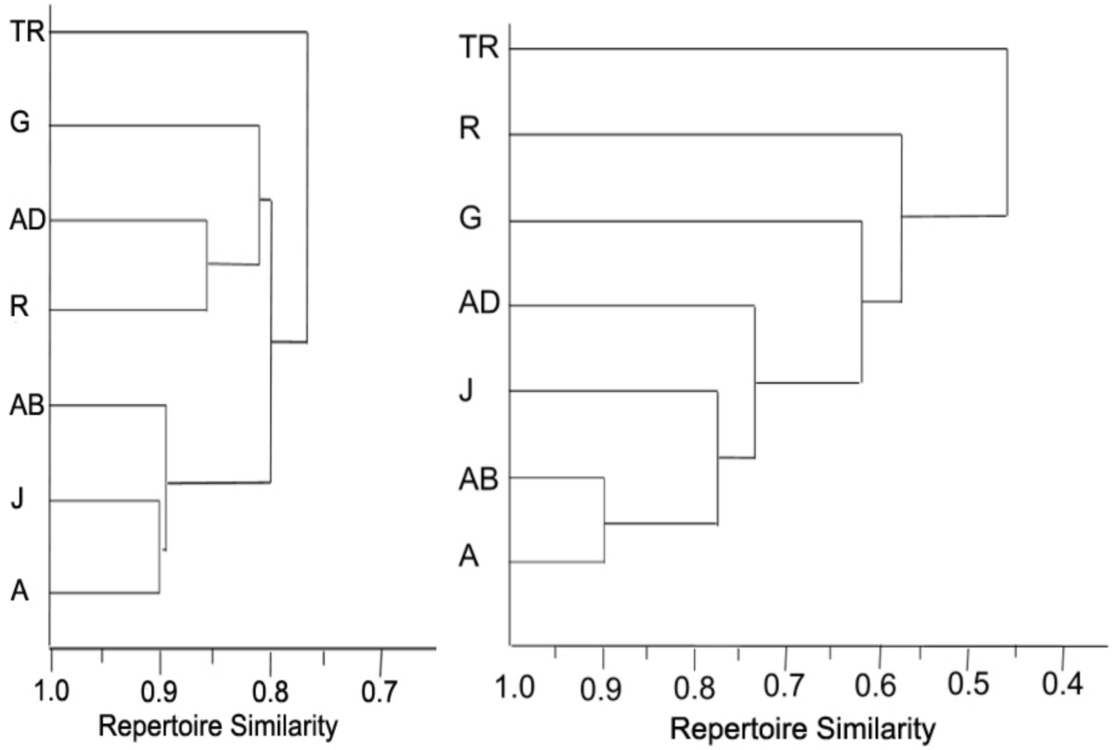

Figure 3.11: Average linkage association diagram giving similarity of repertoires of LFC-syllables (left diagram) and UFC-syllables (right diagram) of resident clans, as well as transients. Acoustic similarity is based on Dice's coefficients of association.

Two clusters of resident clans using similar LFC-syllable types (Fig. 3.11, left diagram) showed equal acoustic distances to the transient community. No distinct clusters were found in the association of UFC-syllable type repertoires (Fig. 3.11, right diagram). Instead, the average acoustic distance between clans steadily increased from the clans with the largest syllable repertoires, A and AB clans, to the clans with the smallest repertoires (G and R-clans, 4) (Table 3.7).

The three clans with the largest syllable repertoires (A, AB, and J) also shared more syllable types than the other clans (Tables 3.6 and 3.7). These three clans also represented different communities. Interestingly, clans from the same community were never neighbours in the UFC association diagram, and the acoustic similarity for UFC-syllable types was the lowest among clans of the Northern Resident community. Consequently, acoustic similarity did not reflect genetic similarity, which is always greater within than between communities (Barrett-Lennard 2000), nor did it reflect geographic distance.

Table 3.9: Variation of LFC syllables and UFC syllables within and between levels of social organization. Numbers in parentheses reflect expected values based on equal ratios among syllable distributions.

	Social Organization Levels	Variation Within	Fixed Between	Total
LFC-Syllables	Clans	275 (286)	201 (190)	476
	Communities	275 (298)	243 (220)	518
	Population	312 (331)	266 (247)	578
UFC-Syllables	Clans	83 (72)	36 (47)	119
	Communities	83 (60)	21 (44)	104
	Population	89 (70)	33 (52)	122
Total	Clans	358	237	595
	Communities	358	264	622
	Population	401	299	700

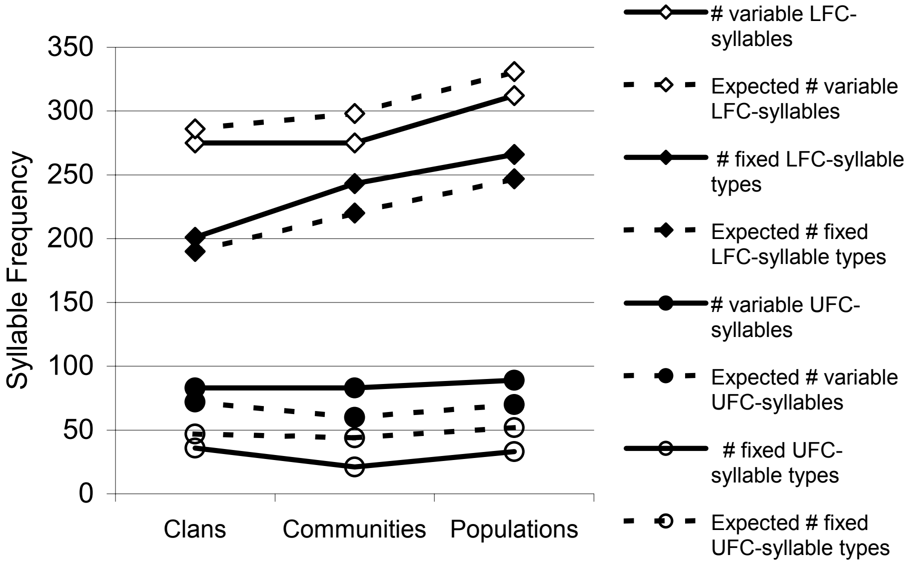

Figure 3.12: Comparison of observed and expected variation of fixed and variable LFC-syllables (upper lines) and UFC syllables (lower lines) within and between population levels.

Test for selection in LFC- and UFC-syllable evolution

The previous section suggested that similarity of repertoires among levels of the social organization could be different for LFC- and UFC-syllable types (Fig. 3.11). The results of the McDonald-Kreitman test (M-K test: Table 3.9 and Fig. 3.12) showed that selection produced syllable repertoire variation among clans, communities and populations.

If selection has acted on call syllables, the ratios of LFC to UFC syllable types fixed between populations should differ from the LFC to UFC ratio within populations. The same LFC syllable types were fixed more often than expected among clans, communities, and populations (shared types). On the other hand there was less than expected LFC syllable type variation within each population level (all syllable types that did not occur in all groups within a population level; Fig. 3.12 - upper graphs). The converse was true for UFCs. While more than expected UFC syllable type variation occurred within population levels, fewer fixed types were found between populations (Fig. 3.12 - lower graphs*)*. Differences between observed and expected values were significant (Fisher exact test (two-tailed) for independence at the clan level: p=0.021; at the community level: p < 0.001; at the population level: p < 0.001).

3.4 Discussion

My results build on earlier findings by Hoelzel and Osborne (1986), Ford (1984; 1987) and Strager (1995) that killer whale call types are composed of acoustically distinct smaller elements (syllables). However, this is the first study to describe syllables as independent structures below the call level and to examine the use of these syllables among different social groups and populations. It is also the first to categorize syllables by their acoustic similarity rather than their acoustic differences among social groups. This approach allowed acoustic similarity to be compared between groups in contact (clans of the same community) versus those that never associate (different communities and populations). The results shed new light on the evolutionary history of cultural divergence among clans, communities, and populations.

Previous research on call divergence concluded that structural variation in calls is most likely the result of cultural drift (Ford 1991; Deecke et al. 2000; Miller & Bain 2000). This study shows that structural variation within calls is also a result of selection on syllable structure. Selection to use certain syllables is most likely the main driving force behind the structural similarity of calls within resident killer whale communities. I hypothesize that the stability of syllable structure is most likely used for long term recognition of community and population membership.

The reliability of syllable type categorizations

Syllable types here were determined based on qualitative judgments of the spectrographic similarities of sound contours. The variation of syllables within a category could have been the result of the arbitrary method used to form categories (see page 13 for description). Arbitrary categorization can cause errors in determining biologically important signal categories (Robinson 1984; Mitani & Marler 1989; Nowicki & Nelson 1990). However, arbitrary classifications combined with ratings are reliable indicators of categorical vocal differences between individuals or groups (Caro et al. 1979; Baptista & Petrinovich 1986; Deecke 1998; Janik 1999). Also, experienced and inexperienced observers are equally successful at rating spectrographic differences (Jones et al. 2001). Human observers are therefore as good, or better, in detecting biologically significant categories as statistical comparisons of acoustic variables (Nowicki & Nelson 1990; Janik 1999).

Computer based comparisons, e.g. with neural networks (Deecke et al. 1999; Deecke 2003 - chapter II), are also effective for determining category similarities. However, these methods sometimes produce more categories than human observers. For example, the number of identified transient killer whale call types (Table 3.1B), produced by neural networks (Deecke 2003), was 14% higher than the number of types determined by human observers (Ford 1987 and Ford, pers. comm.). The same conclusion has been reached in other studies (Janik 1999), suggesting that the method of choice depends on the aim of a study. If assessing similarity among vocalizations is the main goal, human evaluation generates fewer classes, making it more likely to find similarity. When detecting differences between groups is the goal of the study, neural networks or statistical comparison of acoustic variables will allow the detection of finer differences. Because detecting similarity was the main goal of this study, human evaluation combined with statistical testing of the reliability of categorizations was chosen as the appropriate method.

The reliability testing confirmed that there are distinct differences among syllable types. However, there may be more distinct syllable sub-types than the categorizations suggested, because I could not test the reliability of those categories. More sub-types could potentially reflect category differences better unless some of the syllable types have an underlying graded structure (Marler 1977). Graded structure transforms a discrete category into a series of sub-categories, none of which is completely distinct. Graded structure is the result of progressive changes in one or more acoustic variables. The variation in two acoustic variables that I examined here pointed toward an underlying graded structure within syllable categories. This could also explain earlier reports of gradual changes in call structure over time (Deecke et al. 2000).

While testers agreed on different categories reliably, they only agreed upon the same categories in 64% of LFC-syllables and 81% of UFC-syllables. Thirty percent of these disagreements included combinations of one LFC-syllable (LF08) and another UFC-syllable (UF06). These types had similar contour shapes but distinctively different sound frequencies. These disagreements probably would not have occurred if raters could have heard the difference in sound pitch between the syllables. Because spectrograms were used here, that information was not available to the raters. However, LFC- and UFC-syllables could not have been separated correctly using available sound manipulation technology. I suggest that if sound could have been added to the rating procedure this disagreement would have likely not occurred.

LF08 also caused disagreement in 4 more comparisons with other LFC-syllables. However, LF08 was considered distinct a greater number of times (10) than it was considered not distinct (4) from other LFC syllables. Therefore, LF08 was not merged with another category. Further investigation into syllable variation, especially for LFC-syllables, may help to clarify which parts of the call structure may be graded and which are distinct acoustic elements.

Structural variation and divergence of syllables

Structural variation

Deecke et al. (2000) discovered that call structures or LFC structures of a call change gradually over time. Here I found that structural variation exists among syllables within the same syllable category (Figs. 3.5-3.7). Gradual changes in call structure might correspond to gradual changes in syllable structure. That might also explain why Deecke et al. (2000) found that call structure between matrilines remained stable over a 12 year period. The finer call structure (gradual variations of sound frequency and duration parameters) appears to change considerably among calls of closely related matrilines. However, syllabic call structure (discrete variations of sound frequency and duration parameters) remained stable. In fact, syllabic call structure appears to remain stable for more than one generation (Ford 2004).

The lack of significant differences in maximum sound pitch and duration among some syllable types, suggests that type recognition is resilient against fine scale vocal variation. Because call duration varies with environmental context (Ford 1989; Foote et al. 2004), variation may not be very important for syllable type recognition. Nevertheless, differences in duration were used previously to describe variation among calls of closely related matrilines (Ford 1987; Deecke et al. 2000; Miller & Bain 2000). Sound pitch differences on the other hand appear to be reliable indicators of some differences in the gross structure of call types (Ford 1987). However, Ford (1987) also stated that call type distinctiveness was indicated by differences in the occurrence of call parts. This would explain why maximum sound pitch differences were not the only distinctive characteristics for LFC syllable types, but still aided in the process of distinguishing categories. I propose that sound pitch may help whales to identify a particular type over greater distances or in noisy environments if a familiar frequency range is used. Humans also recognize syllables and words better, if the word is pronounced with a familiar accent. Accents usually affect the frequency signature of syllables either in the high-pitch or mid-frequency range (Arslan & Hansen 1997).

UFC-syllables of different communities and some clans were distinctively different on the basis of maximum sound pitch. This appears to support Miller's (2002) idea of independent production mechanisms and functions of the two call components. UFCs are transmitted directionally with most of the sound energy emitting to the front of the whale while LFCs are omnidirectional. Functional differences may follow from these different acoustic properties (Miller & Bain 2000). In addition to possible function of LFCs and UFCs in group recognition, UFCs may also synchronize group movements (Miller 2002). Due to their directional properties, UFC syllables could also be used to address signals towards groups or even individuals. The greater structural variation of UFCs compared to LFCs among clans and communities, suggests that this variation facilitates matriline or clan recognition rather than community recognition. If calls function in mate choice (Ford 1991; Barrett-Lennard 2000), the two independently modulated components of calls could allow senders to convey information of identity, status, and movement direction to potential mates. Multiple functions have been suggested as causes for the evolution of complex vocalizations in other species (Bradbury & Vehrencamp 1998). Structural complexity of signals may also be the result of competition for resources. This function has been suggested for the structure of song repertoires of birds, in particular for repertoire size (Searcy & Nowicki 2000). Songbirds that defend territories as communities tend to have more aligned song structures than those that defend territories as individuals (Lachlan et al. 2004). The similarities of the syllabic call structure of killer whales may have similar functions. Call type repertoires are different in size among matrilines and clans, and syllable type usage differs among communities. Future studies should focus on the relationship of call repertoires and resource utilization as well competition among matrilines, clans and communities.

Evolutionary mechanisms of syllable divergence

Cultural drift through social divergence is believed to be the main process for call divergence within killer whale clans (Ford 1984, 1991; Miller & Bain 2000; Deecke et al. 2000). However, drift does not fully explain the completely distinct call repertoires of clans that interact regularly. Furthermore, if calls are used in mate choice (Ford 1991; Barrett-Lennard 2000), call structure is likely to be under selection to reflect relatedness.

The McDonald-Kreitman test (McDonald & Kreitman 1991) used here suggests that different selective pressures exist for UFC- and LFC-Syllables (Fig. 3.11). The significant differences in occurrence of LFC and UFC-syllable types at each population level implies that either: a) directional selection fixes LFC-syllables more rapidly than UFC variants within a population level, b) purifying selection prevents UFC-syllable variants from rising to fixation more than LFC-syllable variants, or c) balancing selection has maintained usage of UFC-syllable variants within populations longer than for LFC-syllable variants. No decision can be made at this point about which form of selection was responsible for the observed differences. However, while drift might still contribute to LFC-syllable variation, selection seems to have increased the vocal contrast in LFCs between resident communities and between residents and transients.

Based on their independent frequency bandwidths and modulations, UFCs and LFCs could have evolved separately and perhaps have been combined into calls to increase signal efficacy (Endler 2000). Also, if function differs between the two frequency components one would expect selection to act differently. Endler (2000) described efficacy as a measure of how well a signal is received in relation to the cost of signal production. Having a dual generator of sounds with different time and frequency structures makes the cost of combining low and high sound frequencies negligible. The evolution of a dual sound generator was likely facilitated by the advantage of using high sound frequencies to detect food (echolocation) (Cranford et al. 1996). Low frequency sounds, due to their omnidirectional transmission, are more suitable for social communication, as it allows whales to stay in contact (Miller 2002).

The benefits of combining sound with different acoustic properties into calls are manifold:

- Information on distance and direction of senders is improved by the combination of signals with different directional properties and dissipation rates (Miller 2002).
- Variation in lower frequency syllables among communities allows killer whales to distinguish community members from non-members more reliably because of the omnidirectional transmission of LFCs. The existence of vocal markers for communities supports an earlier proposition by Barrett-Lennard (2000) that community recognition may be adaptive. The non-dispersal of residents from their natal group in combination with their group-specific dialects creates a selective advantage for group recognition. Group dialects allow residents to vocally recognize matrilines that they have socialized with previously. However, by chance some matrilines could have little contact, making it difficult for younger whales to learn to recognize all individual members of the community by their call repertoires. This would also make the recognition of certain syllables as community markers advantageous. The same is true for vocal differences among different populations.
- Variation in UFC-syllables within communities will allow whales to track movements of members of their own and other clans similarly to what Miller (2002) suggested for members of matrilines. As a result, UFC syllable variation would assist interbreeding clans to coordinate meeting opportunities in a habitat characterized by long and often narrow channels. Finally, stronger purifying selection on UFC-syllable mutations as one

form of selection suggested by the results of the M-K test, could mean that UFC-syllables play a role in individual recognition. UFC-syllables, particularly those that are produced simultaneously to LFC-syllables, show more discrete contour variations than do LFC-syllables (Miller & Bain 2000). Greater within-category variation means greater contrast among individual whales.

Calls are learned within the matriline (Ford 1991; Miller & Bain 2000; Barrett-Lennard 2000). Future work should address the question of whether LFC- or UFC-syllables are learned separately. One way of addressing this question is by asking whether syllable usage follows syntax rules and whether those rules can explain call differences. By comparing syntax rules among population levels, one can determine whether the syllables themselves or the syllable combinations are learned. The syntax of killer whale call syllables will be examined in the next chapter.

3.5 Summary and conclusions

Previous studies have investigated the divergence of vocal culture from group-specific dialects of matrilines to those dialects describing clans. Because killer whale clans associate within communities, the question remains how clans recognize community members. Killer whales have evolved complex calls that are characterized by syllabic structures. All identified calls of six vocal clans of three resident killer whale communities are made up from combinations of 18 distinct smaller syllable types. Combinations of eight of the same 18 syllable types comprise all identified calls of the transient killer whale population. Eleven of the 18 syllable categories were part of the broadband call component that has its main energy in lower frequencies (< 4 kHz). The remaining seven syllable categories belong to the narrow band call component that has its main energy in frequencies > 4 kHz. Syllable type variation allows whales to distinguish clans from the same and different communities without having to memorize call types. It also may allow them to distinguish between populations.

Previous work suggested that accumulation of random changes to the structure of calls is the sole cause of vocal divergence. My work suggests that directional selection acts on call structure to create differences and similarities among and between clans, communities and populations. While structural variation of upper frequency syllables reflects vocal variation within clans of the same community, repertoire differences of lower frequency syllables are markers of communities and populations. Distinct syllable usage may allow recognition among groups of whales that do not associate regularly. This can be considered evidence for cultural stability that reaches beyond the level of continued social association. It is possible because a small repertoire of syllable types (18) is used to produce a large repertoire of call types (163). Although call repertoires may diverge to create distinct differences, the small syllable repertoire is responsible for cultural stability of vocalizations. So far, such a system has only been described for human languages, where a limited number of syllables can create an almost infinite number of words. My results support earlier suggestions that killer whale call repertoires are adaptive because they can assist in mate choice. In fact, the differences in syllable type usage found here may allow whales to mate within their community to avoid excessive outbreeding. This might represent a cultural mechanism to avoid detrimental effects that can result from outbreeding and is evidence for gene-culture coevolution in killer whales.

4. CALL SYNTAX AND CLAN REPERTOIRE DIVERGENCE IN RESIDENT KILLER WHALES

4.1 Introduction

The structure of communication signals is constrained by an organisms' physical, psychological and social environment (Endler 2000). For example, signals used in long distance communication require properties that allow them to travel much further than signals that are used when sender and receiver are close. While the physical environment and physiological constraints in sound production tend to influence the frequency and temporal structures of signals, the combinatorial structure, or *syntax*, of signals is often influenced by cognitive and social constraints. For example, humans are thought to be capable of understanding an average of four different units of information (range three to seven) instantaneously (Cowan 2001). Words should therefore contain on average no more than four *morphemes* (units of information) in order to be recognized as words and compared to a mental dictionary (Pinker 1998). In fact most languages do follow this rule and languages with higher numbers of morphemes have grammatical rules that divide words into smaller units (Pinker 1994). Similar limitations appear to exist for bird calls (Hailman et al. 1987) and bird songs (Hultsch & Todt 2001), as well as for other combinatorial animal vocalizations (Robinson 1984; Mitani & Marler 1989). Combinatorial complexity of distinct vocalizations is therefore under selection not to exceed an upper limit that cannot be perceived as distinct.

Complex vocalizations are often generated by combining syllables from the same or different categories (types). The degree of combinatorial complexity is dependent on how many distinct syllables are combined, or simply by the total number of combined syllables. These types of complex vocalizations occur in birds (Catchpole & Slater 1995; Hailman & Ficken 1996), humans (e.g. Weissenborn & Hoehle 2000) and other cetaceans (Payne & McVay 1971). Repertoire complexity of combinatorial signals is often measured as the ratio of constituting elements to combinatorial signals. The more distinct combinatorial signals, the more complex the vocal system (Marler 1998). The most complex system is found in humans where thousands of signals are formed from a small number of distinct elements, typically 40 to 45 (range 10 to 141) (Wales & Sangor 2001). In contrast, song type repertoires of birds are always smaller than the repertoires of notes and syllables that an individual bird produces (Hultsch & Todt 2001). The same is true for other vocal learners, such as the humpback whale (*Megaptera novaeangliae*) and the bottlenose dolphin (*Tursiops truncatus*). Humpback whale songs are limited to one or two song types per breeding ground (Payne & Payne 1985; Noad et al. 2000) and bottlenose dolphins produce fewer discrete whistles than whistle elements

(Caldwell & Caldwell 1965; Tyack 1986). The size of the whistle repertoires, however is still a matter of dispute (McCowan & Reiss 1995; Janik 1999). For many other highly vocal cetaceans such as the beluga (*Delphinapterus leucas*), call and syllable repertoire sizes are not yet known.

Because species recognition is sometimes important when learning communication signals (Emlen 1972), conforming selection may lead to structurally fixed signals or fixed species-specific syntax of signals (Marler & Pickert 1984; Nelson & Marler 1994). Examples of fixed syntactical structures are found in the call sequences of dusky titi monkeys (*Callicebus molochus*), the songs of gibbons (*Hylobates* spp.) and in some bird vocalizations (Robinson 1979; Mitani & Marler 1989; Kroodsma 1996).

The syntactical structure of particular human words or sentences or the syntax of particular bird songs is rarely used for species-recognition (Searcy et al. 2003; Steels 2004; Nelson & Marler 1994). Species-recognition seems to be mainly accomplished through recognizing that words or songs are organized into smaller structural features by human infants and young birds (Doupe & Kuhl 1999). The syntactical order of particular signals is mostly arbitrary and sometimes controlled by social or cultural selection (Marler & Peters 1988; Hailman & Ficken 1996). Syntax variation often reflects social separation among individuals and groups within a population (Baptista & Petrinovich 1986; Clucas et al. 2004) or between populations (Balaban 1988; Burnell 1998). This allows the recognition of cultural and social groups based on syntactical differences. However, syntax can also indicate genetic relatedness (Baker 1974; Marler 1976; Balaban 1988; Baptista & Petrinovich 1984). The vocal systems with the highest degrees of signal variation among individuals and groups are often those with the most variable syntax. Examples for those are the black-capped chickadee calls (Hailman et al. 1985), the song types of the European nightingale (Todt & Hultsch 1996), or human languages (Pinker 1998; Steels 2004). Furthermore, syntactical rules in many bird species and in humans are culturally inherited and have primarily interactive social functions, such as promoting cohesion (Baptista 1996; Pinker 1994).

Types of syntax

Marler (1976; 1998) differentiated between *phonetic syntax* and *lexical syntax*. Phonetic syntax is a process by which words, calls, or songs are formed from acoustically distinct phonemes, such as syllables in human speech and notes or syllables in calls or songs of birds. Linguists also call this the morphological syntax or simply language morphology (Pinker 1998). Language morphology is not defined by the meaningful differences of acoustic utterances but by their acoustic distinctiveness, which are also called phonetic differences (Ladefoged 1993).

Similarly, there appears to be no explicit difference in meaning between notes or phrases in birdsongs. In fact, all songs produced by members of the same bird species are thought to have the same meaning (Marler 1998). Lexical syntax on the other hand is a process by which meaning is formed through the combinations of smaller meaningful units. This is done through a mental transformation of the meaning of morphemes (smallest meaningful units in languages) into words, or of words into phrases and sentences.

Lexical syntax has not been found to exist in birds and mammals other than humans (Pinker 1994; Marler 1998). One well studied vocal system that was considered to have lexical syntax is the calls of black-capped chickadees (Hailman et al. 1985). Chickadees have more than 300 distinct *chick-a-dee* calls that are formed from four acoustically distinct note-types (Hailman et al. 1985). Hailman et al. (1987) considered the chickadee system to be the only known 'manifestly combinatorial' communication system other than human language. However, because the note combinations do not differ in meaning from the note types themselves, Marler (1998) claimed that no lexical syntax is present in the chickadee system. Another example for possible lexical syntax is the alarm calls of some members of the genus *Cercopithecus.* Diana monkeys (*Cercopithecus diana*) appear to comprehend the meaning of syntactic changes in alarm calls of the Campbell's monkey (*Cercopithecus campbelli*). Although the two species are closely related, their respective alarm calls are structurally different. However, Diana monkeys can make sense of the syntactical changes in the calls of Campbell's monkeys with respect to the type of predator that educes the alarm call. This understanding allows Diana monkeys to differentiate between different types of predators without using the actual vocalizations (Zuberbuehler 2002). This may represent understanding of lexical syntax because Diana monkeys understand the meaning of the syntactical order of calls but do not use the phonetic call structure that represents the meaning. Killer whales have combinatorial signals that show great complexity (Ford 1987 and Chapter 2 and 3) but so far the potential for lexical meaning has not been investigated.

Killer whale syllabic call structure

Killer whale vocalizations can be divided into three forms, *clicks*, *whistles*, and *calls*. Clicks are mainly used in echolocation. Whistles, with few exceptions, are associated with social behaviour in close proximity (Ford 1989; Thomsen et al. 2002). Calls, which are stereotyped pulsed vocalizations, are the main long distance communication signal (Ford 1989). Calls are often characterized by two independently modulated frequency components, an upper frequency component (UFC) and a lower frequency component (LFC) (Ford 1987; Miller & Bain 2000 and Chapter 2 and 3). While UFCs consist of continuous frequency contours, LFCs are often marked by abrupt contour shifts or contour breaks (Fig. 2.2 in Chapter 2 and Fig. 3.1 in Chapter 3). On the basis of these characteristics, calls can be divided into spectrographically distinguishable syllables (Ford 1987; Strager 1995, Chapter 3). Because this division of calls into syllables occurs in killer whale populations that are geographically and genetically distinct, syllabic structure appears to be a stable characteristic of killer whale calls. Calls produced by the same groups of whales have not shown variation in their syllabic structure for more than 25 years (Ford 2004). Some calls appear to be stable for almost fifty years or two generations (Ford, pers. comm.). This stability allows observers to recognize discrete call categories (types) and determine distinct repertoires of discrete call types (Ford 1987 and chapter 2). The existence of the same syllable types in calls of two reproductively isolated populations (Chapter 3) indicates that call stability might last for an even greater number of generations.

The 147 distinct call types identified from resident killer whales in the Northeastern Pacific are formed through combinations of 18 syllable categories or types (Chapter 3). Resident killer whales also produce stereotyped narrow band whistles that are not divided into syllables (Ford 1989; Thomsen 2001 and Chapter 2). Because there are more resident killer whales in the North Pacific whose calls have not been categorized (Yurk in prep.), there could be a few more distinct syllables in the communication system of resident killer whales. However, because of the low number of syllable types versus call types, call complexity may be primarily a function of syntax complexity.

The goal of this chapter is to examine syntax complexity of killer whale calls and to determine whether patterns of complexity are associated with differences in relatedness and sociality of groups. For this analysis, I focus on the syntactical variability in calls of resident killer whale clans and communities in the Northeastern Pacific. Clans and communities rarely share call types (1 shared type out of 147), and members of different communities seldom socialize, if ever. On the other hand, residents share many of the syllable types that form calls, e.g. 6 of 11 LFC types are shared by all clans (Chapter 3). Migration of individuals between communities has never been observed in thirty years of study (Ford et al. 2000). Mating takes places within communities and most often between different clans (Barrett-Lennard 2000). If mate choice is associated with call type use then syntax should be also associated with mate choice.

I examine stability of syntax in killer whale vocalizations to determine whether killer whales use grammatical rules to combine syllables and therefore have a ‘discrete combinatorial system’ (Pinker 1998). If syllables have their own distinct meaning, the killer whale vocal communication could be added to the short list of ‘manifestly combinatorial’ systems (Hailman et al. 1987). I evaluate whether syntactical order of killer whale calls is associated with the social structure and mating system of resident killer whales. In particular, I ask whether group recognition and mating preferences are based on syntactical differences. Both Ford (1991) and Barrett-Lennard (2000) suggested that discrete calls in killer whales aid in mate selection, with the goal of avoiding inbreeding. Barrett-Lennard (2000) showed that an effective outbreeding mechanism must exist, because residents are completely philopatric, i.e. both males and females remain in their natal groups, and inbreeding coefficients are low. If calls do aid mate choice by reflecting degrees of relatedness, is this because a) the whole call is recognized as an indicator of relatedness or b) the difference in syllable combinations reflects relatedness?

To assess whether syntax-mediated function is plausible in killer whale calls, I first examine whether differences in the positioning of syllables within calls are associated with particular pitch and duration differences. If so, syntax would be tied to acoustic variation among syllables and that would limit the possibilities of syntax being arbitrary. Second, I explore whether syllable type positioning within calls is governed by the same rules at all population levels. This would point toward a population or species-specific fixed grammar that would limit variation of call syntax among levels. I also explore whether associations between syllable placement and type usage exist and consider possible grammatical rules. Third, I examine whether placement of syllable types and transitions between syllables varies among clans and communities. Here, I test whether variation in syllable placement and transition is associated with social contact and/or maternal relatedness among population levels.

Finally, I compare syntactical complexity as indicated by the number of group-specific type placements and transitions of syllables in calls among resident clans and communities. Here, my goal is to find whether complexity is mainly associated with population demographics (e.g. community and clan sizes) or whether it is also associated with social structure. If the latter is true, complexity is likely under social or cultural selection.

4.2 Methods

Syllable selection

I used the same data as in Chapter 3 for this study on syllable syntax. For most clans, the number of calls for which syllables were extracted reflected the total repertoire of identified calls (Ford 1987 and Table 2.2 in Chapter 2). Many discrete calls are separated into two frequency components that are often independently modulated (upper frequency components or UFCs with pulse repetition rates above 3.5 kHz, and lower frequency components or LFCs with pulse repetition rates below 3.5 kHz; Fig. 3.1 in Chapter 3). UFCs have continuous contours with no abrupt shifts and occur once in a call. UFCs are either produced synchronously (Fig. 3.1 - Chapter 3), or sequentially with LFCs (Fig. 3.2 – Chapter 3). LFCs of many calls can be divided further into two or more syllables based on distinct contour and sound pitch changes (Fig. 4.1). Only UFCs that occurred in sequential order with LFC syllables (n = 292) were included in this analysis on syllable syntax.

The actual numbers of LFC syllables examined in each analysis varied with the number of available spectrographic images of syllable types. All of the acoustic analyses are based on measurements and visual interpretation of spectrographic differences. Syllable types were defined in Chapter 3 and are shown schematically in Figure 4.4.

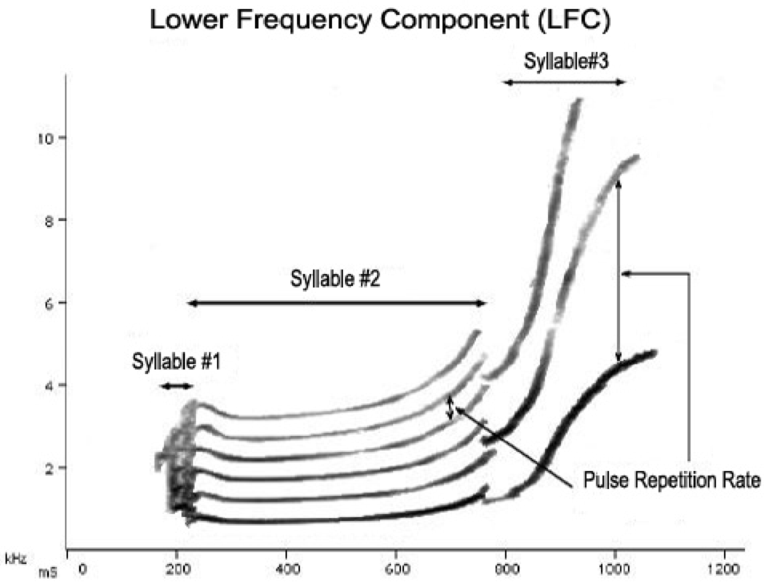

Figure 4.1: Lower frequency component of a stereotypical killer whale call consisting of three syllables. The sound pitch of the pulsed call is produced by the pulse-repetition rate, which is reflected by the side-band interval (PPR) between contour lines in the spectrogram.

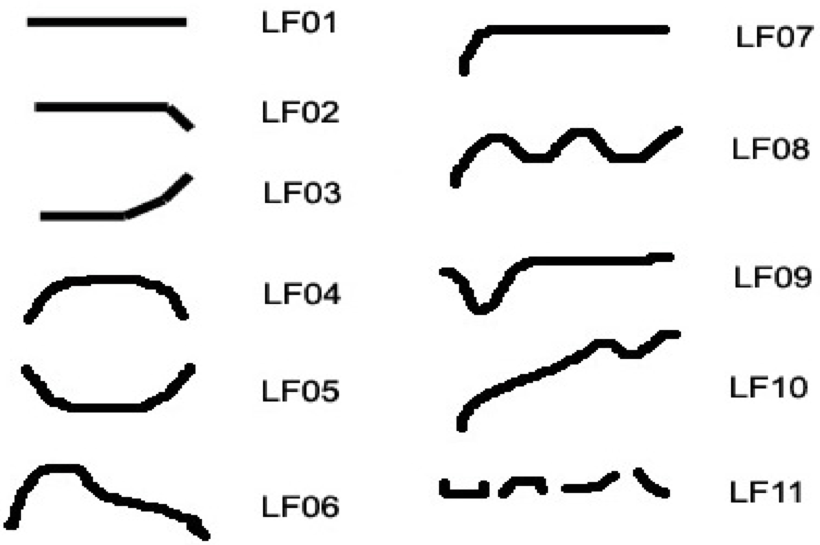

Figure 4.2: Schematic representation of syllable types as defined in Chapter 3. LF01 through LF10 consist of continuous contours, while LF11 is characterized by contour segments.

Table 4.1: Components and syllables extracted from discrete calls of resident killer whales. P-UFCs and LFC appear synchronously in calls, while S-UFCs and LFC-syllables appear sequentially.

Communities	**Clans**	**Calls**	**Components**			
			UFC		LFC	
			#	Syllables	#	Syllables
Southern Alaska	AB	37	18	P-UFC: 10 S-UFC: 8	35	57
	AD	17	10	P-UFC: 10	16	25
Northern	A	38	33	P-UFC: 24 S-UFC: 9	38	79
	G	16	5	P-UFC: 5	16	34
	R	10	4	P-UFC: 4	10	23
Southern	J	29	15	P-UFC: 15	29	57
Total		147	85	P-UFC: 68 S-UFC: 17	144	275

Using reference catalogues (Ford 1987) for calls for which no high quality spectrograms were available, all of the 292 sequential syllables were used in the following analyses. Table 4.1 shows the number of syllables extracted from all identified stereotyped or discrete calls of resident killer whales.

Most sequentially occurring UFC syllables (S-UFCs -Table 4.1) have contours like particular LFC syllable types. S-UFCs of type UF04 (Fig. 3.8 in Chapter 3) are similar to LFC-syllables of type LF07 (Fig. 3.6 in Chapter 3); S-UF05s are similar to LF06; S-UF06s are similar to LF08; and S-UF07s have some resemblance to LF04. Although synchronous UFC syllables are part of the complex structure of killer whale calls, they do not vary with regard to their position within the call. Therefore, they are inconsequential for syntax variation. Sequential UFC syllables can vary with regard to their within-call position and behave more like LFC syllables. Because of contour similarity to LFC syllables and their similar effects on syntax, S-UFC syllables were lumped with their corresponding LFC counterparts in the following analyses. Because S-UFC syllables were rare in comparison to LFC syllables, the lumping did not affect the results considerably. The variation in occurrence of UFC and LFC syllables was subject of Chapter 3.

Test for fixed, non arbitrary call structure

<u>*Sound pitch and duration differences of syllables at particular positions*</u>

First, I examined variation in sound pitch (Pulse Repetition Rate or PRR) and duration among 176 sequential syllables to test if variation of these two acoustic variables depended on syllable positions in calls. The 176 syllables were extracted from different within-call positions. They represented dialect groups or clans in proportion to the numbers of discrete call types used per social unit. I tested for significant associations between duration, PRR, and call positions (Figure 4.3) using *Chi-square* and rank order tests (*Gamma statistics*) (Siegel & Castellan 1988).

Call types are discrete categories that show little change in syllabic structure over several generations (Ford 2004 and chapter 3). Syllables with PRRs > 3 kHz and S-UFC-syllables were always found in second or higher within-call positions. There were few S-UFC syllables (17) in comparison to LFC syllables (275). Placement preferences for S-UFCs were therefore not tested separately.

Test for static syntax rules

Placement of syllable types within a call

Next, I analyzed whether syllable types occurred at fixed positions within calls to see if a deterministic rule governs the order of syllable types in calls. I tested for non-random occurrence of types at particular positions (1st syllable in call, 2nd, 3rd and so on) with a Chi-square test. I then determined which syllable types were shared at the same positions among different levels of the social structure social units and which contrasted communities or clans.

Test for dynamic syntax rules

Call structure based on syntactic relationships among syllable types

Syllable transitions among calls of the same type are stable over several generations (Ford 2004 and chapter 3). Furthermore, most distinct call types of resident killer whales are known. Therefore, any associations between syllable types and within-call positions of each type reflect a stable grammatical organization of these calls at the population level. I examined whether syllabic call structure is characterized by higher than expected levels of syllable type repetition. I used *Goodness–of-fit* Chi square tests (Siegel & Castellan 1988) to test whether particular combinations of syllable types were preceded or followed by the same or different types. Following Ford (1989), I then used a modified *Dice's* coefficient of association to find preferred associations among syllables of different types. *Dice's* coefficients normalize data to account for differences in the abundance of syllable types (Dice 1945; Morgan et al. 1976) .

$$\text{Coefficient of Association} = \frac{2\,(\text{transitions } (a \rightarrow b) + (b \rightarrow a))}{(\text{transitions involving } a) + (\text{transitions involving } b)}$$

where a and b are consecutive syllables. *Dice's* indices are appropriate for the killer whale call data, because the total number of transitions is limited by the number of identified call types, which was known (Cairns & Schwager 1987). A cluster diagram was used to display associations among syllable types.

I next assessed the number of all distinct combinations of syllable types that were shared at each population level and the number that were characteristic for a particular community or clan. I then compared how many of the shared transitions where between neighbouring communities and how many between distant communities. The comparison was restricted to syllable types with similar occurrences in the communities' call repertoires.

I next examined whether syllable transition order was associated with the amount of social contact between groups and/or the existence of close maternal relatedness between clans. I tested whether particular syllable transitions were shared among associating clans that interbreed. Transition order differences among clans (Barrett-Lennard 2000) were described using *Dice's* association indices. I tested for differences in association using a *Wilcoxon* ranking or W test.

Finally, I compared occurrence of syllable types and transition order with demographic parameters, such as the number of matrilines and whales in clans and communities. The goal was to determine whether syntax divergence was correlated with clan or community size. I compared variation in occurrences of unique syllable combinations (combinations not shared between clans) with the number of whales and the number of matrilines at each population level. Then, I tested for linear relationships between demographic parameters and syntax variation using multiple regressions.

4.3 Results

Test for fixed, non arbitrary call structure

Sound pitch and duration variation among syllables

The median pulse repetition rate (PRR) of the 176 syllables analyzed was 1.5 kHz (79% were below 2 kHz) and the median duration was 0.6 seconds (83 % were shorter than 800 milliseconds). Significantly fewer than expected syllables with sound pitches below 2 kHz, were longer than 0.8 seconds and vice versa (Fig. 4.3) (Chi-Square: $\chi^2_1 = 16.97$, $p<0.01$).

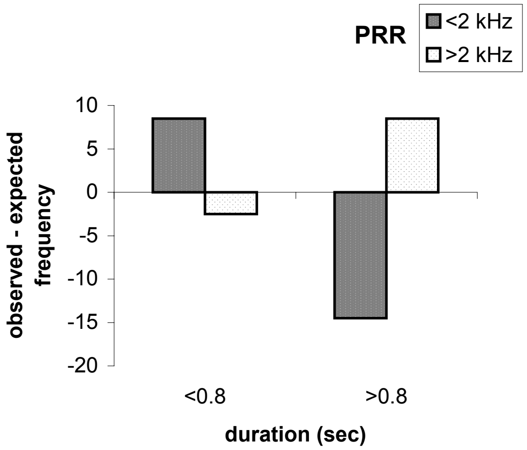

Figure 4.3: Difference in observed and expected frequency of pulse repetition rates of syllables with different durations. Expected frequencies are based on independence of duration and frequency.

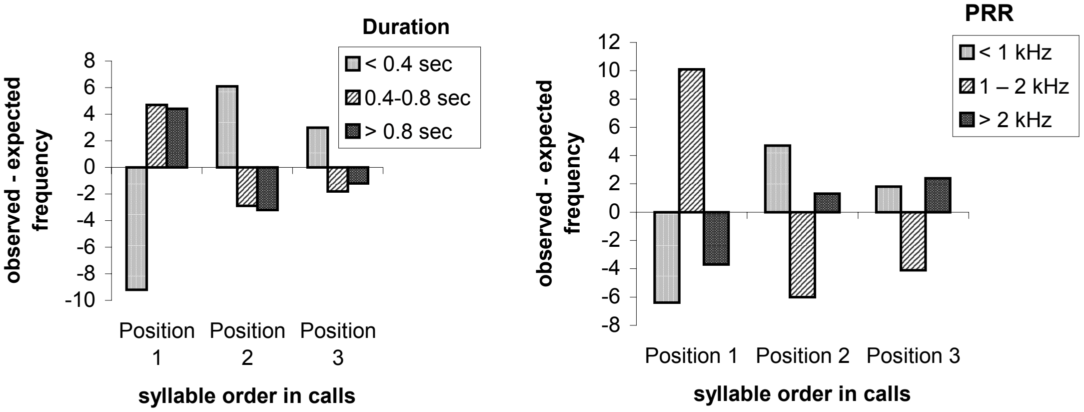

Figure 4.4: Difference in observed and expected frequency of syllable durations and PRRs at different within-call positions. Expected frequencies are based on independence of duration and frequency.

No exclusive within-call placement rules for syllables of any length were detected. Furthermore, no specific frequency occurred exclusively at any particular position within calls. However, shorter syllables (< 0.4 seconds) were found in second or higher positions significantly more often than longer syllables (> 0.4 seconds). These occurred more often at the beginning of calls (Chi-Square: $\chi^2_2 = 8.280, p=0.02$) (Fig. 4.4).

Syllable length decreased slightly from positions one to two to three (Gamma Statistic = *–0.359, p = 0.003).* Call types with four syllables were rare (n=2) and were not included here. Syllables with high and low pitch (PRR > 2 kHz and < 1 kHz) were found slightly more often in second and third within-call positions. In contrast, syllables with medium pitch (PRRs between 1 and 2 kHz) occurred significantly more often at the beginning of the call (Fig. 4.4) (Chi-square: $\chi^2_4 = 11.789$, $p < 0.02$ level*).* No significant decrease or increase in pitch of syllables was detected from the beginning to the end of calls. LFC syllables with high PRRs (> 2 kHz) were not found in single-syllable calls, although two calls consisted of single upper frequency components (S-UFCs with PRRs > 4 kHz). Also, high-pitched LFC syllables (PRR > 3 kHz) rarely occurred in the first position of a call (2 of 18).

In summary, the most common pulse repetition rates were between 1 and 2 kHz and most syllables were between 400 and 800 milliseconds long. Only about 20% of syllables had either sound pitches > 2 kHz, or lengths > 0.8 seconds. Syllables became progressively shorter in later positions of a call. High and low pulse repetition rates occurred more often in the 2nd or 3rd position within a call, while medium ones (1-2 kHz) were more often found in the 1st position. The latter result was partly due to the high frequency of single syllable calls (~20% of all calls).

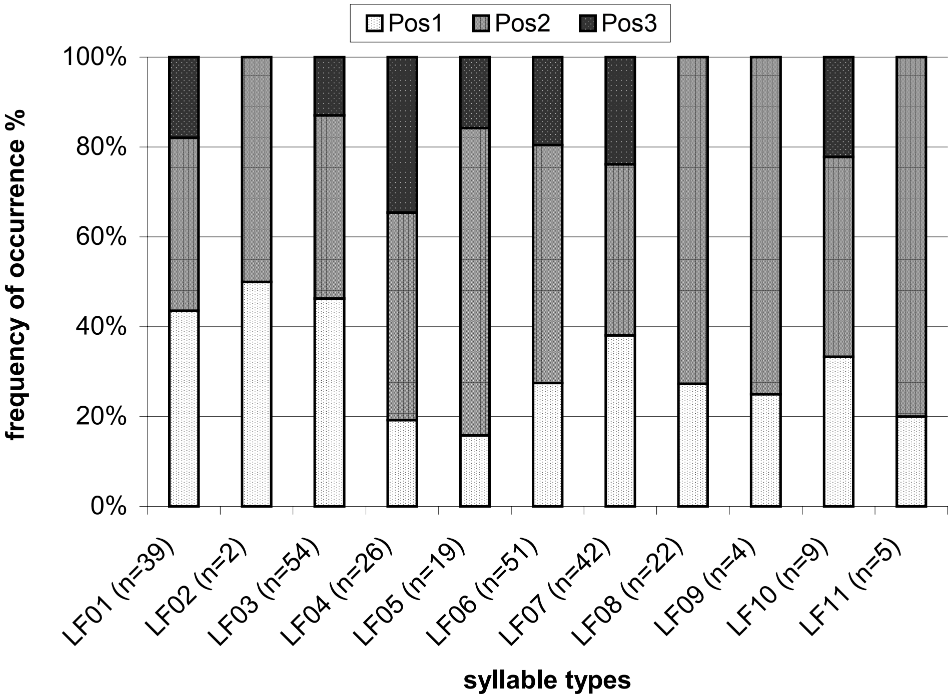

Figure 4.5: Proportional occurrence of LFC syllable types at positions one, two, and three in killer whale calls.

Very high pitch elements (PRRs > 3 kHz) were often short (< 400 msec), while high pitch syllables (2-3 kHz) were often the longest.

Test for static syntax rules

Placement of syllable types within a call

There were no exclusive rules that defined the position of syllable types within calls. Each syllable type was found in first or second position within calls, and 7 of the 11 types (Fig. 4.2) also occurred in third positions (Fig 4.5). The infrequent occurrence of syllable types in the third position reflected the rarity of three syllable calls. Despite the absence of exclusive placement rules, the variation in placement of more common syllable types (occurrence >10) at particular positions was significant (Kruskal-Wallis test, $\chi^2_2 = 8.009$, $p < 0.02$). In particular, LF01, LF03, and LF07 occurred more often in the first position of a call than did LF04, LF05, LF06, and LF08.

Call structure based on syntactic relationships among syllable types

With the exception of LF02 and LF09, all syllable types occurred in calls of all three resident communities. However, there was a distinction between the rare types that occurred in only some clans and the common types used by all clans (LF01, LF03, LF06, and LF07).

Table 4.2: Distribution of syllable types at within-call positions 1, 2, and 3 among clans and communities.

Comms.	SAR						NR									SR			Tot.
Clans	AB			AD			A			G			R			J			
Position	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	
LF01	2	1	1	1	2		3	6	3	5			3		2	3	6	1	39
LF02											1					1			2
LF03	8	2		2	3		7	13	5	1			2	3		5	1	2	54
LF04	1	1	2					3	1		1	3	4	3			4	3	26
LF05	1	2	2		1		2	1			5	1					4		19
LF06	2	7	1	4	4	1	3	4	2	3	4	2			1	2	8	3	51
LF07	3	3	4	2			8	6	5	3	2			1	1		4		42
LF08		7					3	5						4		3			22
LF09	1	1									2								4
LF10					1	1	1	2	1		1					2			9
LF11		2						2								1			5
	18	26	10	9	11	2	27	42	17	12	16	6	9	11	4	17	27	9	273

The occurrence of syllable types LF03 and LF07 at particular positions could have been influenced by clan membership. Generalized linear models applied to the data in Table 4.2 detected influences of clan membership on the position of both types relative to each other. The regression coefficients for both influences were above 0.8 ($F_6 = 4.4$ and 6.6, respectively, both $p < 0.02$). LF03 was common in all clans except G-clan and was used consistently either first or second within calls of all clans. With the exception of A and J clans, LF03 did not occur third in calls. LF07 was used in calls of all clans but only occurred in all 3 positions in AB and A clans. In contrast, LF07 was only in 1st (AD clan), in 1st and 2nd (G-clan), only in 2nd (R-clan), or in 2nd and 3rd position (J-clan). For most syllable types however, usage did not vary significantly among clans in within-call position 1 and 3, but it did so in call position 2 (Kruskal-Wallis test, $\chi^2_5 = 12.514$, $p < 0.03$) (Fig. 4.6).

In summary, there was no evidence for rules resulting in exclusive placements of syllable types in calls at either the clan or the community level. However, commonly used types varied in occurrence at particular positions within calls. Furthermore, variation of syllable type occurrences in 2nd call position differed significantly among all clans. Finally, the variation in occurrence of two syllable types, LF03 and LF07, at particular positions could have been influenced by clan membership.

All syllable types except LF06 were preceded and followed more often by different types than by the same type (Goodness–of-fit $\chi^2_1 = 96.805$ (preceded) and 88.733 (followed), both at $p<0.001$). LF06 type syllables occurred as three distinct sub-types (Fig. 3.6 in Chapter 3), and syllables of a particular sub-type were generally not preceded or followed by the same sub-type.

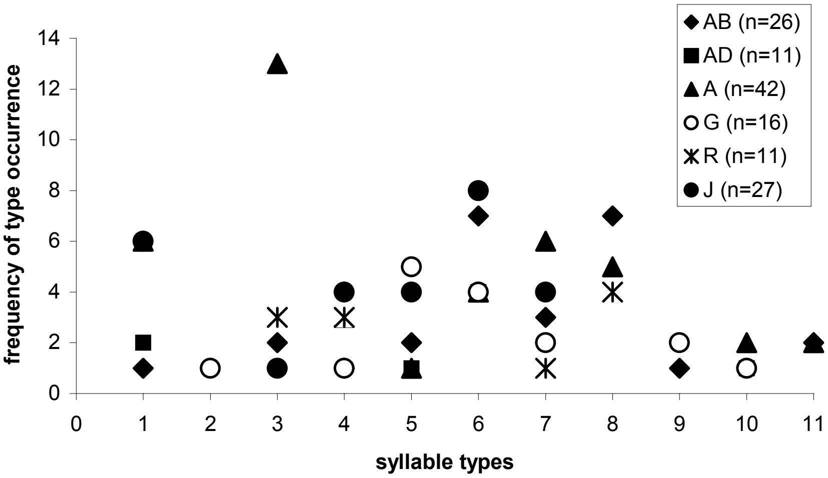

Figure 4.6: Distribution of syllable types among clans at the second within-call position. Numbers on y-axis reflect the number of call types that a syllable type has been extracted from.

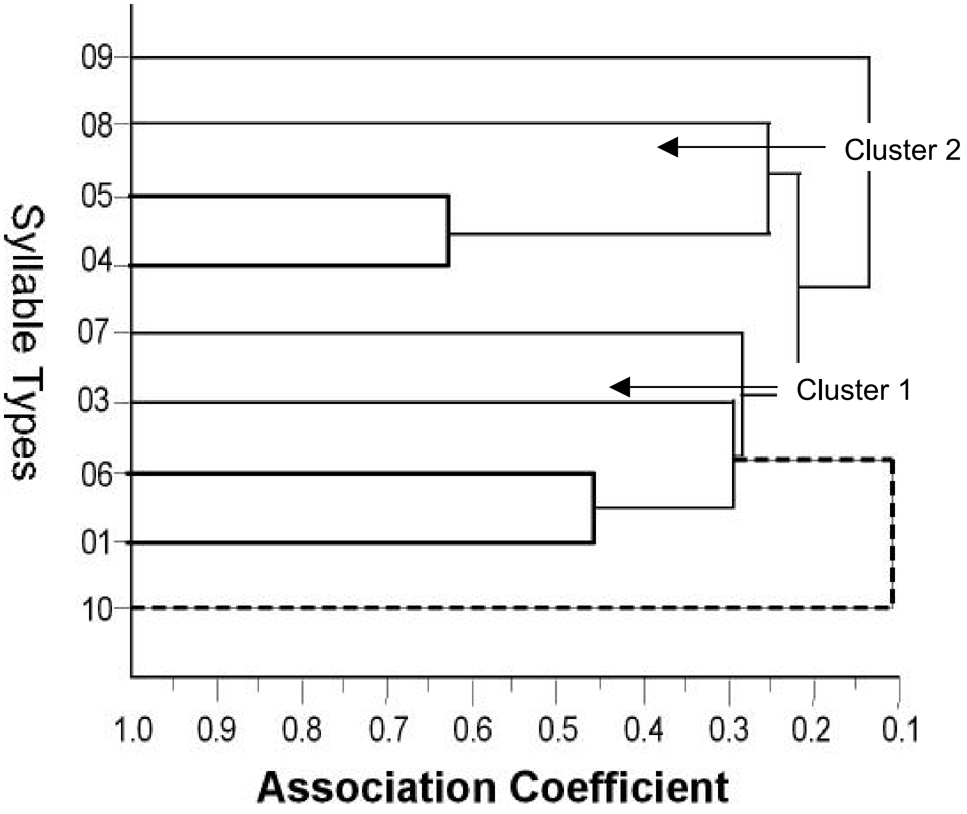

Figure 4.7: Average-linkage clusters of association indices among lower frequency syllables. The dotted line depicts association strength between LF10 and LF01, LF03, and LF06.

Syllable transition order produced clusters of associated syllable types. The association strength is illustrated by using *Dice's* association coefficients. The average linkage of association among syllable types within calls produced two clusters (Fig. 4.7). The occurrence of LF10 within calls was only associated with syllable types LF01, LF03, and LF06.

Cluster 1 included the most common syllable types LF01, LF03, LF06, and LF07 (66% of all syllables, Table 4.2), while cluster 2 included less common (LF04, 12%) and rare syllable types (LF05 at 6% and LF08 at 7%). LF09, which was more abundant among transient calls (see Chapter 3), had low associations with both clusters. It was associated with LF01, LF03, and LF06 of cluster 1, and with LF04 of cluster 2. Together these five types were common among both resident and transient killer whales (Chapter 3), two sympatric populations inhabiting the Northeastern Pacific (Ford & Ellis 1999). LF10 was only associated with three syllable types in cluster 1. Types of cluster 2 showed greater contour similarities than did types of cluster 1. LF04 and LF05 of cluster 2 were both chevron shaped and were mirror images of each other. At least some LF08s could be described as uninterrupted combinations of LF04s and LF05s (see Fig. 3.6 in Chapter 3).

In summary, syllables tended to be used in certain positions of a call in a manner that particular syllable types clustered in occurrence. Common syllable types were more closely associated with each other than they were with less common or rare types, which in turn were more strongly associated with each other. *Dice's* coefficient for loosely or partially associated types (LF09 and LF10) could have been influenced by low occurrences of these types (Table 4.2), which possibly made those indices less reliable. LF02 and LF11 were not considered in this analysis because these types were rare or absent in most clans.

Test for dynamic syntax rules

Dynamic syntax variation is the difference in proportions of distinct (Table 4.4) and shared (Table 4.5) syllable transitions to the total number (Table 4.3) of syllable transitions within calls.

Syntactical distinctiveness of clans and communities

No exclusive clan or community specific syllable order was detected, but frequency variations of particular syllable type combinations were present (Table 4.4).

Table 4.3: The number of observed syllable transitions within identified calls of resident clans and communities

Communities	Clans	Transitions			
		1 → 2	2 → 3	3 → 4	4 → 5
SAR	AB	14	6	2	-
	AD	7	2	-	-
NR	A	19	11	3	1
	G	10	4	-	-
	R	7	3	1	-
SR	J	14	6	2	-
Total		71	32	8	1

Table 4.4: Distinct syllable transitions within all identified calls of resident clans and communities

Comm.	Clans	Distinct Transitions				
		Proportion of total	1 → 2	2 → 3	3 → 4	4 → 5
SAR	AB	1→2: 0.36	LF04-LF06	LF09-LF04	LF01-LF06	
		2→3: 0.17	LF05-LF03		LF05-LF06	
		3→4: 1.0	LF06-LF11			
			LF07-LF11			
			LF09-LF07			
	AD	1→2: 0.29	LF03-LF10			
		2→3: 0	LF07-LF01			
NR	A	1→2: 0.47	LF03-LF01	LF01-LF06	LF01-LF04	LF07-LF01
		2→3: 0.64	LF05-LF06	LF01-LF07	LF03-LF07	
		3→4: 1.0	LF05-LF11	LF03-LF01	LF07-LF01	
		4→5: 1.0	LF06-LF03	LF04-LF06		
			LF06-LF07	LF08-LF04		
			LF07-LF03	LF10-LF03		
			LF07-LF07	LF11-LF03		
			LF08-LF03			
			LF10-LF10			
	G	1→2: 0.5	LF01-LF05	LF09-LF06		
		2→3: 1.0	LF01-LF07			
			LF01-LF09			
			LF06-LF02			
			LF06-LF10			
	R	1→2: 0.29	LF04-LF03	LF04-LF01	LF01-LF07	
		2→3: 0.67	LF04-LF08	LF08-LF06		
		3→4: 1.0				
SR	J	1→2: 0.29	LF02-LF05	LF01-LF04	LF03-LF03	
		2→3: 0.17	LF06-LF04		LF04-LF03	
		3→4: 1.0	LF10-LF01			
			LF11-LF07			

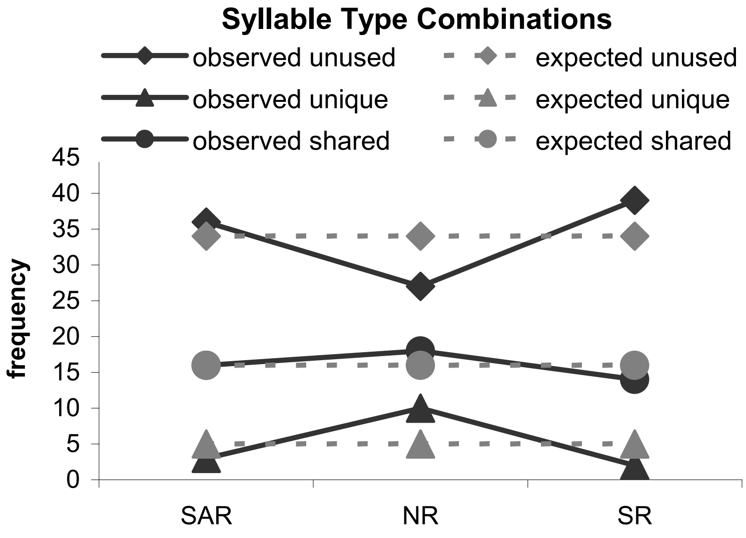

Figure 4.8: Occurrence of unique and shared syllable transitions in comparison to unused transitions by each community: Northern Residents = NR; Southern Alaskan Residents = SAR; Southern Residents = SR. The expected values are based on uniform distributions of syllables.

The proportion of clan-specific syllable type transitions versus all syllable type transitions was higher later in the calls. Consequently, calls of four or even five syllables could easily be distinguished by the syllable types in the fourth or fifth position. However, because most calls were short, the majority of clan-specific type transitions (> 70%) occurred either between the first and second or the second and third syllable of a call. Interestingly, A, G, and R clans of the Northern Residents showed more distinct syllable type transitions between 2^{nd} and 3^{rd} position of calls than the other clans.

The Northern Resident community had the most community-specific syllable transitions (10 unique combinations, Fig. 4.8), followed by Southern Alaskan Residents with three unique combinations, and Southern Residents with two unique combinations (Fig. 4.8). Northern Residents also shared more syllable transitions with other communities (18). Differences between unique and shared syllable transitions in communities were significant (Chi-Square, $\chi^2_4 = 10.394$, $p < 0.04$).

The repertoire of all possible combinations was limited by the number of identified distinct calls in residents. The differences in shared versus unique syllable type combinations between the Southern Alaskan Residents and Southern Residents were therefore minor in comparison to those differences between each of the two communities and the Northern Residents.

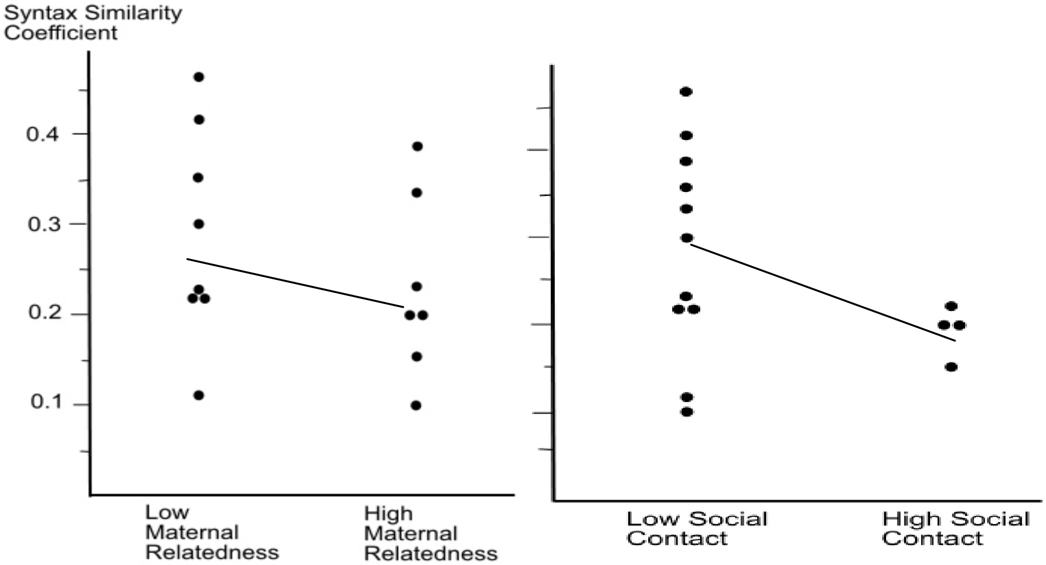

Figure 4.9: Syntactical similarity compared to maternal relatedness and social contact of clans. The coefficient displayed is a simple ratio association coefficient measuring the occurrence of the same syllable combinations in relation to the total number of possible occurrences of these combinations in the compared clans (Table 4.5). The lines depict the mean differences between the distributed values.

Syntactical similarity among clans and communities

Interestingly, syntactical similarity, measured as the ratio of shared syllable combinations to all possible syllable type combinations, appeared to be lower among clans within communities than among clans from different communities (Fig. 4.9-right). However, the difference could not be tested statistically due to the low number of data points for clans within communities. Nevertheless, the Mantel-Haenszel statistic rejected independence between syntax similarity and community membership ($\chi^2_1 = 5.005$, $p < 0.03$). This trend was also present but not significant when I compared syntactical similarity with maternal relatedness (Fig. 4.9-left) (Barrett-Lennard 2000). The maximum number of shared syllable transitions for socializing clans (same community) was two per clan (Table 4.5). These two combinations shared the same starting syllable.

There are two maternal haplotypes among the three resident communities (Barrett-Lennard 2000). SR is the maternal haplotype found in the Southern Residents and AD clan of the Southern Alaskan Residents (SAR). NR is the maternal haplotype of the Northern Residents and the AB clan of the SAR.

The two clans of Southern Alaskan Residents only shared syllable combinations that started with LF06. In NR, shared combinations mostly started with LF01. The Southern Resident community only consists of the J-clan and therefore cannot share syllables among clans within that community. Furthermore, all clans of Northern Residents shared the transition LF01 to LF04, which was also the most frequent shared transition in all communities (6 times). The highest syntactical similarities were between clans that neither socialize commonly nor have the same maternal haplotype (Barrett-Lennard 2000).

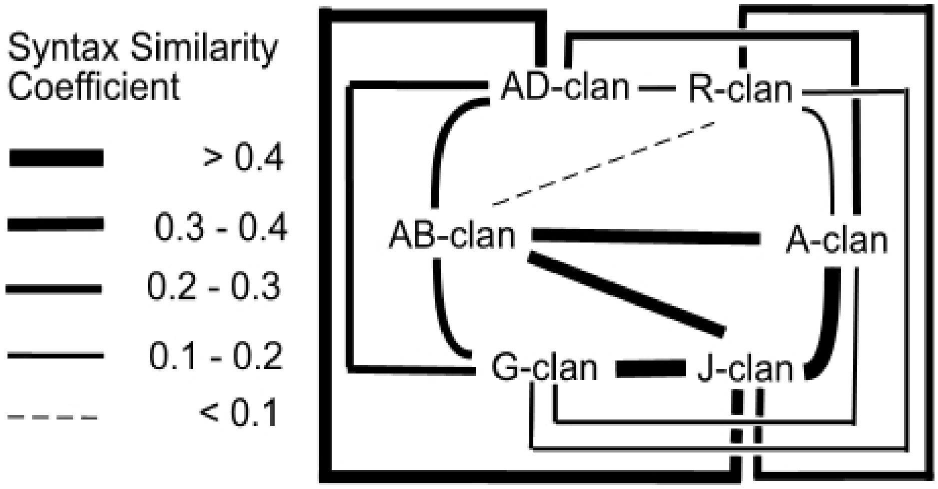

Figure 4.10: Sociogram of syntactical similarity of clans based on the transition similarity coefficient in Table 4.5.

The only exceptions were AD clan and J clan (similarity > 0.3). These two clans shared the same maternal haplotype but inhabit opposite ends of the range of resident killer whales (Fig. 1.1 in Chapter 1). The sociogram (Fig. 4.10) depicts a low average similarity (< 0.2) among all three clans (A, G, and R) of the Northern residents. All clans of the Northern Residents share the same maternal haplotype (Barrett-Lennard 2000). The two clans (AB and AD) of the Southern Alaskan Residents also showed low similarity (0.25). However, these two clans have different maternal haplotypes. The lowest similarity was between AB clan and R clan (< 0.1). Although these two clans share the same haplotype, they belong to different communities. However, some matrilines of these two clans have been seen in close proximity of each other on several occasions (Dahlheim, pers. comm.).

In summary, the number of syllable transitions that occurred was much lower than the possible number of combinations. The usage of group-specific syllable combinations did not reflect exclusive syntax rules that characterized any clan or community (Table 4.4). However, each community used a number of specific syllable combinations. The Northern Residents, which had more clans than the other two communities, used a greater than expected number of unique and shared syllable combinations (Fig. 4.8). Northern Residents also used a greater portion of the pool of observed combinations. Greater numbers of shared syllable combinations (syntactical similarity) may be correlated negatively with frequent social contact among clans but not strongly with maternal relatedness (Fig 4.9). Most shared syllable combinations were of common types (Table 4.4). Syntactical distinction among clans was mainly achieved through clan-specific positioning of syllable type combinations within calls (Table 4.3).

Call type repertoires and syllable type syntax

Based on the ways call types are defined (Ford 1987 and Chapter 2), large call repertoires can be achieved either by combining more syllables or by using distinct syllables. Call type repertoire sizes of clans were positively correlated with the number of matrilines per clan ($r=0.843$, $p<0.05$) and with the number of syllables used by clans (syllable repertoire) ($r=0.951$, $p<0.01$). However, no correlation was detected between repertoire size and the number of whales per clan (Table 4.6). A combination of clan size (matrilines per clan) and syllable repertoire size had the greatest power to predict call repertoire size of clans (multiple regressions, adjusted correlation coefficient $r^2=0.982$, ANOVA $F_1=138.69$, $p<0.01$; Table 4.6). Therefore, call repertoire differences among clans were mainly based on the variation in syllable use among clans. Particularly, A, G, and R clan used calls with multiple syllables more often than the other clans. Call repertoire sizes were also well predicted by transitions between

Table 4.5: Shared syllable transitions between 1st, 2nd, and 3rd call positions among clans and communities. Syntax similarity is the ratio of observed shared combinations to all possible shared combinations. *A sample calculation for syntax similarity is given below the table.

Shared by Comms.	Shared by Clans	Maternal Haplotypes	Shared transitions between syllables in call positions		Similarity Coefficient
			1 → 2	2 → 3	
SAR-SAR	AD – AB	SR-NR	LF06-LF01	LF06-LF06	0.222
SAR-NR	AD - A	SR-NR	LF03-LF03	LF03-LF10	0.222
	AD - G	SR-NR	LF06-LF06, LF07-LF05		0.222
	AD - R	SR-NR	LF03-LF03		0.111
	AB - A	NR-NR	LF01-LF06, LF01-LF08, LF03-LF07, LF03-LF08, LF07-LF04, LF07-LF08	LF03-LF07	0.389
	AB - G	NR-NR	LF01-LF06	LF05-LF04, LF06-LF05	0.231
	AB-R	NR-NR		LF08-LF07	0.1
SAR-SR	AD - J	SR-SR	LF01-LF03, LF06-LF06	LF06-LF06	0.333
	AB - J	NR-SR	LF01-LF06, LF03-LF05, LF03-LF06, LF03-LF07	LF05-LF04, LF06-LF06	0.353
NR-NR	A – G	NR-NR	LF01-LF04, LF01-LF06		0.154
	A – R	NR-NR	LF01-LF04, LF03-LF03		0.2
	G – R	NR-NR	LF01-LF04, LF01-LF07		0.2
NR-SR	A - J	NR-SR	LF01-LF04, LF01-LF06, LF03-LF07, LF08-LF01, LF08-LF05	LF01-LF03, LF07-LF01	0.412
	G - J	NR-SR	LF01-LF04, LF01-LF06, LF03-LF06, LF06-LF06	LF05-LF04, LF07-LF06	0.462
	R - J	NR-SR	LF01-LF03, LF01-LF04, LF03-LF04		0.3

* The total number of 1 → 2 transitions was 14 in AB clan and 7 in AD clan, while the total number of 2 → 3 transitions was 6 and 2 respectively (Table 4.3). Thus, the total number of possible shared combinations was 9 (Minimum of (14,7) + Minimum of (6,2)). As only two shared transitions were observed, the similarity coefficient was 2/9 or 0.222.

Table 4.6: Comparison of the number of whales, matrilines and calls per clan with the size of the syllable repertoire, the number of distinct syllables, and the number of syllable transitions per clan.

	Repertoire Users		Calls	Syllables			
				static syllable order		dynamic syllable order	
Clans	# of matrilines *	# of whales *	# of distinct calls in repertoire	# of syllables in repertoire	# of distinct syllables in repertoire	# of different syllable combinations in repertoire	# of unique syllable combinations in repertoire
AB	35	201	37	65	11	19	3
AD	12	46	17	25	7	8	0
A	18	106	38	88	9	28	4
G	10	76	16	34	9	13	5
R	5	32	10	23	7	11	1
J	20	75	29	57	11	20	2
Total	100	536	147	292	54	99	15

*** 2000 Census**

different syllables (r^2=0.981, ANOVA F_1=85.087, p<0.02). Consequently, large call repertoires also occurred when matrilines used a greater number of different syllables (e.g. G-clan).

4.4 Discussion

The position of syllable types in resident killer whale discrete calls is highly flexible. Almost every type can occur as the first, second, or third syllable of a call. Some syllable lengths and maximum sound pitch levels were preferentially located at particular positions in calls. However, syllables of particular length or pitch level had no exclusive positions within calls. Nevertheless, some syllable types showed preferred associations. These preferences limited the syntactical variability of calls.

Syntax variation

Syntax variation commonly produces distinct signal types in bird songs (Catchpole & Slater 1995), human speech (Doupe & Kuhl 1999), and killer whale calls (Ford 1987). The syllable syntax of killer whale calls is more flexible than in many bird songs, although syllable type order is more variable in birds with individual song repertoires (Podos et al. 1999). As in killer whales, syntactical orders of elements, such as notes, phrases, and motifs in bird songs, often vary among groups. This syntax variation may characterize socially and geographically different song types (Baptista & Petrinovich 1986; Catchpole & Slater 1995; Slabbekoorn et al. 2003). However, the association of notes and syllables within songs often represents a species- or population specific ordering in birds (Marler & Tamura 1962; Marler & Pickert 1984; Hultsch & Todt 2001). Although syllable order is fixed within a particular killer whale call (Ford 1987 and Chapter 2), syllable types are combined differently in different calls of the same clan, community or population. Also, repetition of the same song elements reduces the syntactical complexity of bird songs in comparison to that of killer whale calls. Repetition occurs in strings of killer whale calls, but repeated calls are often not from the same individual (Ford 1989; Miller et al. 2004).

Killer whale call syntax is more flexible than any other combinatorial mammalian vocalizations other than human speech. Some vocalizations of neotropical monkeys (Robinson 1979, 1984) and male humpback whales (Payne & McVay 1971) have considerable syntactical flexibility in the order of syllables. However, their syllable phrases and sequences are more repetitive and have fewer distinct types than killer whale calls. Also, the sequence order is often innate, such as for vocalizations of the Dusky Titi monkey (*Callicebus molochus*) (Robinson 1979). The syntax of killer whale calls is learned socially because call types produced by members of a matriline are identical in syllable order and almost indistinguishable within a matriline (Ford 1987; Miller & Bain 2000).

Some killer whale syllables are often found in pairs (Fig. 4.7). These preferred associations could reflect historic relationships among these syllables, i.e. reflect the cultural history of calls, because they are not characteristic of particular within-call positions. The syllables with the highest association coefficients among them occurred not only in resident killer whales but also in transient killer whales (Chapter 3). These populations separated a long time ago, and may represent incipient species (Barrett-Lennard 2000). The preferred associations may reflect simpler organizational levels of calls used by ancestors of both residents and transients. Furthermore, these patterns of syllable association could reflect an intermediate level of organization within calls similar to song phrases (distinct strings of notes or syllables) in bird songs (Marler & Peters 1988; Nowicki & Nelson 1990). Because they limit the way certain syllable types are ordered, preferred associations limit the arbitrariness of killer whale call syntax. Syllable associations in human speech are limited by grammatical rules (Nichols 1998) and certain associations reflect historical relationships among languages (Nichols 1998; Cavalli-Sforza 2000). However, humans use more distinct syllables than killer whales and have fewer fixed associations of syllables among loosely related language groups (Nichols 1998). Thus, humans can store an almost unlimited amount of information in words. Due to smaller syllable repertoires (Chapter 3) and less syntax variation, killer whale calls are less likely to reach information contents of human words.

Syntax divergence and its possible functions

Although call repertoires diverge among matrilines according to their degree of relatedness (Ford 1987; Deecke et al. 2000; Miller & Bain 2000 and Chapter 2), innovations at the level of the call type are rare (Ford 1991; Ford 2004 and Chapter 2). New call types evolve by either replacements of syllable types at particular positions, or by additions of syllables to existing calls (Table 4.6) (Ford 1987). Because choice is limited to 11 lower frequency and 7 synchronously produced upper frequency syllable types (Chapter 3), divergence of call type repertoires is mainly a function of syntax variation (Table 4.6). So far 147 distinct calls of residents have been identified and recent recordings of residents from other areas of the North Pacific show additional call types but no new syllables (Yurk et al., unpubl. data). Divergence in call syntax therefore reflects the social or cultural history of resident killer whale clans, while innovation and loss of syllable types explains vocal divergence among resident killer whale communities and between residents and transients (Chapter 3).

If killer whale syllable syntax is analogous to song type syntax in birds, it is most likely without function. Each of the organizational components of bird songs appear to have the same meaning as whole songs (Marler 1998). Song type variation or differences in song type repertoire are considered the only carrier of important biological information (Podos et al. 1992). In contrast, human language is an open communication system, in which a finite number of syllables or phonemes can be combined arbitrarily to produce an infinite number of words, phrases, and sentences (Pinker 1998). The more complex structural element carries a different meaning than each of the simpler structural elements of which it is comprised. This process that transforms meaning in human languages is called lexical syntax (Marler 1998). It is too early to say whether killer whales have lexical syntax. However, a relationship between syntax and mate choice exists that allows syntactical variation to function differently from syllable choice.

In the Northern Resident community, mating occurs predominantly between clans. Although all three clans are maternally related, genetic distance between them is greater than within each clan (Barrett-Lennard 2000). Differences in syntactical call structure are associated with clan membership within communities (Fig. 4.10), and syntactical similarity appears to be associated with social contact among clans rather than maternal relatedness (Fig. 4.9 and Table 4.5). It is possible that selection stabilizes call syntax within clans and promotes divergence between clans to avoid inbreeding. Syntax variations can assist whales in choosing mates that are genetically less related (fathers of calves always come from different maternal lineages), but still belong to the same community without having to memorize calls of each matriline of a community.

Alternatively, syntax variation among those clans could be a by-product of call repertoire divergence. This result, however would also mean that syllabic call structure is a by-product of call development. In this case drift and not selection has produced distinct clan repertoires.

This outcome is less likely, because it requires that clans with distinct call repertoires in the same community are older than communities whose repertoires are not completely distinct. Although calls are not shared between communities, syntactical similarity is often greater between than within communities (Fig. 4.10). Also, the proximate mechanisms responsible for greater call repertoires appear to differ among clans. While AB and A clans generate larger call repertoires by using more syllables, G- and possibly also R-clan produce more distinct combinations of syllables to achieve the same result. Selection for syntax to diverge in response to social contact of clans would allow call repertoires to change faster than does drift influencing all parts of calls equally (Ford 1991). It may be easier to replace or add syllables in existing repertoires to create variety than to create new syllables. White-crowned sparrows (*Zonotrichia leucophrys)*, whose syllable type repertoire is under selection to conform to a region-specific type, may use this mechanism to invent new song types (Slabbekoorn et al. 2003). Also, recombining syllables to produce novel calls is a cost efficient way to produce complex signals (Endler 2000; Johnstone 2000).

Resident killer whale clans maintain distinct call repertoires (Ford 1991 and Chapter 2) despite frequent social and vocal interactions with other clans in their community. Because call syntax is learned within the matriline, syllable choice is limited during learning. If syntax learning were not restricted to the tutor model, syllabic call structure would be completely arbitrary as it is in some bird songs (Marler 1997). Due to the copying of the syntax of close relatives, each clan or community uses considerably fewer combinations of syllables than could be generated from the syllable repertoire (Fig. 4.8). It is not known whether killer whales understand more combinations than they use. However, because selection acts to contrast communities through syllable type choice (Chapter 3), they would not need to know all combinations to recognize community members. The restriction in syllable choice to only 18 types might also limit the call repertoires of matrilines. Call repertoires of matrilines in the Northern Resident and Southern Alaskan Resident communities appear not to exceed 17 to 18 call types (Ford 1987 and Chapter 2). In contrast, humans can learn and produce syntactical ordering of more than one language. Furthermore, by combining phonemes of more than one language into a far greater number of grammatically correct words, humans can create huge word lexicons (Pinker 1998). Killer whales may lack that ability to create meaningful grammatical constructs. Call syntax is therefore not likely to be lexical syntax as defined by Marler (1998).

Resident killer whales communicate more often with close relatives of the same matriline, than with distantly related groups. If syllables already carry most of the information that killer whales need to exchange with their group mates, call syntax divergence could result from the need to distinguish matrilines and clans. In this case, calls might function similarly to family or clan names in human societies, or to the chemical markers used by terrestrial mammals to mark social boundaries (Bradbury & Vehrencamp 1998). The fact that larger call repertoires of communities are associated with larger numbers of matrilines and clans seems to support this notion. In songbirds, the sizes of song type repertoires are sometimes correlated with the number of neighbours in a given area (Williams & Slater 1990; Beecher et al. 2000). Alternatively, call repertoires could have functions other than as group identifiers. In some songbirds, repertoire sizes are associated directly with the success of the singer in male-male competition for territory (Searcy & Nowicki 2000; but see Beecher et al. 2000). Song repertoire sizes also appear to be influenced by the need to attract females (Catchpole 1996) and can indicate the reproductive success of males (Reid et al. 2004, 2005a).

Future studies on call repertoires of resident killer whales should make an effort to find out who is calling to whom and when. For example, males could use particular calls more often than females. If so, there could also be structural differences among those calls. However, there appears to be no obvious difference in call repertoire use between males and females of the same matriline (Ford 1989), nor do closely related matrilines with and without males show considerable repertoire differences (Ford, pers. comm.). It is also possible that females use more complicated calls that are less likely to be copied accurately. This could help them to assure that their vocal markers do not get used by other matrilines, unless they are related. Although call mimicking does occur, the rendition of the mimicked call always allows receivers to identify them as copies produced by a matriline with a different dialect (Ford 1991).

4.5 Summary and conclusions

A number of studies on bird songs and human vocalizations have shown that syntax variation is one of the important mechanisms to produce changes in dialects. Previous studies on killer whale vocalizations have asserted that this is also true for call dialects. Here, I have shown that resident killer whales of the Northeastern Pacific lack the region- or species-specific syllable order seen in other mammalian and some avian vocal signals. Although syllable order is fixed within a particular killer whale call, syllables can be combined differently in different calls. Positioning of syllable types within calls is predominantly arbitrary, although some syllable lengths and maximum sound frequencies show preferential positioning. The combination of syllables, however, is not completely arbitrary, because certain syllables occur more often together than others. This pattern might reflect historical relationships among syllables. The syntactical order of syllables is also constrained by syntax or call learning, which occurs mainly between parent and offspring generations in the natal matriline. This vertical transmission of syntax and calls stabilizes syllable order in matrilines and has led to a constraint on syllable combinations in clans. Consequently, this learning process may also explain long-term syntax stability in clans.

Syntax divergence appears to be greater among clans of the same community than between clans of different communities. Clans of the Northern Residents have the same mtDNA haplotype but consistently low syntax similarity. This can mean that syntax divergence is correlated with social contact but not with maternal ancestry. Previous studies suggested that distinct call repertoires of clans are the products of cultural drift. However, given that divergence is most rapid in groups having on-going contact, it is more likely that selection causes dialects to diverge within communities.

Call repertoires could be used in mate choice to reduce inbreeding by choosing vocally dissimilar mates. A prior genetic study showed that inter-clan mating or mating among members of vocally dissimilar groups is typical for residents. Because mating predominantly occurs within communities, syntax divergence among clans may result when relatedness falls below a certain threshold. My results point toward gene-culture coevolution in killer whales, because syntax variation constrains gene flow.

5. GENERAL CONCLUSIONS

The proximate and ultimate mechanisms of vocal divergence, which I set out to examine in killer whales, have been the focus of intense research in birds and other mammals (Mundinger 1980; Slater 1986; Janik & Slater 2003; Lachlan & Feldman 2003). The question of whether vocal culture in birds is adaptive has received special attention (Slater & Ince 1979; Slater 1986; Payne 1996). While some cultural differences might be adapted to particular locations (Payne 1996), most vocal cultures are seen as by-products of vocal learning at geographically different locations (Slater 1986). In a few instances where song is transmitted from father to son, cultural differences may be used in mate choice and can be considered adaptive (e.g. Grant & Grant 1996). Differences among human languages and dialects of traditional societies are considered to function as cultural barriers between communities that also affect gene-flow (Renfrew 1998; Cavalli-Sforza 2000). In this thesis, I compared and contrasted syllabic call structure and syllable-type distributions of various killer whale clans, communities and populations of killer whales of the Northeastern Pacific. The goal of this comparison was to investigate the extent to which call structure influences social structure and mating patterns.

Cultural lineages (Clans)

I began this dissertation by analyzing acoustic recordings from an area of the resident killer whale population range (Southern Alaska) for which vocal similarity among matrilines and pods had not been previously determined. This analysis led to the identification of two vocal clans which, when compared to results of genetic studies (Barrett-Lennard 2000), were found to represent different maternal haplotypes. The results showed that vocal clans of killer whales, which were initially defined by Ford (1991) based on their distinctive call repertoires, may also reflect genetic relatedness (Barrett-Lennard 2000). This result confirmed that vocal clans do indeed meet the broadly accepted definition of a clan as a cultural lineage that reflects relatedness (Murdock 1960).

Syllable repertoire divergence among clans, communities and populations

To determine if there are vocal markers for social and genetic relatedness above the clan level, I examined whether call types could be subdivided into distinct smaller acoustic elements, or syllables. Syllabic signal structure is present in human speech (Ladefoged 1993), birdsongs (Catchpole & Slater 1995; Hultsch & Todt 2001) and songs of baleen whales, such as the humpback whale (Payne & McVay 1971). In birds and humans, syllable similarities and differences can be used to trace population divergences (Lynch & Baker 1993; Nichols 1998). I found that all 163 call types described from two killer whale populations, residents and transients, in the Northeastern Pacific can be broken down into syllables belonging to 18 distinct types.

Syllable type repertoires showed distinct differences among resident clans, communities and between two populations, transients and residents. Particular groups of syllable types were shared between these two populations, while others only occurred in resident killer whales. It appears that syllable type repertoires of residents have diverged more than those of transients. This pattern may reflect differences in the stability of social group composition between residents and transients but may also indicate a functional difference of syllable repertoires in the two populations. While syllable and call repertoire differences among residents reflect the different levels of the social organization in this population, the vocal repertoires of transients are not stratified. All transients share all of the syllable types and most of the calls of their repertoire with other transients of their population (Ford & Morton 1991; Deecke 2003).

Transient killer whales are characterized by groups that change composition through dispersal (Ford & Ellis 1999; Baird & Whitehead 2000). Residents appear not to disperse from their natal groups, called matrilines, for more than a day (Ford et al. 2000). It may be more important for a transient killer whale than a resident killer whale to sound similar to other community members because of a need to restore social affiliation following dispersal. Transient killer whales hunt cooperatively (Ford & Ellis 1999) and may regulate group size through the use of calls. Because transients often travel in small groups or alone (Ford & Ellis 1999; Baird & Whitehead 2000), calls may be used to find other members of the community (Deecke 2003). Resident killer whale signals appear to reflect the potential need of these whales to communicate group membership at different levels of the social organization. As a possible result, syllable type and call type repertoires are greater in residents than in transients.

Syntax divergence among resident clans and communities

While syllable type repertoires identify community or population membership in killer whales, the syntactical order of syllables is characteristic for each call type. However, syntactical order varies greatly among different call types. Variable syntactical order of notes and syllables also characterizes bird songs (Peters et al. 2000; Searcy et al. 2003) and human words (Ladefoged 1993). However, syntax variability in killer whale calls is lower than in birds and humans because some killer whale syllables occur together in calls of different communities or populations. Because the preferred syllable combinations also involve the more common syllable types, it is possible that these combinations reflect historic associations. These combinations appear in calls of residents and transients (Chapter 3).

There are three main ways in which syllabic call structure in killer whales changes: a) deletion of syllables, b) replacement of syllables, and c) addition of syllables (Chapter 4). None of these changes happen very often as the syllabic structure of call types is highly stable. Call types are learned within the matriline and are mainly transmitted from parent generation to offspring generation, although some horizontal exchange between matrilines also occurs (Deecke et al. 2000). However, syntax stability is greatly reduced above the clan level leading to distinct call repertoires, and syntax differences seem greater among clans within communities than between communities. If syntax divergence results passively from call divergence, i.e. due to drift, it should follow social divergence of groups. However, this would mean that clans with greater syntax differences are older than communities with greater syntax similarities. Because social contact occurs mainly within communities, drift is unlikely the cause for syntax divergence among clans of the same community. I propose that selection has acted to maintain stable differences in syntax among clans within communities. Furthermore, I believe that distinct call repertoires are a result of syntax divergence. Syntax variation produces call distinction faster than other forms of call structure divergence. Rapid vocal divergence may allow whales to find mates that belong to the same community but that are not closely related. There is good reason for clans to stay within communities, because mating between communities seems to be virtually absent. If mate choice is associated with vocal difference as suggested earlier (Ford 1991; Barrett-Lennard 2000), call type repertoires should diverge as relatedness decreases. The most efficient and least costly way to change call types is by changing syntactical order. If mate choice depends on acoustic differences, selection could act to maintain and even increase dialect distinction among clans within communities.

Cultural selection and gene-culture co-evolution in killer whales

Selection is present when either: 1) the function of calls or call structures influences individual fitness (natural selection), or 2) the production of appropriate calls is socially advantageous and is selected by members of the group (cultural selection). Both mechanisms typically occur in communication systems where group-specific vocalizations help individuals to increase or maintain their reproductive success (Lachlan et al. 2004). Cultural selection is then maintained through conformity-enforcing behaviour, e.g. communal territory defense, while individual fitness benefits, e.g. territory acquisition, select for conformity. This has been suggested for song dialect similarities of related and unrelated birds that act together to drive away intruders with different song-types (Lachlan et al. 2004). The cooperative behaviour of unrelated individuals is facilitated through increases in individual fitness for territory holders.

Bird songs are usually learned through copying the songs of neighbours. However, song type acquisition is often under selection to restrict songs to species- or region-specific types (Baker et al. 1987; Nelson & Marler 1994; Peters et al. 2000). If signal production is under selection to conform to a social model instead of a species or regional model, such as a group-specific dialect, the selection is cultural. Resident killer whale call dialects, which exist at the level of matrilineal groups, are most likely under cultural selection.

Cultural selection that affects gene distributions is generally seen as evidence for gene-culture co-evolution (Feldman & Laland 1996; Lachlan & Slater 1999; Lachlan & Feldman 2003). Aside from being a characteristic of human evolution, gene-culture co-evolution has been also noted in the development of shared song types among generations of Darwin finches *Geospiza fortis* and *Geospiza scandens* (Grant & Grant 1996). Darwin finches learn song repertoires by copying the songs of their fathers. To reduce inbreeding, dialects appear to affect mate choice because finches only chose mates that were using different dialects. Syntax differences are greater among interbreeding killer whale clans than among reproductively isolated communities. This indicates that gene-culture co-evolutionary processes may have played a role in the evolution of call repertoires.

Barrett-Lennard (2000) showed that resident killer whales prefer to mate with members of different clans. Since call type repertoires of clans are completely distinct, this could mean that there is a social rule: Mate preferentially with partners that use different call types. However, while some killer whale communities do not mate within clans, other communities are characterized by some within-clan mating. One community consists of only one clan, and therefore all mating takes place within that clan. Barrett-Lennard (2000) therefore decided to rephrase the rule to: Mate only with the acoustically most dissimilar individual or group encountered. This seems to be the case in Alaskan resident killer whales, where mating takes place within and between clans but always between acoustically very dissimilar matrilines (Barrett-Lennard 2000; Matkin et al. 2002). The rule leads to a vocal bias in reproductive associations among groups of a community and would explain why associations between members of different clans are frequent and prolonged during times when mating may take place (Ford, pers. comm.).

If genetic diversity within resident communities is maintained by the simple rule of mating with the most vocally dissimilar individual, syllable type choice and syllable syntax differences are more reliable indicators of relatedness than are calls. Syllable type choice reflects community membership and could be used to avoid breeding outside of the community. Clans in two of the three communities examined here have only one distinct mtDNA haplotype (Barrett-Lennard 2000). Because all mating occurs within communities, this might explain why mitochondrial DNA diversity is low in resident killer whales. Because syllable type differences among communities are culturally selected, this may also support the idea of cultural hitchhiking of genes (Whitehead 2005). Syntax differences are responsible for distinct repertoire differences beyond gradual call variation and would allow individuals to recognize vocally dissimilar partners reliably. Syntax similarity does not decrease proportionally with social divergence. It appears to be high as long as social contact is frequent (Ford 1991; Deecke et al. 2000; Miller & Bain 2000). Syntax stability may be achieved by regular vocal exchanges between groups (Deecke et al. 2000). When relatedness decreases, social contact among matrilines also decreases. It may be that if year round social contact falls below a certain threshold, cultural selection pressures become reduced, allowing syntax similarity to decrease. The driving force for this vocal divergence may be that the number of available mates depends on the number of matrilines within a community.

The largest syntax difference should exist among matrilines of the same community that associate the least. Recent observations, however, show no obvious relationship between degree of social association and vocal relatedness of Northern Resident groups (Ford & Ellis 2002). These observations were predominantly made during summer months. However, during late fall, winter, and early spring, acoustically monitored resident killer whales in Southern Alaska associated exclusively with members of their own clan (Matkin et al. 2001, 2002). Further investigations into the winter associations of residents are needed to determine whether year round social contact is higher for closely related matrilines. Summer distribution of residents could be influenced by patchy prey abundance (mainly salmon – Ford et. all 1998; Saulitis et al. 2000), which brings whales of the same community into greater contact than during the winter. Salmon abundance along the coastline varies over the course of a year and is highest near spawning areas and in migration corridors during summer and fall. Furthermore, mating in killer whales takes place during summer and fall (Ford et al. 2000), which is another reason to seek contact during this time. Overall contact frequency over the year among loosely related matrilines may be considerably lower.

Summary and outlook

My results support the notion that resident killer whales use vocalizations in mate choice (Bigg et al. 1990; Ford 1991; Barrett-Lennard 2000). Resident killer whales have neonate mortalities that can reach 60% (Olesiuk et al. 1990). Detrimental effects to their survival due to inbreeding could therefore be considered a high risk for these killer whales. Considering the relatively small sizes of some resident communities (e.g. 75 Southern residents in 2000), resident killer whales need an effective strategy to avoid inbreeding. This becomes even more vital because assortative mating further reduces effective population size (Barrett-Lennard 2000), The vocal system of residents includes complex signals that reflect not only degrees of relatedness but also degrees of social affiliation. As a result, resident killer whales are able to consistently outbreed by choosing an acoustically dissimilar mate among members of the same community. Conversely, within-community mating reduces the negative effects of disease spreading (Barrett-Lennard 2000). Because visual and chemical markers are ill-adapted to aquatic environments, effective out-breeding would be very difficult without the relative stability of call type repertoires of resident killer whales. The stability of vocal repertoires is likely a product of vertical and oblique cultural transmission of syllabic call structure. Because calls are socially learned, so is group-specific syllabic call structure. Social affiliation and divergence regulates vocal similarity and vocal difference but not in a linear fashion. Because killer whales do not leave their matriline and matrilines gradually split over time, vocal similarity reflects genetic lineages among matrilines with frequent social contact. However, when relatedness falls below a threshold, call type divergence accelerates possibly due to changes in syllable syntax.

Future studies should focus on the usage of syllables by killer whales, particularly whether they are recognized independently of calls and whether differing syllable combinations elicit different reactions. These studies could be achieved through playbacks of syllable types and combinations to different groups. Furthermore, special attention should be given to possible differences in syllable use between males and females. Due to the complete philopatry of residents, males have only a limited ability to maximize mating frequency. If males are vocally more active and use different calls based on syllable choice and syntax, vocal divergence could be driven by two competing strategies: a male strategy that drives the change of syllabic call structure and a female strategy that promotes structural stability. Call use in resident killer whales is an excellent candidate for studies on gene-culture coevolution (Feldman & Laland 1996).

Finally, it appears that resident killer whales do not have an open communication system in which signal structure has a different meaning than each of the signal components, as does human speech (Pinker 1998). The basis for such a system is present because a low number of small acoustic units can be combined differently to produce more distinct vocal units. However, cultural rules, such as the confinement of call learning to matrilineal groups, appear to limit the evolution of an open communication system in killer whales. Group recognition and mate choice seem to drive the cultural evolution of the system. It is possible that killer whales are able to create more meaningful syllabic call structures, but this question could not be addressed with this study. Well-designed playback experiments that test cognitive capabilities of killer whales might shed more light on this question.

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APPENDIX

Acoustic Test Help

This rating procedure is meant to provide information on the similarity of call elements and components of discrete calls used by killer whales in the North Eastern Pacific.

What you see are spectrograms of formative parts of calls responsible for their discreteness. Spectrograms illustrate changes in the sound frequency contour over time. The intensity of particular frequency bands is indicated by the darkness of the contour band. There are multiple contour bands visible because the signals are pulsated. Number of visible bands usually depends on the clarity of the signal (e.g. distance from the recording source) not on frequency parameters. However, darkness of a particular band could be considered a deliberate emphasis used by a vocalizing whale. The elements and components are standardized for frequency. The duration of elements and components is presented in four classes (FRAME SIZES): Frame size reflects class size, e.g. smaller window - calls of shorter duration.

ELEMENTS AND COMPONENTS DO NOT HAVE TO HAVE THE SAME LENGTH IN ORDER TO BE CONSIDERED SIMILAR. CONTOURS CAN BE CONSIDERED SIMILAR IF THEY OVERLAY WHEN STRETCHED OR COMPRESSED HORIZONTALLY (NOT VERTICALLY). NUMBER OF BANDS VISIBLE ARE NOT INDICATORS FOR SIMILARITY! SO, LOOK FOR SIMILAR MODULATION AND DISTANCE BETWEEN CONTOUR LINES NOT FOR IDENTICAL LENGTH. ALSO, LOOK FOR POSITION AND DIRECTION OF CONTOUR CHANGES.

RATE SIMILARITY OF TWO SPECTROGRAMS BY ESTIMATING WHAT PERCENTAGE OF THE CONTOURS IS THE SAME. BASE YOUR ESTIMATE ON THE FOLLOWING PARAMETERS USING THE PRESENTED HIERARCHY:

1. **HIGHEST PRIORITY**
   MAKE YOUR INITIAL RATING BASED ON: CONTOUR MODULATION: Trend of contour: upwards or downwards, amount of contour changes, position of changes within contour. Decide on the rating class: If the contours are neither identical nor completely dissimilar decide on whether they show low, medium, or high similarity.

2. **2ND HIGHEST PRIORITY**
   ADJUST YOUR INITIAL RATING USING: DISTANCE BETWEEN SPECTROGRAPHIC BANDS: The more the distances between bands differ the less similar they are. If similarity is either high or low, decide whether they can be considered very high or very low.

3. **3RD HIGHEST PRIORITY**
   ADJUST YOUR PREVIOUS RATING USING: POSITION OF DARKEST BAND: The greater the vertical distance of the darkest bands is between the two spectrograms the

lower the similarity is. If more than one band can be considered the darkest compare the lowest bands in each spectrogram. Finalize your decision on whether similarity is higher or lower within rating class. If based on previous decision similarity is close to a boundary switch to the next class.

4. **LOWEST PRIORITY**
   LENGTH OF SPECTROGRAM: Use the frame size as an indicator of length. This parameter is the least important and should only be used to increase or decrease your rating after the above parameters have given you an idea of how similar contours are according to the rating scheme. Adjust rating only if your previous decisions have placed the similarity close to the boundary of a rating class.

   EXAMPLE: IF THE CONTOUR IN SPECTROGRAM 1 IS SMALLER THAN THE CONTOUR IN SPECTROGRAM 2 BUT CAN BE STRECTCHED OR COMPRESSED TO MATCH CONTOUR IN SPECTROGRAM 2 COMPLETELY THAN THE SIMILARITY IS HIGH. WHETHER THE SIMILARITY IS VERY HIGH DEPENDS ON THE DISTANCE AMONG CONTOUR LINES AND WHERE THE DARKEST CONTOUR IS LOCATED. IF CONTOUR IN SPECTROGRAM 1 CAN BE STRETCHED OR COMPRESSED TO MATCH A PART OF CONTOUR IN SPECTROGRAM 2 THAN THE PERCENTAGE OF MATCH IN CONTOUR OF SPECTROGRAM 2 INDICATES THE AMOUNT OF SIMILARITY.

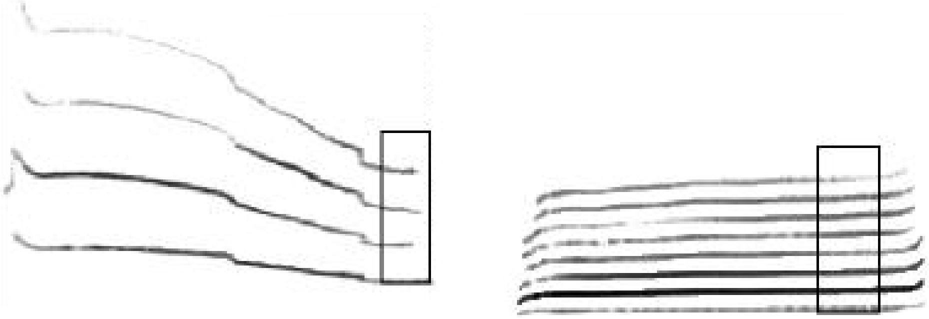
RATINGS:

NO SIMILARITY	less than 10% contour similarity
VERY LOW SIMILARITY:	between 10%- 20% of contours are similar
LOW SIMILARITY:	between 20%-40% of contours are similar
MEDIUM SIMILARITY:	between 40%-60% of contours are similar
HIGH SIMILARITY:	between 60%-80% of contours are similar
VERY HIGH SIMILARITY:	between 80%-90% of contours similar
IDENTICAL:	more than 90% contour similarity*

* Less than 100% similarity is acceptable for the contours to be considered identical because individual variation is not tested.

VIEW RATING EXAMPLES BEFORE STARTING TO RATE. RATE BY CLICKING CORRESSPONDING RADIO BUTTON AND PRESS NEXT. DO NOT SPEND MORE THAN 15 SECONDS ON EACH RATING!!!

Rating Examples

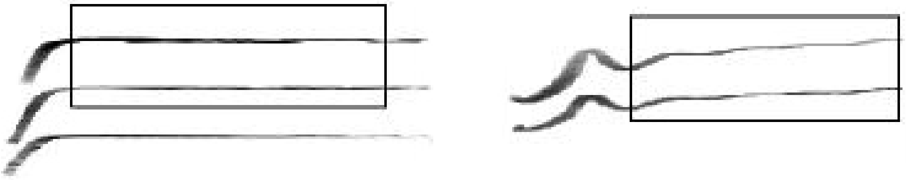


~ 5-10%
similarity

No to Very Low Similarity

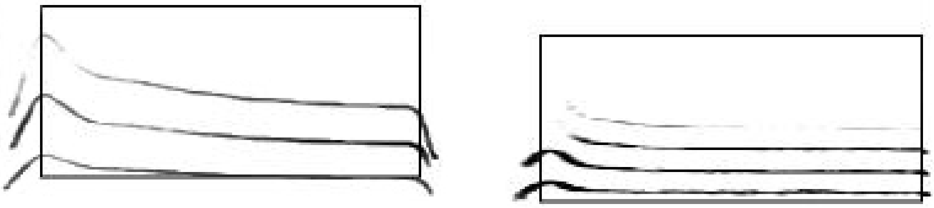
~ 35-40%
similarity

Low to Medium Similarity



~ 60-80%
similarity

High Similarity



~ 70-90%
similarity

High to Very High Similarity