# Repertoire Usage of the Southern Resident Community of Killer Whales (*Orcinus orca*)

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Monika Wieland

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# Preface

The happiness of the bee and the dolphin is to exist. For man it is to know that and to wonder at it.

*-Jacques Cousteau*

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# Abstract

The Southern Resident Community of killer whales (*Orcinus orca*) frequent the waters of Washington State and British Columbia. The three pods that make up the community (J-, K-, and L-Pods) have been well studied since the 1970s. These long-lived marine mammals live in stable social groups and they are known for their complex communication system that involves a shared set of 26 discrete calls. Each pod has its own repertoire, or group-specific subset of the calls that are socially learned. While intensive acoustic studies occurred in the 1980s, much about discrete call function and repertoire structure remains unknown. Using recordings made on the west side of San Juan Island in the summers of 2005-2006, this study considers current repertoire usage of all three pods. Call type usage, frequency of call usage, two-call sequences, and mean call durations are analyzed for each pod and compared to 1978-1983 data to assess changes that have occurred in repertoire usage. Information theory and Zipf's statistic are also used to quantitatively compare the killer whale communication system to other species. Call types have been added and dropped from every pod's repertoire, demonstrating an unprecedented rate of change for killer whale communication systems. Other calls have changed in frequency of occurrence and many calls have increased in mean duration, perhaps as a result of increased vessel noise. Many two-call associations are also found, indicating sequential structure in the repertoire. Analysis using Zipf's statistic also demonstrates a non-random repertoire structure. These observed changes all have implications for call function and overall repertoire complexity. These results demonstrate cultural evolution, complex repertoire structure, and potential impacts of anthropogenic noise. The increased understanding of the killer whale discrete call system presented here will set the stage for future studies of this endangered population of killer whales.

# Chapter 1: Introduction

## An Introduction to the Study

This study considers the acoustic communication system of the Southern Resident Community of killer whales (*Orcinus orca*) that live in the waters off of the Pacific Northwest coast. This introduction will begin by exploring communication in general, and then focus will turn specifically to animal acoustic communication and methods of quantifying and analyzing it. Next, the natural history of the killer whale will be reviewed, with special detail given to the Southern Residents and what is already known about killer whale communication. By exploring the theoretical basis for animal communication and describing the available methods of analyzing it, the main goals and significance of the current study will be brought into focus.

## Communication

In the most basic of terms, communication is defined as the provision of information by a sender to a receiver and the use of that information by the receiver in deciding how to respond (Bradbury and Vehrencamp 1998). Information can be loosely defined as knowledge about the sender and how the sender will act, so the provision of information allows receivers to more accurately estimate the behavior of a sender. Information is transferred via signal that passes through the physical environment between the sender and the receiver. In the field of animal behavior, a signal can take the form of a sound, a visual display, an electrical pulse, a touch, or a chemical scent.

### The Basics of Animal Communication

Among animals, communication occurs for a wide variety of reasons, including mate selection, predator avoidance, conflict resolution, parental behavior, foraging, identification, and coordination of group activities (Bradbury and Vehrencamp 1998; Simmons 2003). Animal communication is fascinating to study because it is "the glue that holds animal societies together" (Bradbury and Vehrencamp 1998). As animal communication systems are studied further, the types of information animals transmit will be better understood. It becomes possible to comprehend the signals animals use and how they use them, and such an understanding of signal evolution can inform us about the evolution and adaptations of the species itself. For many species, an understanding of their communication system can also play a critical role in their conservation. For example, in the case of the giant panda, knowledge of chemical signaling has increased the success of zoo-based breeding programs (Lindburg and Fitchsnyder 1994; Bradbury and Vehrencamp 1998; Swaisgood et al. 1999). In the case of cetaceans, knowledge of acoustic communication patterns of specific species or populations can increase the usefulness of remote hydrophone monitoring, which can provide information on species abundance and distribution, knowledge that, for marine mammals, can otherwise be difficult to obtain.

Animal communication is a vast field that is widely interdisciplinary. Depending on the type of communication to be studied, it is imperative to incorporate physics (through details of signal properties), physiology, neurology, chemistry, psychology, mathematics, economics, and anatomy. Animals use different modalities to communicate depending on their particular environments and adaptations. Visual signals are more useful in wide-open spaces, while acoustic signals are more beneficial in dense habitats or for nocturnal communication. Tactile communication can only occur over a very short distance. Acoustic communication can occur across a wide distance, while chemical communication in the form of scent marking can occur across time (Krebs and Davies 1993).

This study focuses on acoustic signals. Auditory signals are especially useful for covering long ranges at very high speed, traversing obstacles, and resulting in the emitter of the signal being highly locatable. One of the detriments of an acoustic signal is that it is usually energetically costly to produce. Another detriment is if the signaler is localized by a receiver they didn’t intend to signal to, such as a predator if the signaler is the prey (Krebs and Davies 1993). Acoustic communication is the most-studied type of communication. The reason for this is that sounds are easy for humans to detect, record, and quantify. Also, at least relative to other modalities, acoustic communicative function is easy to assess; when an animal makes a loud noise, it is likely serving a communicative function, whereas whether or not a visual display is communicatory is less distinct (Bradbury and Vehrencamp 1998).

## Acoustic Communication

It is necessary to establish some basic vocabulary for further consideration of acoustic communication. In the case of acoustic communication, signals often occur in the form of vocalizations. Each vocalization is referred to as a call, and stereotypical categories of calls can be defined into call types. A repertoire is defined as the entire range of distinct calls made by an individual or a population. While the variation in the number of call types within a repertoire gives some idea of potential information transfer and complexity, this is only the first step to understanding a communicative system. In what contexts calls are used, the frequency of signals, and the order of sequences of signals are also important elements to consider (Bradbury and Vehrencamp 1998).

In addition to how call types are used, it is now widely recognized that the variation within call types is also of great importance, and may even be where the majority of the information is contained (Hailman and Ficken 1996; Bradbury and Vehrencamp 1998; Tyack and Miller 2002). That is to say that while an animal producing call type A is providing some level of information to a receiver, the true content of the message may be contained in the particular version of call type A given. For acoustic signals, the main parameters that contain within-call type variation are frequency, amplitude, and duration.

While descriptive studies have demonstrated that mammals have fairly large repertoires, the evolutionary basis for this, especially with regards to social living, remains elusive. The function of shared repertoires is unknown, which makes this aspect of animal communication especially intriguing. (Boughman and Moss 2003; Janik and Slater 2003; McComb and Semple 2005).

Dialects are shared group-specific vocalizations or variations on a vocalization. Dialects are common in birds, but are relatively rare in mammals (Ford and Fisher 1983; Catchpole and Slater 1995). When two groups have different dialects, it is often correlated to a difference in geographic location; some define true dialects as differences in vocal behavior between potentially interbreeding groups, which excludes geographic dialects (Conner 1982; Rendell and Whitehead 2001). In these cases, it is likely that variations arise from isolation and genetic drift or local adaptation to acoustic environments. In a few cases of some birds and mammals, it has been proposed that cultural drift or directed cultural evolution via vocal learning is responsible for dialectical difference (Noad et al. 2000; Rendell and Whitehead 2005). The understanding is that errors and innovations appear in the call types, and as repertoires are learned, different populations vocally diverge. Most evidence for vocal learning as a source of vocal divergence comes from studies of cetaceans, including bottlenose dolphins, humpback whales, and killer whales (Ford 1991; Miller and Bain 2000; Janik and Slater 2003).

When rapid change in dialects occurs, for instance at a rate faster than a generation, cultural evolution must be involved (Rendell and Whitehead 2005). The most striking example of this is humpback whale songs. Male humpback whales are known to sing elaborate songs that gradually shift and evolve between breeding seasons so that all the whales in the same area will change their song in the same ways from year to year. In an especially remarkable case in Australia, the entire song of the east coast population changed to match the song of the west coast population after the immigration of just a couple of “foreign” singers from that western population (Noad et al. 2000).

## Methods of Studying Acoustic Animal Communication

This study is interested in the structure and function of the repertoire of a community of killer whales. Questions include: How much information is being transmitted? What are animals communicating about? Are the calls within the repertoire interdependent? Is there any sort of sequential structure within the repertoire?

To study the information being transmitted via a signal or within an entire repertoire, a method to measure the amount of information being transferred is needed. Above, information was defined as knowledge about the sender and how the sender will act; this can be rephrased to say that information provides a receiver with probabilistic knowledge on how the sender will act. The change in probability estimates (or reduction of uncertainty) associated with information being transferred can be used as a measure of informational exchange by using a method called information theory (Bradbury and Vehrencamp 1998).

Information theory has only recently been applied to studying animal behavior. There are many other, more traditional, methods that are used to answer some of the basic questions surrounding acoustic communication. These include studying call sequences to assess repertoire structure, determining important aspects of information transfer by looking at variation within and between call types, and estimating call function by looking at contexts in which calls are used.

### Information Theory

Information theory was developed as part of Shannon and Weaver’s mathematical theory of communication (Shannon and Weaver 1949). In this case, information is defined in a statistical sense as the reduction of uncertainty provided by a signal, where uncertainty is a measure of the predictability of a communicative system.

To get a better idea of what it means to have a reduction of uncertainty, consider an example given by Bradbury and Vehrencamp (1998) about the amount of information that can be provided by one signal. Imagine a female bird that needs to choose a mate. Suppose she has to divide courting males into one of two conditions: healthy or sick. Before a female has any information about a male, there is an equal chance of him falling into either condition. In other words, there is a 50% chance he will be healthy and a 50% chance he will be sick. This scenario can be generalized by stating that when there are N alternative conditions and all conditions are equiprobable, the probability of any particular event occurring is 1/N. Before making a decision whether or not to mate with a male, she can use information provided by the male to improve her probability estimates of whether he is healthy or sick.

To determine whether or not the male is healthy, the female needs to know the answer to a yes or no question: is the male sick? This is called a binary question, and the answer to it will eliminate the uncertainty in her probability estimates. Of course, in reality, very few cases can be resolved by a single binary question, but any problem that has a finite set of answers can be figured out by some set number of binary questions (Bradbury and Vehrencamp 1998). Hailman (1977) demonstrates how this could be the case by considering a slightly more complex situation that has four possible answers: A, B, C, and D, as summarized in the schematic below:

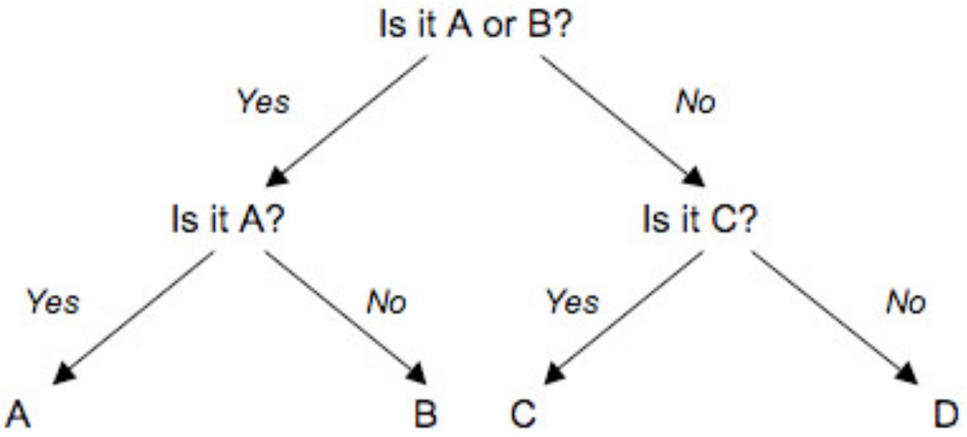


**Figure 1: Schematic demonstrating the basic principle of information theory**

The minimum number of binary questions, H, needed to resolve a situation with N conditions can be summarized by the following equation: $N = 2^H$. This can be rewritten as follows:

$$H = \log_2 N$$

This equation represents zero-order entropy, where the only measurement of concern is the repertoire's diversity or number of signals. Entropy is defined here as an informational degree of organization (McCowan et al. 1999). First-order entropy measures simple internal organization of a repertoire and is represented by a manipulation of the above equation that takes into consideration the probability of occurrence of each event. The equation for second-order entropy, which considers two-signal interactions within a repertoire, also takes into account conditional probabilities.

The equations become correspondingly more complex for higher-order entropic equations that consider longer signal sequence interactions (three-signal sequences, etc.) (McCowan et al. 1999). Information theory applies these entropic equations to communication systems to assess potential amounts of information transfer.

So far a perfect communication system has been assumed: a system where there is one signal for every condition, the sender always sends the proper signal, the receiver never makes an error in interpreting which signal was sent, different signals occur with equal probabilities, and there are no signal interdependencies. In perfect communication systems, all uncertainty is lost when communication occurs. In reality, this is rarely ever the case. Signals and conditions don't necessarily correspond in a 1:1 ratio for a variety of reasons. For example, senders and receivers may have different coding schemes, or interpretations of how the signals map onto the conditions. Senders may try and deceive receivers, such as a sick male singing the signal that, in general, means "healthy". A receiver may misinterpret a signal and thus come to the wrong conclusion about what the sender is trying to say. If different scenarios are not equiprobable and not independent of one another, less information is also being provided than by an optimal communication system (Hailman 1977). Thus, in imperfect communication systems, uncertainty is never removed entirely.

Just because a communication system is not perfect does not mean it is not useful. In the English language, for example, the signals (in this case, the letters) are highly interdependent and occur with differing probabilities. In English, for example, certain letters are far more frequent than others, and certain letter combinations are not allowed because they are meaningless, such as "x" following "z", or are mandatory, such as "u" following "q" (Bradbury and Vehrencamp 1998). Imperfect communication does not always have negative consequences, because it can help a receiver understand the message even if there was interference with the signal. If an English speaker saw the signal: "qXite", their probability of placing the correct letter where X denotes a missing letter is far better than the 1/26 chance that would occur if every letter occurred in equal probabilities. Instead, using our previous knowledge of the English language, it can be said with nearly 100% certainty that the signal was supposed to be "quite" (Hailman 1977; Bradbury and Vehrencamp 1998). Any type of structure within a communication system increases its efficiency at transferring information.

Information theory is an intriguing model for studying communication because it involves quantitative tools. It has been applied more to engineering and computer science, but in recent years its use in the field of animal behavior has been growing (Owings and Morton 1998). Information theory has been used to assess interactions between individuals, such as the advertisement calls of male bullfrogs (Suggs and Simmons 2005), the songs of birds (Hailman and Ficken 1986; da Silva et al. 2000) and songs of humpback whales (Suzuki et al. 2006), and a wide variety of other taxa from grasshoppers to shrimp to macaques (McCowan et al. 1999). While it has been useful for looking at interactions on the level of the individual, information theory was originally designed as a tool for considering the structure of entire communication systems. McCowan et al.'s animal communication studies on bottlenose were the first to apply information theory at the repertoire level (McCowan et al. 1999, 2002). Information theory gives us a tool to quantitatively compare signal use between different populations and species, which will lead to a greater understanding of the evolution of animal communication systems (McCowan et al. 2002).

In order to use information theory to extrapolate from sequential signaling between individuals to the structural organization of an entire repertoire, a large sample size is needed. It is precisely due to this limitation that so many studies have focused on the individual level and more restricted behavioral interactions (McCowan et al. 1999). Entropic equations can be used to evaluate different orders of complexity in a communication system's organization. For instance, when applied to human language, structure can be considered at the level of the letter, the word, or the sentence. Complexity can be analyzed at different levels ranging from repertoire diversity to simple internal repertoire organization to two-signal sequences (and beyond) and this corresponds to zero-order, first-order, and second-order entropy respectively.

McCowan et al (1999) reported that an ideal sample size for a first-order analysis of a communicative system is ten times the number of signal types, although four or five times the number of signal types may be sufficient. Even this estimate may be modest, as other sources suggest that a system with R signal types should have $10R^2$ signals included in the analysis to achieve statistical significance (Fagen and Young 1978). The English language, which contains an estimated 600,000 words according to the Oxford English Dictionary, would therefore need a sample size of between 2.4 million and 3.6 x 10^13 words to conduct a first-order analysis. It is even more difficult to apply higher order entropies because as more and more sequential possibilities become possible, a larger data set is needed to achieve significance (McCowan et al. 1999). Of course, animal communication systems have much smaller repertoires so the required sample size, while large, is theoretically attainable.

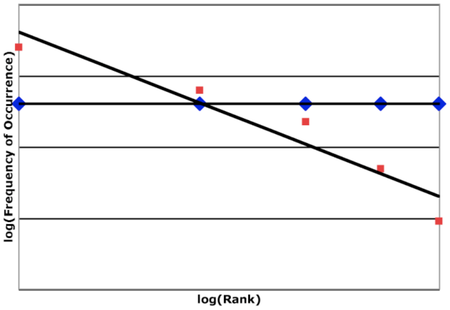
It is still difficult to fit something as variable and undefined as an animal communication system into this rigid mathematical model. It is important to note that information theory does not quantify how much information is *actually* being communicated by a system, but rather how much information is being *potentially* communicated. It is a useful tool to help examine the structure and capacity of communication systems, which will in turn give clues to the function of the system and the content that is being transmitted (McCowan et al. 1999, 2002).

## Zipf's Statistic

Zipf's law was originally formed to model language and is a mathematically simpler way of assessing the same level of repertoire complexity as a first-order entropic equation: the signal composition of a repertoire (Zipf 1949; McCowan et al. 1999). Zipf's law considers the frequency of use of all the signals in a repertoire relative to their rank, where rank is determined by ordering the signals from most frequent to least frequent. In human language, it has been applied at the level of the word. Zipf's law states that in languages, the frequency of a word is inversely proportional to its rank in a frequency table. The most frequently used word is given a rank of "one", the second most frequent word is given a rank of "two", and so on. The most common way to quantify Zipf's law is via Zipf's statistic, which is the slope of the regression line that results when you plot the data with the x-axis as the log(signal rank) and the y-axis as the log(actual frequency percentage) for every signal. For a wide variety of human languages, Zipf's statistic has been shown to be -1.00, giving a reference point when defining the statistic for other species (McCowan et al. 1999). If a language or other signal system has a Zipf's statistic of -1.00, it is said to be in accordance with Zipf's law. A schematic demonstrating Zipf's statistic for two hypothetical repertoires is shown below:

Repertoire 1

| Signal Rank | Frequency |
|---|---|
| 1 | 20 |
| 2 | 20 |
| 3 | 20 |
| 4 | 20 |
| 5 | 20 |



Repertoire 2

| Signal Rank | Frequency |
|---|---|
| 1 | 50 |
| 2 | 25 |
| 3 | 15 |
| 4 | 7 |
| 5 | 3 |

**Figure 2: Zipf's statistic demonstrated for two hypothetical repertoires**

A diagram plotting hypothetical data from two repertoires to obtain Zipf's statistic. Repertoire 1 contains equiprobable signals, resulting in random repertoire structure represented by a slope of 0.00. Repertoire 2 contains internal structure and conforms to Zipf's law by having a slope of -1.00.

Zipf's statistic considers the optimal amount of information transfer occurring and relative amounts of diversity and repetition. If a repertoire is too diverse, a message is over-represented by multiple signals and less communicative complexity is conveyed, where communicative complexity is defined as information transferred. Extreme diversity would be represented by a randomly distributed repertoire. Diversity is represented by a less negative Zipf's statistic. If a repertoire is highly repetitious, a message is under-respresented by only a few signals and less communicative complexity is also conveyed. Extreme repetition would be one signal for all messages. This is represented by a more negative Zipf's statistic. Zipf's law states that these two opposing forces will create a balance where the optimal amount of communication could occur, resulting in a slope of -1.00 (McCowan et al. 1999).

While Zipf's statistic is not a linguistic tool, it does indicate the relative balance of diversity and repetition within a communication system and therefore whether or not the repertoire structure is non-random (McCowan et al. 1999). If a balance is found via a slope of -1.00, this indicates that information is potentially stored in higher orders (such as signal sequences), giving a reason to examine the repertoire in terms of higher-order entropies (McCowan et al. 2002). Beginning to understand repertoire structure using tools such as Zipf's statistic can give us clues to how a communication system works and is especially useful for beginning to assess repertoires with an unknown function (McCowan et al. 1999). Zipf's statistic is one tool for comparing repertoire structure across populations and species.

## Cross-Species Comparisons

One reason information theory is an intriguing tool for studying communication is that it can help to quantitatively compare and contrast very different communication systems by using a common measure of information. Cross-species comparisons are useful to help understand the evolution and function of signal communication systems, and the complexity of a vocal communication system can be assessed by comparing it to other communication systems including human language. By using methods such as Zipf's statistic and information theory to quantitatively characterize a repertoire, it is possible to develop an unbiased measure to evaluate the comparative complexity between communication systems across divergent taxa.

Even with information theory as a tool for comparing repertoires across species, such studies have been limited by lack of extensive data sets. In 1999, McCowan et al. published a paper using information theory to analyze the structure of bottlenose dolphin whistle repertoires, and reported that despite conducting an extensive literature review, was unable to find any other species that had a large enough quantitative data set to include in their initial analysis (McCowan et al. 1999).

In 2002, however, McCowan et al. published a paper in which such a cross-species comparison was conducted using bottlenose dolphin whistles, human English words, and squirrel monkey chuck calls. The vocalizations in all species are similar in that they are important in maintaining social relationships within that species' social structure. This paper was the first study to quantitatively examine the amount of information transferred in repertoires of different species, and it did so by making use of information theory. First, the frequency of occurrence for each call type among each species was tallied and the call types were organized by rank so that Zipf's statistic could be generated. Additionally, sequences of vocalizations were used to calculate zero-through third-order entropic values.

The results were stunning. Zipf's coefficients for all three species hovered around -1.00, indicating that the repertoire structure of bottlenose dolphin whistles and squirrel monkey chucks are comparable to that found in human language. Entropic numbers were also given, but results were likely influenced by a limited sample size for dolphin and squirrel monkey vocalizations (McCowan et al. 2002). Still, this study showed for the first time that, given a robust data set, interspecific vocal complexity can be quantitatively compared.

## Sequential Analysis

In addition to information theory, there are other statistical methods for considering the structure of a communication system. One such way of considering repertoire structure is by looking for sequences in the order calls are used. Given the particular demands of sequential structure, however, one must be careful in choosing which statistical test to apply. Usually, when conducting statistical analyses on a data set, one of the underlying assumptions is that the data are independent, but when conducting sequential analysis, an interdependency of the data is expected.

A common method of studying sequences is through Markov chain analysis which tests the degree to which an event can predict which events will follow. For instance, in the occurrence of event A, how likely is event B to follow it? If events are found to have no influence on what will follow, the sequences are entirely random and the data are said to fit the Markov property. If events are absolute predictors of what will follow, the data are said to be an example of a Markov process (Suggs and Simmons 2005). Sequences of animal behavior are described as semi-Markovian because they fall somewhere between a Markov property and a Markov process (Fagen and Young 1978).

In other words, a behavioral event may be a good, but not absolute, predictor of what will follow.

Markov chain analyses involve transition matrices of behavioral events. For vocal communication, matrices showing the frequencies of call transitions can be generated and carefully chosen statistical tests can be applied to compare observed frequencies with those that would be expected by random.

### Determining Call Function

A central question when studying animal communication is, of course, what are the animals communicating? To begin to answer this question, it is necessary to determine what function a vocalization is playing in the interactions of that species.

When trying to determine the function of a vocalization, there are two interpretations as to where a message can be encoded: in the type of signal used (ie, the call type) or in the variation within a signal type (Catchpole and Slater 1995). It is important to consider the significance of both types of variation, and in order to do so, it is important to study not only repertoire use but also variation within a repertoire (Baker and Cunningham 1985). With acoustic vocalizations, variation can occur in duration, amplitude, and/or frequency. It is unlikely that all variation is directly related to communicative function, so it is important to try and determine what type of variation is carrying important information for the signal receiver (Catchpole and Slater 1995). In marine mammals, there is a general trend for acoustic variation in temporal rather than frequency variables (Tyack and Miller 2002).

Information theory's measure of repetition and diversity of a repertoire can also provide clues to call function. Social and intragroup calls are usually diverse, whereas alarm calls and intergroup calls are more stereotyped and redundant (McCowan et al. 2002). McCowan et al. (2002) give an example of humans communicating in their native language to other native speakers versus communicating in a second language. When speaking in their first language with others familiar with that language, communication is often complex and diverse. When speaking a second language or speaking their native language to an unfamiliar speaker, speech is more stereotypical and redundant to facilitate communication.

## The Basics of Cetacean Communication

The utility of using information theory to compare communication systems across species was discussed, and indeed the comparative method can be very useful when considering the mechanisms and functions of behavior. It can be enlightening to compare the behavior patterns of cetaceans with everything from primates to elephants to songbirds (Mann 2000), but when comparing marine and terrestrial animals, important factors must be kept in mind. When comparing communication systems, the vastly different mediums in which the messages are traveling must be recognized, as well as the distinct mechanisms of, in this case, sound production. In air, sound can travel perhaps a kilometer, while underwater, cetaceans produce sounds that are audible up to tens or even hundreds of kilometers away. The speed of travel is also vastly different, with sound traveling in air at approximately 340 m/s, and traveling through water 1500 m/s. (Tyack and Miller 2002).

The term “vocalization” may even be misleading when it comes to cetaceans. Specifically, a vocalization refers to a sound produced in the larynx. Sound production in cetaceans is not well understood, but it is known that sounds are generated by air flow causing vibrations in sacs of the nasal passages (Bradbury and Vehrencamp 1998; Tyack and Miller 2002). In cetaceans, vocalizations are directed into the water through the melon, a fatty organ in the forehead of dolphins that has a density similar to water. Sound reception occurs not through an external ear and the auditory canal as in terrestrial mammals but through the oil-filled tissue of the lower jaw, which transmits sound waves directly to the inner ear (Stenersen and Simila 2004).

Another difference between terrestrial and marine mammals is the source of acoustic variation. For the vast majority of non-human terrestrial mammals, vocalizations vary primarily due to genetic variation, whereas for marine mammals vocal learning and cultural variation are more widespread (Miller and Bain 2000; Tyack and Miller 2002). One main theory about why this may be is evolutionary pressure for individually distinct vocalizations. In terrestrial mammals, natural variation in the vocal tract (the air passages above the larynx, including the mouth and throat) leads to individuals having recognizable voices. In marine mammals, and cetaceans in particular where all vocalizations are made underwater, this method of differentiating between signalers doesn’t work. As animals dive, the pressure change results in physical alterations of sound production apparatus that modify the frequency of the vocalizations. This likely masks any more subtle natural variation due to differences in the vocal tract. As a result, if it is important to have individually distinct vocalizations, vocal learning presents a solution (Tyack 2000; Tyack and Miller 2002).

# Killer Whales

## Life History and Diversity

Killer whales (*Orcinus orca*), also known as orcas, are technically the largest members of the dolphin family (*Delphinidae*) (Baird 2002). They are one of the most widespread mammals on the planet, perhaps second to only humans, as they are found in all of the world's oceans, usually in highly social groups (Baird 2000, 2002; Stenersen and Simila 2004). Orcas are long-lived creatures, with some females in the Pacific Northwest estimated to be in their mid-nineties (van Ginneken et al. 2005). Their life history is, in many respects, remarkably similar to humans. Calves are born after a 16-17 month gestation period, and are about six feet long and several hundred pounds at birth (Ford et al. 1999; Baird 2002). They nurse for one to two years, but are still considered juveniles until the age of ten or twelve (Baird 2000). At this point, they begin to become sexually active, and throughout the course of their teenage years the two genders become sexually dimorphic (Baird 2002). Females grow to a maximum size of about 25 feet and weigh three or four tons. Their dorsal fins grow to about three feet tall. Males grow to up to 30 feet long, weigh over six tons, have larger pectoral fins and tail flukes, as well as a dorsal fin that reaches up to six feet in height (Baird 2002). Both males and females are reproductively active into their 50s, which is about the maximum lifespan for a male (van Ginneken et al. 2005). Females, however, go through menopause, and, at least in the Pacific Northwest, are known to live on for several decades as a post-reproductive adult (Baird 2002). Such an extended post-reproductive period is a rarity in the animal kingdom, found only among humans and orcas (Baird 2002).

Individual orcas are identifiable to researchers by distinct markings, particularly the grayish saddle patch that sits behind the dorsal fin and is visible when the whale surfaces (Ford et al. 1999; Baird 2002; van Ginneken et al. 2005). The saddle patch is unique on every single whale, as well as on the left and right side of every whale. The size and shape of the dorsal fin, as well as any nicks or notches in the fin, also aid in identification (Ford et al. 1999).

In at least some killer whale societies, whales are organized into a hierarchical social structure of stable interactions (Miller and Bain 2000). The smallest unit is the matriline, made up of a female, all of her offspring, her daughter's offspring, and any surviving members of the mother's natal matrilineal group. A matriline can include up to five living generations at a time (van Ginneken et al. 2005). Matrilineal groups rarely separate from each other for more than a couple of hours (Baird 2000). Often, several related matrilines associate together into a pod, which is defined as a group of whales that spend more than 50% of their time together (Baird 2000, 2002). A pod, therefore, is essentially a large family group (Ford et al. 1999). Associations of pods that interact socially and share at least some aspects of their vocal communication system are known as communities or populations.

The killer whale is the top predator in the sea. They have adapted to their local habitats all across the globe, becoming foraging specialists for a wide range of prey, which is just another indicator of their intelligence. In Norway, killer whales cooperatively feed on schools of herring (Stenersen and Simila 2004). Off the coasts of Argentina, orcas have learned to intentionally beach themselves to snag sea lions off of the beaches (Baird 2000, 2002). In the Pacific Northwest, there are three sympatric ecotypes of killer whale: offshores, transients, and residents (Ford et al. 1999). Each variety is defined by diet, behavior, travel patterns, social structure, and vocalization system (Ford 1987). None of these ecotypes have been seen to intermix except on very rare occasions. Studies have shown that the transient and residents are as genetically distinct from one another as they are from other geographically isolated populations (Hoelzel and Dover 1991).

Little is known about the offshore killer whales, which, just as their name suggests, spend the vast majority of their time way out at sea. They are usually seen 15-25 miles offshore, and encounters are rare (Center for Whale Research 2006). They live in large groups of 30 or more, and only very rarely pass near the coasts (Ford et al. 1999).

The other two types of killer whales are, on the other hand, primarily coastal. The transient killer whales live in small groups, usually of no more than 2-6 individuals (Ford and Ellis 1999). This is because they hunt almost exclusively marine mammals such as seals, sea lions, porpoises, and other whales, and optimal foraging strategy keeps their group size small (Baird 2002). They roam widely with unpredictable movements, ranging all the way from southeast Alaska down into Mexico. More than 400 transients have been individually identified along the Pacific Coast, and the entire population shares at least some vocalizations. Repertoires of each transient seem to be quite small at only 4-6 vocalizations (Ford and Ellis 1999). The call repertoire of the entire transient community is only eight vocalizations (Ford 1987).

The third and final group of killer whales is the resident, which is the focus of this study. Resident killer whales are known to be exclusively fish eaters, feeding primarily on salmon. There are two communities of resident killer whales: the Northern Residents off of the northeast side of Vancouver Island in British Columbia, and the Southern Residents which primarily reside off the southern tip of Vancouver Island and the inland waters of Washington State, as well as the coastal waters off of Washington, Oregon, and

California. The two communities of residents do share an overlapping range, but they are not known to interact socially or interbreed (Ford et al. 1999; Baird 2000). The Northern Resident community is made up of 16 pods totaling about 220 whales in the 2006 census, while the Southern Resident Community is made up of 3 pods totaling 86 whales as of November 2006. This study considers the Southern Residents: J-Pod, K-Pod, and L-Pod. As of November 2006, J-Pod had 24 whales, K-Pod had 20 whales, and L-Pod had 42 whales (Center for Whale Research 2006).

Resident killer whales are unique among mammals in that there is no dispersal from the natal pod for either gender: both male and female offspring stay in their maternal pod for their entire lives (Baird 2000). Even in other social mammals such as elephants (Fernando and Lande 2000) and sperm whales (Rendell and Whitehead 2005), which have highly stable matrilineal social groups, there is dispersion of males from natal groups or occasional shifting of group members from one group to another. Multipod associations within a community are common, however, and one major reason they occur is mating (Baird 2002). Males from one pod will mate with females from another pod, but when the pods split up again he will return to his maternal group. This unusual lack of dispersal is a main reason killer whales have extremely stable social groups.

Additionally, aggression between killer whales is extremely uncommon. Aggression within ecotypes is undocumented, and aggression between ecotypes is limited to a few rare interactions of transients and residents (Baird 2000).

While resident killer whales have been heavily studied over recent decades, remarkably little is actually known about them due to their elusive underwater lifestyle. Still, their intelligence, complex social behavior, and mysterious communication system has led them to be a highly charismatic species that we are continually striving to understand better.

## <u>Orca Communication – What is Known</u>

### Types of Vocalizations

A primary aspect of orcas that makes them unique is their complex communication system. Killer whales can make three types of vocalizations: clicks, whistles, and discrete calls (see Figure 3 for a spectrographic comparison of these three different types of vocalizations). Clicks are short, broadband pulses of sound that are used primarily for echolocation, which aids the whales in navigating and foraging, especially in waters with low visibility. Whistles are pure sounds with little harmonic structure that usually contain some level of frequency modulation and appear on spectrograms as single, narrowband tones (Ford 1989). While whistles are the primary social vocalization of many dolphins, they are relatively rare and highly variable in killer whales and hence are little studied (Ford 1987). Discrete calls are the main social vocalizations among killer whales. Evidence for this is that the emission of a discrete call elicits response from conspecifics and calling rates are also highest when the whales are socializing (Baird 2000). As of yet, the function and many aspects of discrete call usage are poorly understood.

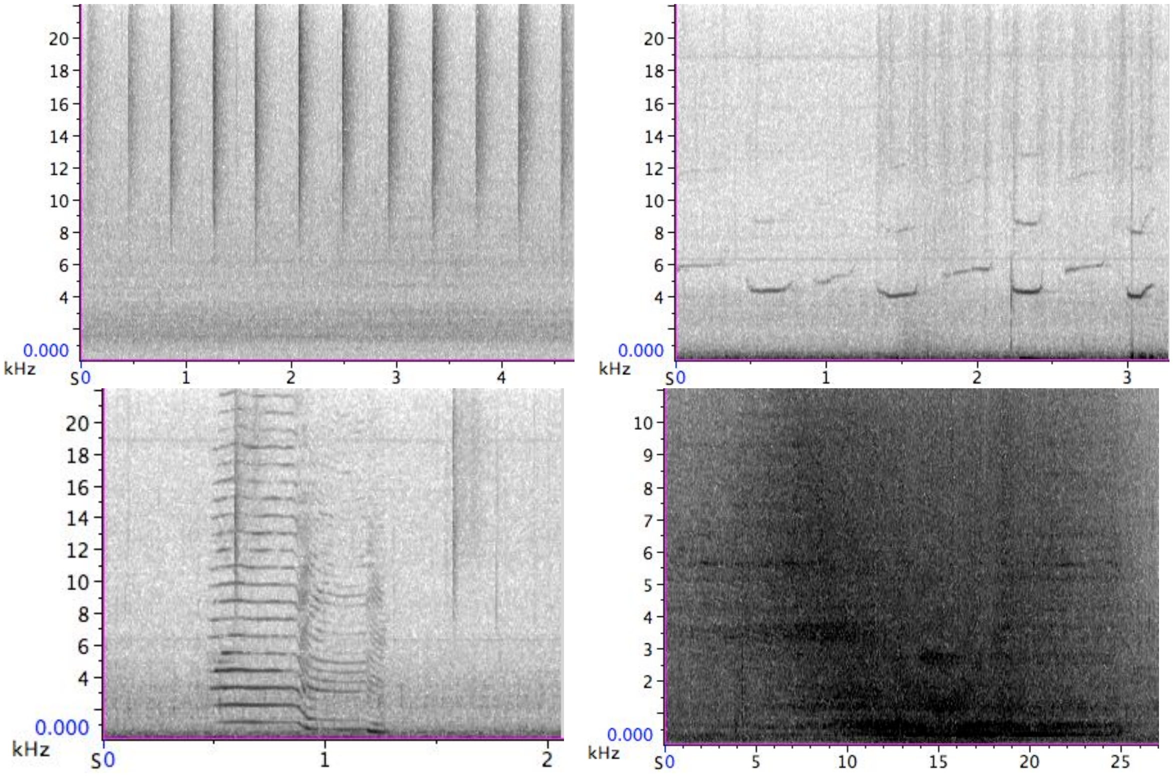


**Figure 3: Spectrograms of clicks, a whistle, a discrete call, and boat engine noise**

Short, broadband clicks (upper left) are repeated and used in echolocation. Pure tonal whistles (upper right) have little harmonic structure. They are highly variable and rare among killer whales. Discrete calls (bottom left) are the main social vocalization of killer whales. Each call type has a distinct harmonic structure visible as a unique spectrographic pattern. Boat engine noise (bottom right) causes loud, broadband interference of any ambient noise. The Y-axis on every graph indicates frequency in kHz. The X-axis indicates time in seconds. The darkness of the color on the graph indicates the amplitude (or strength) of that particular frequency.

Discrete calls are stereotyped tonal pulsed calls that have been categorized into conventional categories (Ford 1987). Pulses are bursts of sound generated at high repetition rates that appear as oscillations on a waveform. High pulse rates create the tonal sounds that are discrete calls. When the whale alters the rate of pulses within a call, the result is a modulation in the tone (or frequency), giving each call type a distinct sound discernable by ear (Ford 1987). The calls are mostly 0.5-1.5 seconds in duration, and while some components extend above 20 kHz, the primary energy (or the peak amplitudes) of the call is usually between 1-10 kHz and therefore well within the range of human hearing (Ford 1987). Discrete calls also have complex harmonic structure, in some cases including an independent high-frequency whistle-like component. Due to their unique tonal structure, discrete calls are often easily differentiated by the human ear and also provide a unique spectrographic structure.

## Discrete Call Usage

Long-term studies of acoustic communication in the marine environment are rare, as study subjects can be elusive and data collection difficult and time consuming (Janik 2005). Discrete call usage in resident orcas is one of very few cases where such extensive studies have occurred, thanks in part to John K.B. Ford, a scientist who has studied killer whale communication for the last several decades. In 1987, Ford published a catalogue of calls produced by Northern and Southern Resident killer whales as well as by transients. Each call type was given an alphanumeric designation depending on which community of whales it belonged to: “T” indicates a transient call, “N” a call from the Northern Residents, and “S” a call from the Southern Residents. Calls were numbered in the order that they were identified; it is important to note that numbers have no indication of rank within the repertoire and are completely arbitrary (Ford and Fisher 1983). Using recordings made between 1978 and 1983, Ford presented detailed information on each call type including usage by different pods and a representative spectrogram of every call. In this catalogue, he identified 26 discrete calls and several call sub-types used by the Southern Resident orcas (Ford 1987). It soon became apparent that pods had group-specific dialects, and Ford determined that each pod had a distinct repertoire of 7-17 call types (Ford 1989). In killer whale pods, dialects are defined as all pod-specific calling behavior, which includes calls not used by other pods, different production rates of call types shared with other pods, and differences in the structure of shared call types (Miller and Bain 2000).

While dialects are fairly common among animals with stable social groups or intensive sexual selection, the dialects of killer whales are unusual in several ways. First of all, killer whale dialects are not associated with geographic location. Many of the reported cases of dialects in mammals have been attributed to geographic isolation, where populations are separated and vocalizations drift apart as a result (Conner 1982). In the case of birds, where dialects are a widespread phenomenon, dialectical differences are nearly always associated with geographic isolation or territorial defense (Mundinger 1982; Baker and Cunningham 1985; Catchpole and Slater 1995). Neither of these associations are found in the non-territorial, non-aggressive killer whale, which roams freely and often comes into contact with populations using other dialects (Ford 1991).

Secondly, orca dialects are learned and not genetic. Song learning is common in birds, occurring in about half of all species including songbirds, parrots, and hummingbirds. Among mammals, vocal learning is much less common and is found only in cetaceans, pinnipeds, bats, and humans (Janik and Slater 2003). Evidence for vocal learning in killer whales comes from the fact that there are calls unique to each pod, but the pods in the Southern Resident Community interbreed with one another. Therefore, unless there is a bizarre maternal inheritance system of vocalizations involving mitochondrial DNA, the calls must be learned socially (Miller and Bain 2000; Rendell and Whitehead 2001). Additional evidence supporting this fact is that vocal learning and acquisition of unique vocalizations had been demonstrated in both captive and wild killer whales (Ford 1991; Foote et al. 2006). It has been claimed that learned dialects with no geographic association are unique to cetaceans and humans (Rendell and Whitehead 2001).

Finally, killer whale dialects are intriguing because call types are not easily linked to behavioral context, leading to an unknown function for many of the calls. While some calls have been loosely linked to broad behavioral categories such as foraging and socializing; most of a pod's repertoire is heard regardless of the activity the pod is engaged in and no one-to-one matching of call type to behavior has been possible. (Morton et al. 1986; Ford 1989). Additionally, captive animals have produced the entire repertoire of their native pods despite being in a stable social and physical environment (Ford 1989).

While each community of whales among the Southern Residents, Northern Residents, and transients share at least some call types with the other pods in their community, no calls are shared between communities (Ford 1987). Each individual learns the dialect of their specific pod during their first few years of life, and Ford determined that the similarity of dialects between pods is an indicator of historic relationships. The degree of acoustic similarity between pods has been shown to be an accurate reflection of genealogical relatedness (Ford et al. 1999). As historic pods split into the subgroups the whales are in today, the ancestral shared dialect shifted apart over time, allowing vocal divergence to be a measure of relatedness among pods. Even for calls that are shared between pods, each pod often as a unique “accent” to the call (Ford and Fisher 1983).

Most acoustic studies have focused on the Southern and Northern Resident Communities of killer whales. Since they spend a large portion of their time in inland waters they are easily accessible to researchers and are also subject to shore-based recordings. Residents are also more vocal than transients. This is in part due to their large social groupings, but is also understood to be dependent on prey type. Transients’ marine mammal prey are susceptible to pick up on predator presence via vocal cues, while resident’s fish prey are insensitive to killer whale vocalizations (Ford and Ellis 1999). It has also been found that echolocation patterns vary between residents and transients, with residents echolocating more frequently and in longer bouts than transients. The fact the transients often produce only single or paired clicks rather than longer click trains has been attributed to remaining cryptic during hunting and not alerting mammal prey to their presence (Barrett-Lennard et al. 1996).

Listing the call types of J-, K-, and L-Pods was just the beginning. Several papers have been published that consider many aspects of orca vocal behavior including the behavioral contexts of call usage, the occurrence of two-call sequences, rates of calling, and frequency of call usage. In a 1989 paper, Ford determined that killer whales produce the most calls and highest variety of call types while socializing. When foraging or traveling, they are vocal but use a smaller number of call types, and while resting the Southern Residents are completely silent (Ford 1989). While generalizations can be drawn about behavioral state and level of vocal activity, Ford concluded that it wasn’t possible to correlate any specific call with any particular behavioral context. Most of a pod’s repertoire was heard regardless of what behavioral activity the group was engaged in. While certainly a couple of the calls served to maintain group contact, especially when whales are spread out and foraging in waters with low visibility, that could be achieved with a repertoire of only one or two calls. The function of such a large repertoire of vocalizations remained, and indeed still remains, uncertain.

Several other observations have been made about the general call usage of resident orcas. Although it is difficult to record vocalizations of a whale isolated from the rest of its pod, when a whale is near the hydrophones and far enough from any conspecifics it can be assumed it is the whale that is vocalizing. From a series of such recordings, Ford was able to conclude that each whale’s repertoire is the same as that of their entire pod. Further evidence came from captive whales that still made the entire repertoire of their natal pod (Ford 1989). Miller and Bain studied recordings made of matrilines isolated from the rest of their pod. While they found that each matriline among a pod of Northern Residents made all the calls of their pod, they found that different call types were more common among different matrilines (Miller and Bain 2000). This study provided the first evidence that vocal convergence may occur at the matriline-level instead of at the level of the pod. It was later confirmed that all the members in a matriline produce all the calls characteristic of that matriline (Miller et al. 2004).

It has also been hypothesized that discrete calls that vary in frequency or duration indicate an individual's emotional state or level of arousal (Ford 1989). While the majority of pulsed calls fall into Ford's designated discrete categories, the whales also make aberrant calls that are unique variants on the discrete call types or variable calls that were not categorizable. These calls often occur when the whales are in an excited state, such as when pods reunite. Such calls are rare, however, and have not been studied in detail.

In his 1989 study, Ford also considered two-call sequences by creating a contingency table of 9698 call transitions among Northern Residents. The main trend found was that a given call type was most likely to follow itself. Indeed, certain discrete calls were especially likely to occur in repetitive sequences. A significant association was also between calls N7 and N8 (Ford 1989).

In a 1991 paper by Ford, repertoire use over a period of 25 years was considered. By looking at recordings of Northern Residents made between 1958 and 1986, Ford concluded there was little difference in pod repertoires, although he noted some differences in frequency of call usage. For example, S14 made up 10% of the calls heard by J-Pod in recordings made in the 1960s, but was heard only twice among 6000 vocalizations analyzed between 1979 and 1983. Ford thought changes in frequency of call usage are likely part of the vocal divergence process between pods, and perhaps he was witnessing the extinction of the S14 call type from J-Pod's repertoire. Still, he recognized it was difficult to assign a time scale to the process of dialect development without further measures of vocal change, and said it was yet to be determined whether actual generations or cultural generations were the more appropriate time scale for such analyses (Ford 1991).

While Ford's 1991 paper was the first assessment of changes in call type usage in resident pods, changes of the structure of an individual discrete call weren't analyzed until 2000 by Deecke et al. This study looked at the modification of two discrete calls used by two matrilines in the Northern Resident Community over the course of 12 years. Using neural network models to measure the similarity of pulse rate contours, Deecke et al. found that the N4 call type changed significantly over the time period, but interestingly did not diverge between the two matrilines. By contrast, the N9 call type did not change significantly for either matriline. They concluded from this that orca dialects don't only change at the level of the repertoire, but at the level of the discrete call. Indeed, discrete calls are not static behavioral traits, but traits that are subject to changes over time. The rate of change among calls is not standard, however, as one call type didn't change at all (Deecke et al. 2000).

## Aims of This Study

The main goal of this thesis is to advance the understanding of the communicative complexity of the Southern Resident killer whale dialects with the ultimate aim of furthering the understanding of the function of their discrete call usage. This goal will be accomplished via two main aims:

- Aim 1: Compare current call usage of each pod with past data presented by Ford (1987, 1989, 1991) including
    a. Which calls are used by which pods
    b. Frequency of call usage by each pod
    c. Mean duration of each call type
- Aim 2: Assess the complexity of the communication system using
    a. Sequential analysis
    b. Cross-species comparisons using Zipf's statistic and the published data of McCowan et al (1999, 2002)

Under the first aim, it is predicted that call type usage, frequency of call usage, and mean duration of each call type will be different between the past (Ford's recordings from 1978-1983) and the present (the author's recordings from 2005 and 2006). Under the second aim, it is expected that there will be sequential structure in the Southern Resident killer whale discrete call communication system. It is also hypothesized that Zipf's statistic will have similar value to that found for other species.

# Chapter 2: Methods

## Data Collection in the Field

Recordings included in this study were collected during the summers of 2005 and 2006. All recordings of J-, K- and L-Pods were made from shore as part of the SeaSound Project of The Whale Museum in Friday Harbor, Washington. Hydrophones were located on the west side of San Juan Island, Washington just off the lighthouse at Lime Kiln Point State Park (N48°30.954, W123°09.143). In 2005, two Cetacean Research Technology C340 hydrophones were used and data were recorded onto a PC computer in Lime Kiln Lighthouse using Sound Forge, a digital audio software program developed by Sony. Sampling rate, which refers to the number of samples per second made from a continuous signal, was 44.1 kHz. In 2006, an altered Navy Sonobuoy hydrophone was used and recordings were made using LightHouseVocalObserver, a piece of software specially developed by Val Veirs for the SeaSound Project. Due to the differences in technology as well as environmental and technical variation, recording quality was not completely consistent.

In the San Juan Islands there is a substantial ecotourism industry surrounding the whales, and as such the pods are heavily tracked during the daylight hours in the summer months. Pods are located every day by land-based spotters as well as commercial whale-watching vessels. Information about the identity, location, and direction of travel of the Southern Resident pods is sent out every half-hour throughout the day via a pager through a subscription service run by Orca Spirit Adventures, Ltd (Victoria, BC). The Whale Museum subscribes to this service, and so the location of the pods are usually well-known by researchers at Lime Kiln Lighthouse.

Recordings were made whenever the whales were in the vicinity of the research station between the months of May and August in the summers of 2005 and 2006. Recordings were started when whales were within one mile of the hydrophones and were generally terminated when the whales were between one-half and one mile from the hydrophones. The majority of the recordings were made by the author, but in some instances Dr. Robert Otis and his research team, also stationed at Lime Kiln Lighthouse, made recordings when the author was absent. Every time the whales swim through the area in front of Lime Kiln Point State Park is considered one “passby”.

Specific data on the identity of the whales present and their behavior was recorded either by the author or by other researchers for every whale passby. Pod identity was determined by visually identifying individuals using Orca Survey field guides (van Ginneken et al. 2005). Although it was rare to identify every individual present, pods are such cohesive units it is safe to assume that when certain members are present, the rest of their family group will be as well. Pod identification was confirmed with the pager data and by obtaining a count of the total number of whales.

The time (accurate to the minute) any whale or group of whales passed over the hydrophone(s) was recorded for every passby. The location of the hydrophones was estimated using an imaginary line between the research station at Lime Kiln Lighthouse and Mt. Douglas, a distinctive hill visible on Vancouver Island across Haro Strait. The watches of everyone obtaining data were synchronized with the PC saving the hydrophone recordings so a time sync between visual observation data and the recording was possible.

## Data Collection in the Lab

Criteria for including a recording in this study are as follows. Recordings were only included if a single pod was present. For J-Pod, the entire pod (24 whales) was present whenever this occurred. For K-Pod, which had 20 whales in 2005 and 21 whales in 2006, there are two recordings from 2006 included where 5 members of the pod were absent. At more than 40 individuals, L-Pod is a large pod that, in recent years, has been splitting into smaller groups and spending more time in the Strait of Juan de Fuca and the Pacific Ocean during summer months. As a result, there are no recordings with the entirety of L-Pod present, but included recordings still involved only sub-groups of L-Pod with no members of J- or K-Pods present.

Recordings were analyzed from five minutes before the “first cross” of whales passing over the hydrophones until five minutes after the “last cross” where the last group of whales passed over the hydrophones. For the majority of recordings, information on the time of first and last crosses came from the research of Dr. Otis. Due to this criterion, recordings that did not have a five-minute buffer on either side of the first or last cross or that did not have data on crossing times were also eliminated. Finally, in the case of turnarounds where the pod suddenly changes direction of travel, not all of the whales present pass within vicinity of the hydrophones. As a result, recordings with turnarounds were not included if the whales turned around while within a half-mile range of the hydrophones.

As a result of the above criteria, this study included twelve recordings of J-Pod, eleven recordings of K-Pod, and eight recordings of L-Pod, all together making 31 recordings totaling 16 hours. In three of L-Pod's eight recordings, the whales were silent, resulting in a functional sample size of only five recordings. See Appendix 1 for a complete table of included recordings and their parameters.

Recordings were listened to on a Macintosh computer using Raven Pro 1.2.1, a bioacoustics sound analysis software program developed by the Cornell University Lab of Ornithology. Calls were classified based on the now-conventional alphanumeric categories developed by John Ford using his catalogue of discrete calls (Ford 1987). Call type identification occurred aurally and, when necessary, was confirmed visually by inspecting the call's spectrogram. Each call type is characterized by a unique tonal pattern that is distinguishable to the human ear and also manifests as a unique pattern of frequency/time contours on a spectrographic representation of a call. It has been demonstrated that human observers can categorize killer whale discrete calls with the same accuracy as a computer program categorizing calls based on similarity of sound parameters (Yurk et al. 2002).

Call types S2i and S2ii are highly similar and were not distinguished in this study so are referred to simply as S2. As a result, calls were identified as one of 22 call types. Two call types had two subtypes, S2 (into S2 and S2iii) and S37 (into S37i and S37ii), making for a total of 24 different call categories heard in the recordings of this study. Spectrograms showing the distinct tonal structure of each of these 24 call types are shown in Figure 4. Additionally, calls were classified as "Unknown" if they were pulsed calls that failed to fall into one of the stereotypic call categories or "Faint" if they were too faint to be identified. Whistles, rare and highly variable among killer whales, as well as clicks, which are primarily used for navigation and not social communication, were not included in this analysis. A total of 3472 discrete calls were categorized.

The begin time, end time, and duration (length of the vocalization) were recorded for every discrete call by making measurements in the spectrogram window of Raven. Data were stored, along with call identity, in Raven's Selection Table. After a recording was listened to, the Selection Table data was exported as a text file and imported into Microsoft Excel 11.3.3 where a spreadsheet was stored for every passby.

Observer bias is an important issue to consider when analyzing behavioral data. It has previously been demonstrated that inter-observer reliability in identifying killer whale discrete calls is fairly high, with experienced listeners agreeing on 88% of the time (Yurk et al. 2002). Often these issues are dealt with by keeping the observer naïve to certain elements of the experiment or assessing agreement between multiple observers. Due to the constraints of this study, such options were not plausible. Within-observer reliability can be measured by the same observer measuring the same behavioral sample on more than on occasion (Martin and Bateson 1993). In one instance the author listened to a recording twice on separate days to assess intra-observer agreement. Out of 164 call types in that recording, 98% (161 of 164) were coded the same in both assessments.

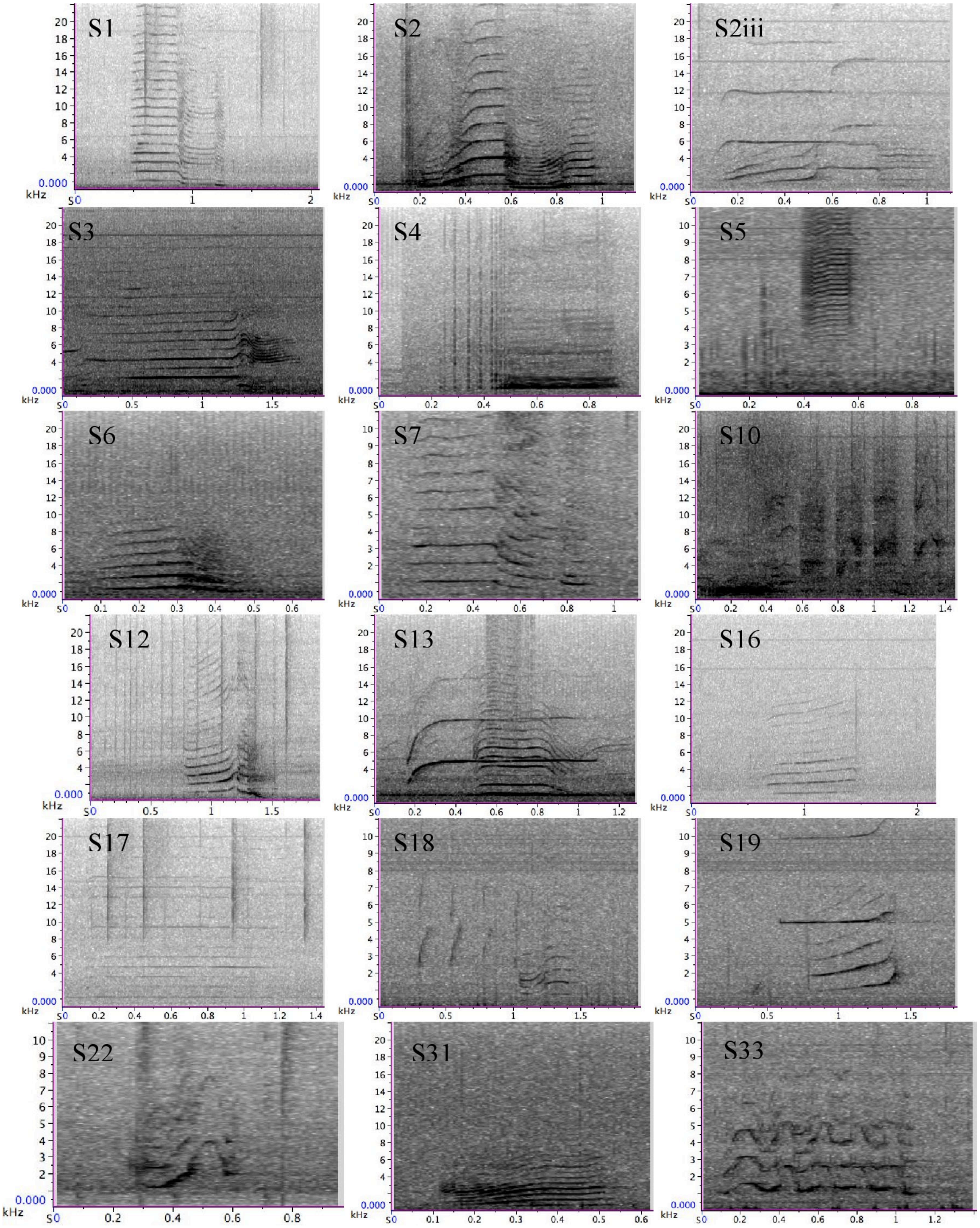


**Figure 4: Spectrograms of the 24 call types used in this study**

Y-axis indicates frequency in kHz. X-axis indicates time. Call designations are based on the conventional categories developed by John Ford. Note: Due to recordings being made in different conditions and on different equipment, the scale is different for each spectrogram. *Continued on next page*.

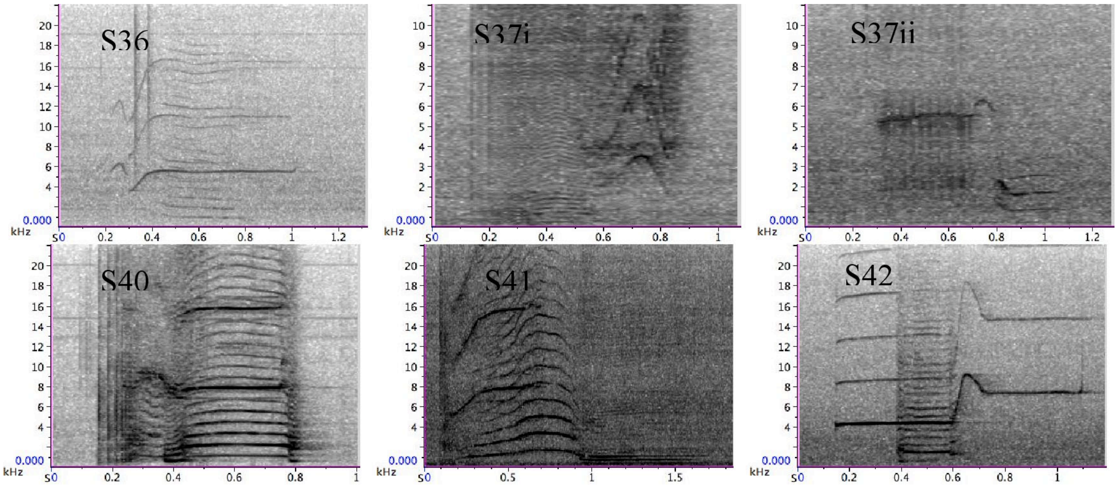


**Figure 4 continued: Spectrograms of the 24 call types used in this study.**

## Data Analysis

Statistical analyses were performed with R 2.4.1, a free software environment for statistical computation (available at www.r-project.org), using a combination of built-in and specially developed functions. See Appendix 2 for the custom R functions and an explanation of the code used. Custom functions were written to import data into R, create a data set for each pod, and to transform the data tables into frequency state transition matrices showing the number of times every call type was followed by every other call type.

Every frequency state transition diagram represents the number of occurrences of each possible two-call transition. A simple question to ask about these matrices is whether any of the cells contain a higher count than would be expected if all the transitions occurred by random. A common statistical procedure for measuring observed frequencies against expected frequencies is the chi-squared test. However, for the chi-squared test to be accurate, a sufficiently large sample size is needed. Sufficient sample size is defined as the expected frequency being at least five, where expected frequency is determined as the number of total observations divided by the number of cells in the transition frequency matrix. In the case of J-Pod, which used 23 call types (21 discrete calls plus the “Faint” and “Unk” categories), the number of cells is 23x23 or 529. The total number of calls observed was 1801, and 1801/529 = 3.40. Another problem for the chi-squared test is having more than 20% of the matrix be zeroes, which is also the case for these data. Since the expected frequency is below 5 and so many of the cells are zeroes, the chi-squared test could not be used to test for significant sequences in this case. Due to these problems with the standard chi-squared test, a Poisson distribution (and the built in “qpois” function in R) was used to determine expected cell counts.

When assessing a large matrix and testing every cell for a significant transition it is important to take measures to avoid the Type I error problem of false positives. With an alpha value of 0.05, five out of 100 tests will reveal a cell as falsely significant. One simple and conservative way to deal with this problem is with the Bonferroni correction, which lowers the alpha value appropriately to account for running multiple statistical tests simultaneously. If k tests are performed and an alpha value of 0.05 is desired, then the adjusted alpha value should be 0.05/k (Bakeman and Gottman 1997). For instance, if 20 tests are being conducted, the alpha value for each test should be 0.05/20, or 0.0025. The Bonferroni correction was added into the Poisson test in R to more accurately determine significance. Details of the analysis are in Appendix B.

A common method of visualizing significant transitions is via a transition state diagram that represent discrete events as separate circles connected via arrows that indicate significant transitions. Transition state diagrams were created in Power Point 11.3.2 with circles corresponding to the frequency of call usage of each discrete call and arrows indicating transitions that were significant under the Poisson distribution.

Frequencies of call occurrence were calculated for the 2005-2006 data set by dividing the number of times that call was observed by the total number of calls observed for that pod. Frequencies of call occurrence for the 1978-1983 data set were estimated from bar graph figures in Ford (1991).

Mean call durations were calculated in R and analyzed using t-tests. Zipf’s statistics were calculated in Excel 11.3.3

# Chapter 3: Results

A total of 3471 vocalizations were heard in the 31 recordings, 2765 (80%) of which were identifiable and placed into one of 24 discrete call categories. Of the 3471 total vocalizations, 1801 were made by J-Pod, and 1388 (77%) of these were identifiable into one of 21 discrete call categories. K-Pod made 1290 vocalizations, 1047 (81%) of which were placed into one of 17 call categories. L-Pod made 380 vocalizations, and 330 (87%) of these were identifiable and placed into one of 14 call categories.

Data from the present study are compared to published data from Ford (1991). Ford's study included 40 recordings of the Southern Residents: 18 for J-Pod with 6005 vocalizations, 10 for K-Pod with no reported vocalization count, and 12 for L-Pod with 2312 vocalizations.

## Call Type Usage

In order to establish an overall shift in the specific calls used by each pod, the presence or absence of each call type was determined and compared to the call type usage previously reported by Ford (1987, 1991). Every pod exhibited changes in calls that made up their repertoire between the past time period (1978-1983) and the present time period (2005-2006) as shown in Table 1. J-Pod no longer uses four call types and has added nine call types to their repertoire. K-Pod has lost three call types from their repertoire and has added ten call types. L-Pod no longer uses five call types and has added three call types. Of the 22 instances where a call type was added to a pod's repertoire, the newly added call type was heard in more than a single recording 13 times, as shown in Table 2.

It has been reported that 80% of call types are shared among Southern Resident pods (Hoelzel and Osborne 1986). In this study, the exact same percentage was found with 20% of call types (5 out of 25) observed in this study being unique to a single pod and 80% of call types (20 out of 25) being shared. This is greater than the number of calls shared in other resident groups; resident pods in southern Alaska share 48% of their call types (Yurk et al. 2002).

Figure 5 indicates the frequency of call usage by pod. Each pod has one or two vocalizations that make up the vast majority of their repertoire. The percentage of variable tonal vocalizations (between 1% and 5% depending on the pod) is comparable to that found in other studies (Miller and Bain 2000).

Figures 6 and 7 show the call frequencies of J-Pod and L-Pod in the past (1978-1983) time period and the present (2005-2006) time period. This graph shows that in addition to some call types being added or lost from a pod's repertoire, other calls have shifted in their frequencies of occurrence. Such a comparison was not possible for K-Pod.

## Call Transitions

Transitions between calls were counted and placed into transition frequency matrices using a custom R function (see Appendix B). Tables 3-5 show the frequency of two-call transitions observed for every pod. Significant transitions, as identified by the quantile Poisson function in R, are highlighted in every table. Accompanying each table is a state transition diagram (Figures 8-10) demonstrating the call transitions for that pod that occur significantly more often than expected by random. J-Pod had the highest number of significant transitions at 25. K-Pod had six significant transitions and L-Pod had seven.

## Call Durations

The mean duration for most call types in the past and present time period are presented in Figure 11. The pod that produced the vocalization most often as determined by Ford (1987) is the pod for which the durations were measured. The S10 vocalization is represented multiple times as it was measured for each pod separately, as indicated on the graph.

16 of the 21 call types analyzed showed a significant change in mean duration between 1978-1983 and 2005-2006 (t-test, $p < 0.05$). Of these 16 call types, 14 of them showed a significant increase in duration.

## Zipf's Statistic

Zipf's statistic, which is the slope of the regression of log(signal rank) versus the log(frequency of occurrence), was calculated for the pooled data from all three pods in the Southern Resident Community. Figure 13 shows the resulting graph with the corresponding regression line. The slope of the regression line for human languages is approximately -1.00; for the Southern Residents it was found to be -1.47. The Zipf's statistics reported by McCowan et al. (1999) for randomly generated data, human language, and bottlenose dolphin whistles are presented in Figure 13 for comparison.

Zipf's statistic was also calculated for each pod separately. J-Pod had a value of of -1.72, and K-Pod and L-Pod both had a value of -2.01 (data not shown). When considering these results it is important to remember that by most standards the data were undersampled compared to the requirements for this analysis.

**Table 1: Call types used by J-, K-, an L-Pods in the past (1978-83) and present (2005-2006)**

A colored square indicates that the call type was used by that pod during the specified time period. Each color represents a different pod: J-Pod (blue), K-Pod (red), L-Pod (yellow). All past data (*) were taken from Ford (1991).

| Call Type | J Past* | J Present | K Past* | K Present | L Past* | L Present |
|---|---|---|---|---|---|---|
| S1 | 🟦 | 🟦 | 🟥 |  |  |  |
| S2 | 🟦 | 🟦 |  |  |  | 🟨 |
| S2iii |  | 🟦 |  | 🟥 | 🟨 | 🟨 |
| S3 | 🟦 | 🟦 |  | 🟥 |  |  |
| S4 | 🟦 | 🟦 | 🟥 | 🟥 |  |  |
| S5 | 🟦 | 🟦 | 🟥 | 🟥 |  | 🟨 |
| S6 | 🟦 | 🟦 | 🟥 | 🟥 | 🟨 |  |
| S7 | 🟦 | 🟦 | 🟥 |  |  |  |
| S8 | 🟦 |  | 🟥 |  | 🟨 |  |
| S9 | 🟦 |  |  |  |  |  |
| S10 | 🟦 | 🟦 | 🟥 | 🟥 | 🟨 | 🟨 |
| S12 | 🟦 | 🟦 |  |  |  |  |
| S13 | 🟦 |  |  | 🟥 | 🟨 |  |
| S14 | 🟦 |  |  |  |  |  |
| S16 |  | 🟦 | 🟥 | 🟥 | 🟨 | 🟨 |
| S17 |  | 🟦 | 🟥 | 🟥 | 🟨 |  |
| S18 |  | 🟦 |  |  | 🟨 | 🟨 |
| S19 |  | 🟦 |  | 🟥 | 🟨 | 🟨 |
| S22 |  | 🟦 |  |  | 🟨 | 🟨 |
| S31 |  |  |  | 🟥 | 🟨 | 🟨 |
| S33 |  | 🟦 |  | 🟥 | 🟨 | 🟨 |
| S36 |  |  |  | 🟥 | 🟨 | 🟨 |
| S37i | 🟦 | 🟦 |  | 🟥 |  | 🟨 |
| S37ii |  | 🟦 |  | 🟥 | 🟨 | 🟨 |
| S40 |  | 🟦 |  | 🟥 | 🟨 | 🟨 |
| S41 | 🟦 | 🟦 |  |  |  |  |
| S42 | 🟦 | 🟦 | 🟥 | 🟥 | 🟨 |  |
| S44 | 🟦 |  |  |  |  |  |
| **Total # of Call Types Used** | **17** | **21** | **10** | **17** | **16** | **14** |

**Table 2: Call Types Added To Each Pod's Repertoire**

The call types added to each of the three pods in the 2005-2006 time period showing the number of times that call type was heard and the number of recordings in which that call type was present.

| Pod | Call Type | # Vocals | # Recordings |
|---|---|---|---|
| J | S2iii | 20 | 1 |
| J | S16 | 90 | 11 |
| J | S17 | 5 | 3 |
| J | S18 | 1 | 1 |
| J | S19 | 17 | 4 |
| J | S22 | 13 | 3 |
| J | S33 | 6 | 2 |
| J | S37ii | 2 | 1 |
| J | S40 | 71 | 3 |
| K | S2iii | 12 | 1 |
| K | S3 | 1 | 1 |
| K | S13 | 3 | 1 |
| K | S19 | 9 | 2 |
| K | S31 | 10 | 2 |
| K | S33 | 15 | 5 |
| K | S36 | 178 | 7 |
| K | S37i | 4 | 2 |
| K | S37ii | 5 | 3 |
| K | S40 | 5 | 3 |
| L | S2 | 1 | 1 |
| L | S5 | 1 | 1 |
| L | S37i | 13 | 1 |

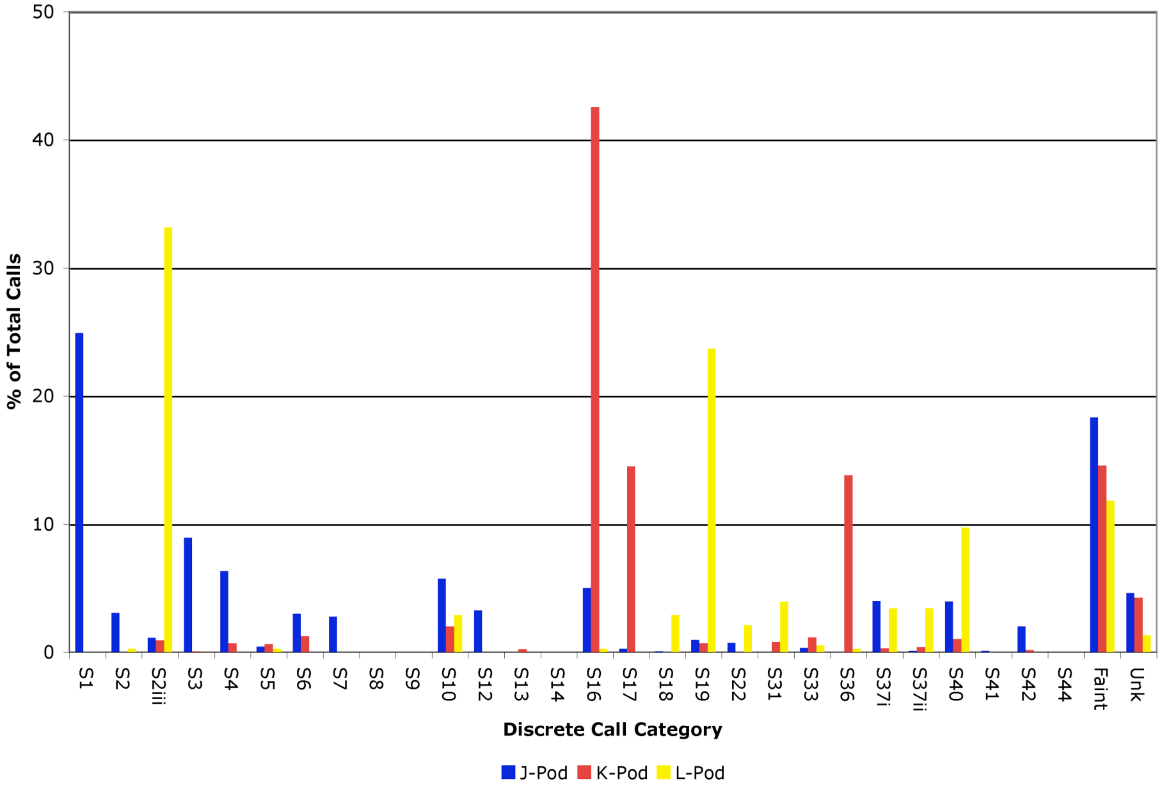


**Figure 5: Discrete call usage by pod**

Discrete call usage by each pod represented as a percent of the total vocalizations heard by that pod in recordings analyzed from 2005-2006. “Faint” refers to vocalizations that were too faint to positively identify. “Unk” refers to variable tonal vocalizations.

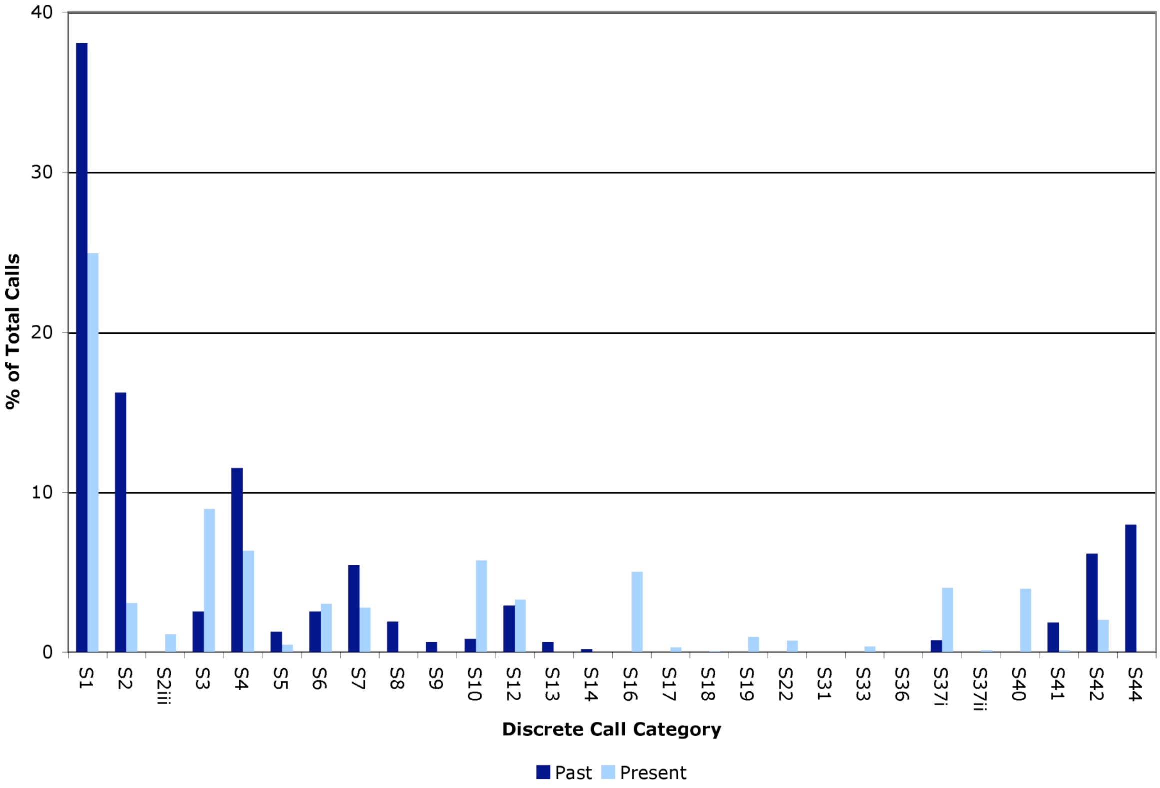


**Figure 6: J-Pod Call Frequency Past (1978-1983) and Present (2005-2006)**
Frequency of call usage for J-Pod in the 1978-1983 time period (dark blue) and 2005-2006 time period (light blue). The 1978-1983 data set was made up of 6005 calls from 18 recordings. The 2005-2006 data set was made up of 1801 calls from 12 recordings. Data for the past time period was estimated from Ford 1991 and pooled across recordings where J-Pod was categorized as either traveling or foraging. No such behavioral distinctions were made in the present study.

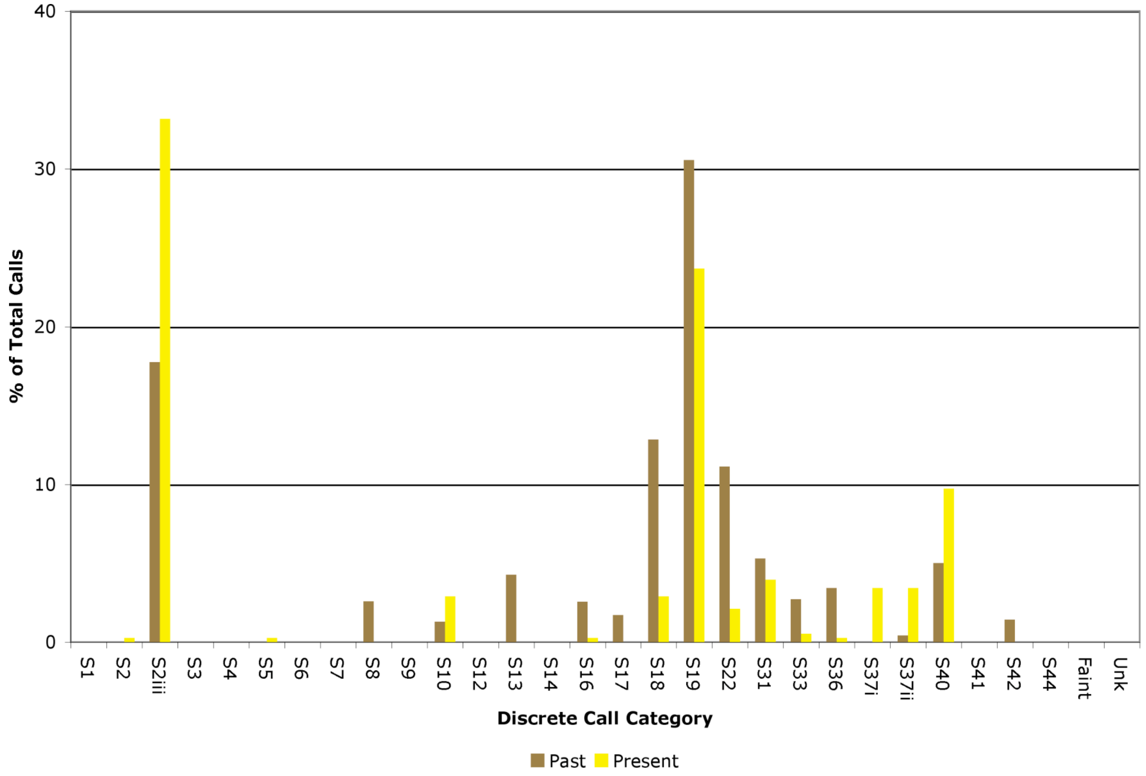


**Figure 7: L-Pod Call Frequency Past (1978-1983) and Present (2005-2006)**

Frequency of call usage for L-Pod in the 1978-1983 time period (dark yellow) and 2005-2006 time period (light yellow). The 1978-1983 data set was made up 2312 calls from 12 recordings. The 2005-2006 data set was made up of 380 calls from eight recordings. Data for the past time period was estimated from Ford 1991 and pooled across recordings where L-Pod was categorized as either traveling or foraging. No such behavioral distinctions were made in the present study.

**Table 3: J-Pod Frequency State Transition Matrix**

Transition matrix showing the observed frequencies of two-call transitions in J-Pod. The first column indicates the preceding call type and the first row indicates the following call type. Blue cells are transitions that are significant at the p < 0.001 level based on the qpois function in R.

| | S1 | S2 | S2iii | S3 | S4 | S5 | S6 | S7 | S10 | S12 | S16 | S17 | S18 | S19 | S22 | S33 | S37i | S37ii | S40 | S41 | S42 | Faint | Unk |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S1 | **256** | **14** | 0 | 8 | **20** | 0 | 8 | **15** | **16** | **12** | **13** | 0 | 0 | 1 | 2 | 3 | 11 | 0 | 6 | 0 | 3 | 54 | 7 |
| S2 | **13** | **12** | 0 | 1 | 1 | 0 | 3 | 0 | 4 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 1 | 7 | 5 |
| S2iii | 0 | 0 | **17** | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S3 | **13** | 0 | 0 | **107** | 3 | 0 | 1 | 0 | 3 | **12** | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 1 |
| S4 | **29** | 1 | 2 | 2 | **35** | 1 | 3 | 3 | 3 | 3 | 4 | 0 | 0 | 1 | 1 | 0 | 4 | 0 | 1 | 0 | 2 | 15 | 4 |
| S5 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| S6 | 8 | 2 | 0 | 1 | 1 | 0 | **13** | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 4 | 0 | 1 | 1 | 3 | 11 | 5 |
| S7 | 7 | 0 | 0 | 1 | 5 | 0 | 1 | **13** | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 11 | 2 |
| S10 | **16** | 8 | 0 | 4 | 1 | 0 | 0 | 2 | **25** | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 9 | 1 | 7 | 0 | 0 | 20 | 7 |
| S12 | 11 | 0 | 0 | **12** | 4 | 0 | 0 | 0 | 1 | **17** | 2 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 5 | 2 |
| S16 | 11 | 2 | 0 | 1 | 4 | 0 | 3 | 0 | 0 | 2 | **32** | 4 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 2 | 14 | 8 |
| S17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 |
| S18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S19 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S22 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S33 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S37i | **16** | 2 | 1 | 0 | 6 | 0 | 1 | 2 | 9 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | **13** | 0 | 7 | 0 | 3 | 4 | 3 |
| S37ii | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S40 | 4 | 2 | 0 | 0 | 2 | 1 | 5 | 1 | 8 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | **30** | 0 | 5 | 6 | 3 |
| S41 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| S42 | 0 | 2 | 0 | 0 | 1 | 1 | 4 | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 6 | 0 | 6 | 4 | 2 |
| Faint | 47 | 7 | 0 | 21 | 24 | 3 | 6 | 9 | 18 | 8 | 18 | 0 | 1 | 4 | 0 | 1 | 5 | 0 | 4 | 0 | 7 | 136 | 10 |
| Unk | 8 | 3 | 0 | 0 | 3 | 0 | 6 | 1 | 9 | 1 | 4 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 3 | 0 | 2 | 17 | 22 |

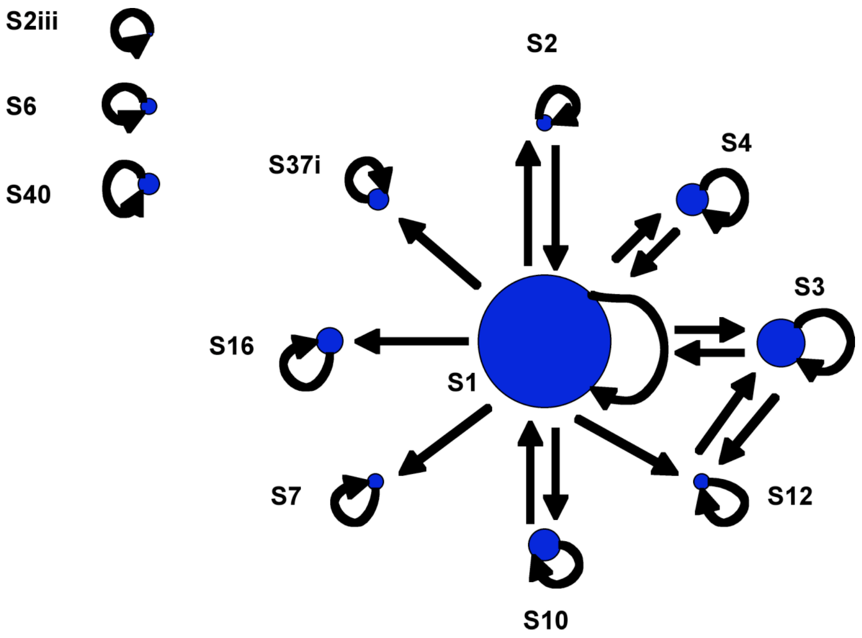


**Figure 8: Significant two-call sequences in J-Pod.**

State transition diagram where arrows indicate call transitions in J-Pod that occur significantly more often than expected by random (qpois function in R, p<0.001). Each circle represents a different call type and the size of the circle indicates the relative frequency of that call. An arrow that returns to the same circle indicates the call follows itself.

**Table 4: K-Pod Frequency State Transition Matrix**

Transition matrix showing the observed frequencies of two-call transitions in K-Pod. The first column indicates the preceding call type and the first row indicates the following call type. Red cells are transitions that are significant at the p < 0.001 level based on qpois function in R.

| | S2iii | S3 | S4 | S5 | S6 | S10 | S13 | S16 | S17 | S19 | S31 | S33 | S36 | S37i | S37ii | S40 | S41 | S42 | Faint | Unk |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S2iii | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S4 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S5 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| S6 | 0 | 0 | 0 | 0 | 2 | 4 | 0 | 2 | 1 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S10 | 0 | 0 | 0 | 0 | 5 | 6 | 0 | 6 | 1 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| S13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| S16 | 1 | 0 | 1 | 2 | 3 | 6 | 2 | **279** | **120** | 0 | 4 | 6 | 9 | 1 | 0 | 3 | 0 | 2 | 81 | 28 |
| S17 | 1 | 0 | 1 | 0 | 2 | 2 | 0 | **104** | **38** | 1 | 0 | 3 | 4 | 0 | 1 | 1 | 0 | 0 | 23 | 6 |
| S19 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S31 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S33 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 10 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S36 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | **22** | 2 | 3 | 0 | 1 | **120** | 1 | 1 | 0 | 0 | 0 | 20 | 3 |
| S37i | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S37ii | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S40 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 4 | 0 | 0 | 3 | 1 |
| S41 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S42 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Faint | 2 | 0 | 0 | 2 | 1 | 2 | 0 | 80 | 17 | 3 | 0 | 0 | 27 | 0 | 1 | 1 | 0 | 0 | 44 | 8 |
| Unk | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 30 | 4 | 0 | 0 | 1 | 3 | 1 | 0 | 1 | 0 | 0 | 4 | 7 |

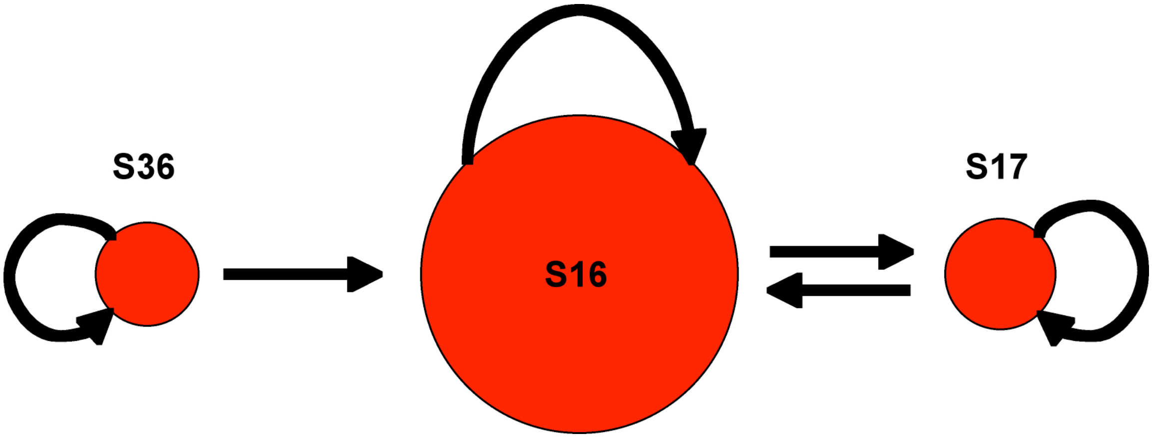


**Figure 9: Significant two-call sequences in K-Pod.**

State transition diagram where arrows indicate call transitions in K-Pod that occur significantly more often than expected by random (qpois function in R, p<0.001). Each circle represents a different call type and the size of the circle indicates the relative frequency of that call. An arrow that returns to the same circle indicates the call follows itself.

**Table 5: L-Pod Frequency State Transition Matrix**

Transition matrix showing the observed frequencies of two-call transitions in L-Pod. The first column indicates the preceding call type and the first row indicates the following call type. Yellow cells are transitions that are significant at the $p < 0.001$ level based on the qpois function in R.

| | S2 | S2iii | S5 | S10 | S16 | S18 | S19 | S22 | S31 | S33 | S36 | S37i | S37ii | S40 | Faint | Unk |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S2iii | 0 | 62 | 0 | 5 | 1 | 0 | 20 | 0 | 0 | 0 | 1 | 2 | 4 | 13 | 16 | 2 |
| S5 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10 | 0 | 4 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 0 |
| S16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S18 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 3 | 1 | 0 | 0 | 0 | 2 | 0 | 2 | 0 |
| S19 | 0 | 23 | 0 | 0 | 0 | 1 | 55 | 1 | 1 | 0 | 0 | 2 | 1 | 2 | 4 | 0 |
| S22 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| S31 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 11 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| S33 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S36 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S37i | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 0 | 4 | 1 | 0 |
| S37ii | 0 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 3 | 1 | 1 |
| S40 | 1 | 18 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 2 | 7 | 3 | 0 |
| Faint | 0 | 10 | 1 | 1 | 0 | 3 | 6 | 1 | 0 | 0 | 0 | 2 | 0 | 6 | 14 | 0 |
| Unk | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |

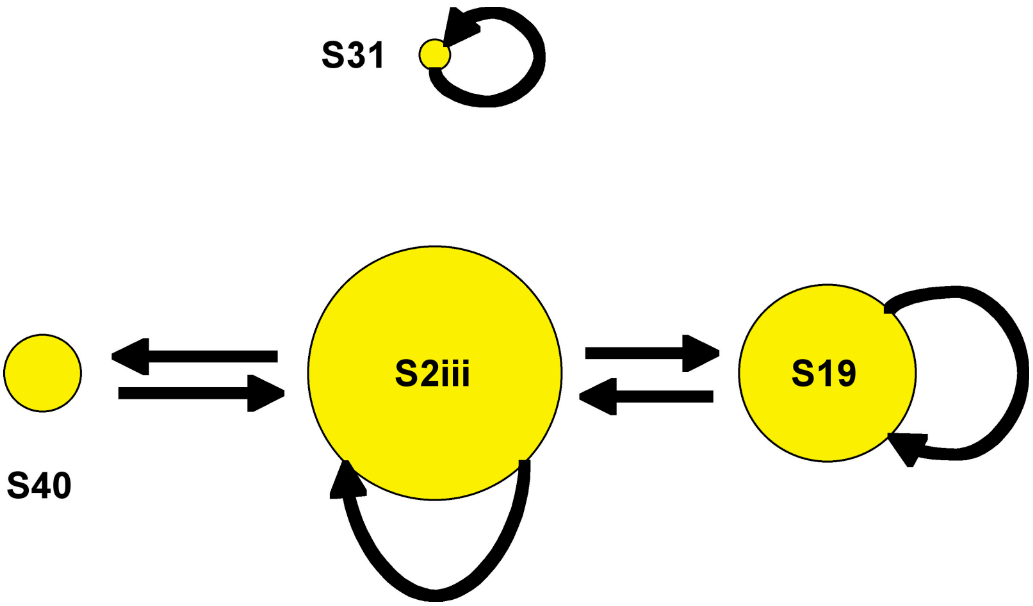


**Figure 10: Significant two-call sequences in L-Pod.**

State transition diagram where arrows indicate call transitions in L-Pod that occur significantly more often than expected by random (qpois function in R, p<0.001). Each circle represents a different call type and the size of the circle indicates the relative frequency of that call. An arrow that returns to the same circle indicates the call follows itself.

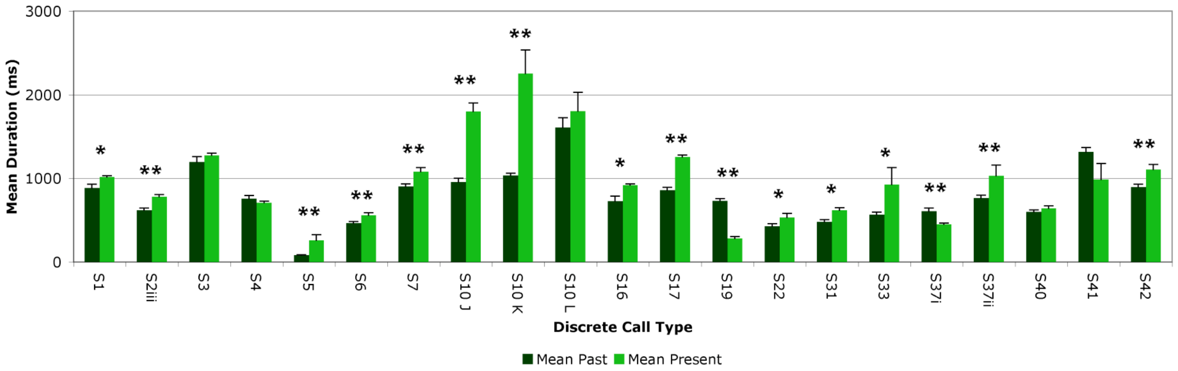


**Figure 11: Comparison of mean call durations**

Mean durations for call types in the 1978-1983 time period (dark green) compared to those from the 2005-2006 time period (light green). Durations for call types in the 1978-1983 time period were taken from Ford 1987. Durations for the 2005-2006 time period were measured in Raven. All measurements are in milliseconds. Each call type was only tested for the pod that produced it most frequently with the exception of S10 which was tested for all three pods. Significance was determined via a t-test. * indicates the results are significant at the $p < 0.05$ level. ** indicates the results were significant at the $p < 0.0001$ level. Bars indicate standard error.

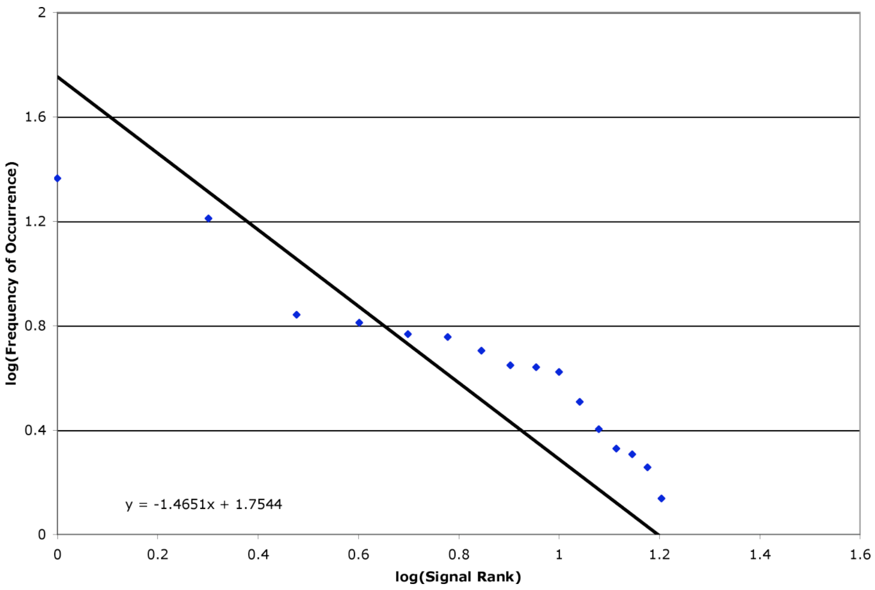


**Figure 12: Zipf's relation of repertoire complexity graphed for the Southern Resident Community of killer whales**

Log(Call Rank) versus Log(Call Frequency) for discrete call usage in the Southern Resident Community. Data were pooled across all three pods before discrete call types were ranked. In humans, the slope of the Zipf's relation (the Zipf's statistic) is roughly -1.00. Here the slope is -1.47.

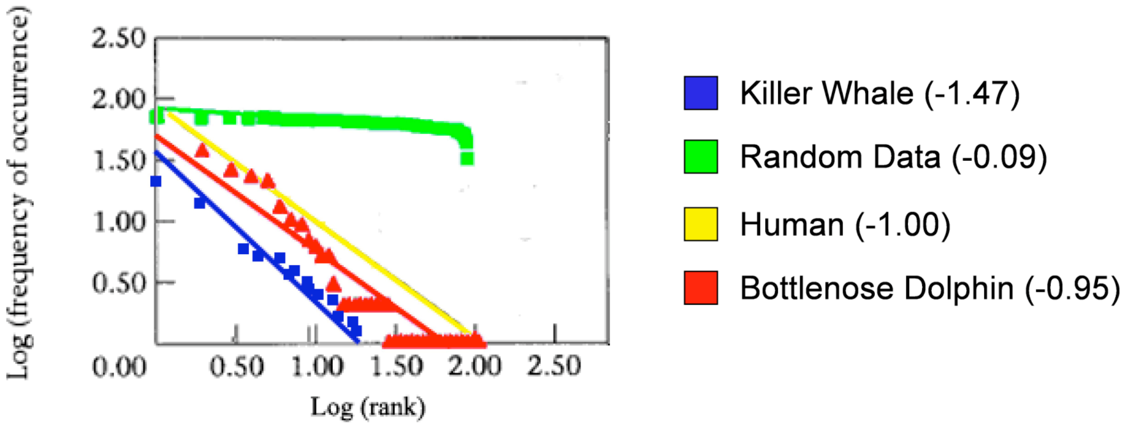


**Figure 13: Cross-species comparison of Zipf's statistic**

Comparison of Zipf's statistic values for Southern Resident discrete calls (blue) from this study to a randomly generated data set (green), human language (yellow), and bottlenose dolphins whistles (red) modified from McCowan et al. 1999 The slopes of each line are indicated next to the corresponding entry in the legend.

# Chapter 4: Discussion

The acoustic communication of the killer whale is vastly intriguing because of their highly social nature, their intelligence, and the fact that it is a unique communication system where many questions have yet to be answered. Whereas many studies on acoustic communication occur in terrestrial, territorial animals such as birds and primates, studying cetaceans allows us to consider signal evolution in an entirely different underwater world. The killer whales in this study were observed to make 24 different stereotyped vocalizations and the functional use of such a large repertoire of discrete calls is unknown. The purpose of this study was to understand discrete call usage better in order to help guide future studies. This goal has been met as this study sheds light on the repertoire structure of the Southern Resident killer whales by discerning shifts in discrete call usage in each pod, establishing call frequency by pod, finding patterns in two-call sequences, and finding significant differences in call durations. This study also provided the first cross-species comparison of killer whale dialects using Zipf’s statistic.

## Shifts in Call Type Usage

Striking differences were found by considering repertoire usage at the most basic level: which discrete calls each pod used. All three pods both lost and added discrete calls from their repertoires. J-Pod lost four call types from its repertoire and added nine, changing its total repertoire size from 17 to 21 calls. J-Pod’s historic repertoire of 17 call types was the largest of any resident pod reported by Ford (1987), so 21 is a new maximum repertoire size for resident killer whales. K-Pod lost three call types from its repertoire and added ten. The most dramatic repertoire shift of the three pods was that of K-Pod. The former repertoire size of K-Pod was 10 call types, and the new repertoire size found in this study is 17 call types. L-Pod showed the smallest shift in their repertoire. While five vocalizations were lost from the repertoire, three call types were added, shifting the repertoire size from 16 call types in the 1978-1983 time period to 14 call types in the 2005-2006 time period. This reduced repertoire shift by L-Pod may be confounded by the undersampling of L-Pod compared to J- and K-Pods.

All three pods were undersampled compared to Ford’s analysis from 1978-1983. In the present study, 1388 calls were categorized for J-Pod compared to 6005 in Ford’s study. 330 calls were categorized for L-Pod in this study compared to 2312 in Ford’s study. No such comparison was possible for K-Pod since no vocalization count was published for the 1978-1983 time period. It is surprising that despite this undersampling, such dramatic repertoire shifts were still observed.

Such shifts in call usage of each pod are startling given that killer whale discrete call systems are known for their stability and have been used to measure degree of relatedness between pods and populations (Ford et al. 1999). It has been reported that certain pods in the Northern Resident community have had no shifts in call types used over a period of at least thirty years (Deecke et al. 2000), and it has been claimed that pod ancestry may be more accurately represented by acoustic similarity than association patterns since association patterns change more frequently than dialects (Ford 1991). Recent studies have shown, however, that there is within-call variation at the matrilineal level (Miller and Bain 2000) and individual level (Nousek et al. 2006), and now this study has shown shifts in repertoire usage at the pod level. This indicates that killer whale discrete calls are more complex than previously appreciated and are likely encoding information at multiple levels; this should be kept in mind when using the discrete call as the unit of analysis in evaluating social communication.

## Gained Calls

In 22 cases a call type was added to the repertoire of a pod. Ford has reported that there are rare cases where a pod will mimic the calls of another pod (Ford 1991), so it is necessary to consider whether some of these cases are mimicking rather than true adding of a call to a repertoire. It is a matter of debate how often a call must be made to be considered part of a pod's repertoire, but observing the gained call type used by the pod on more than one occasion is a good starting point as rarely mimicked calls are unlikely to be heard on multiple recordings. As can be seen in Table 2, of the 22 call types added to a pod's repertoire in the 2005-2006 time period, 13 of them occurred on more than one occasion and therefore should be considered part of a pod's repertoire. Of the nine call types that were only heard during one recording, four of them occurred only once while the other five were heard multiple times within that recording. A threshold to determine how often a call has to be used in order to be included in a pod's official repertoire has not yet been defined.

Looking at what percentage of calls heard are made up of newly added call types can provide information on what role new call types are playing in each pod's repertoire. Of the nine call types added to J-Pod's repertoire in the current study, eight of them occurred only in low frequencies of less than 5%. The one call type that occurred more often was S16, making up exactly 5% of J-Pod's calls. Similarly, in the ten call types added to K-Pod's repertoire, nine occurred in frequencies of less than 5%. The one exception is K-Pod’s S36 call, which was not part of the repertoire in 1978-1983 and now makes up 13% of all K-Pod’s vocalizations. For L-Pod, all three call types added occurred in low frequencies of less than 5%. This indicates that, in general, when a call type is added to a pod’s vocabulary, it, at least initially, plays only a small role in the overall content of the repertoire.

All three pods showed changes in call type usage, but it is important to note that this study was not looking for novel call types added, just shifts in call types between pods in the Southern Resident Community. For instance, the majority of calls added to J- and K-Pods are calls that used to be specific to L-Pod. In the future it would be interesting to consider all the calls that were classified as “Unknown” in this study to look for the possible occurrence of a new call type. In some cases, an unknown vocalization was distinctly repeated several times in succession, but repeated use of unknown call types and potential introduction of novel call types into the Southern Resident repertoire was not the focus of this study. This study only considered the call types previously established by Ford (1987).

There is a unique case study to consider when generating new hypotheses about call usage and calls being added to the repertoire of a pod: the case of L98. L98 was a two-year-old calf from L-Pod that was found on his own on the west side of Vancouver Island in Nootka Sound. He is one of only two recorded instances in more than thirty years of observations of a resident whale being separated from its natal group for a long period of time; in L98’s case, he was solitary for five years before dying in a collision with a tugboat. Observing L98’s vocal repertoire can provide clues to how calls are used within killer whale society. L98 made four discrete call types (Foote et al. 2006). Three of them were found in the repertoire of the Southern Residents and one was a novel call type designated “Lu1”. This is the only known instance of a novel call type being permanently added to the repertoire of a wild resident killer whale. The most common call L98 emitted was, surprisingly, the S1 vocalization most common to J-Pod (Foote et al. 2006). This call type is not even recognized as being part of L-Pod’s repertoire, but clearly L98 had learned this vocalization during the two years of his life he spent within the Southern Resident Community. In addition, L98 mimicked other sounds in his environment such as the barks of California sea lions (Foote et al. 2006).

L98’s unique situation and repertoire can provide insights into the way call types are used and the function they serve within killer whale society. As a member of L-Pod, L98 still must have had the opportunity to learn J-Pod’s S1 call. After being removed from the resident killer whale society, L98 showed the ability to add both calls from other pods and novel vocalizations to his repertoire, demonstrating that such a repertoire shift is at least possible. The calls added to a pod's repertoire in this study are another example of vocal learning from the other pods in the Southern Resident Community. While L98 is the only resident killer whale that has been documented to add novel calls to his repertoire, this study provides the first information of call types of any sort (in this case, from another pod) being added to an entire pod's repertoire under normal social conditions.

## Lost Calls

While no call types were noted to be added to the repertoire of the community, some call types were apparently lost. Especially notable is the S8 vocalization, which was used by all three pods and has now been entirely lost from the Southern Resident Community repertoire. The S9, S14, and S44, all call types that were specific to J-Pod in the 1978-1983 time period, were no longer heard in 2005-2006. Ford had already noted the great decline in S14 call usage in his studies (Ford 1991). While it made up nearly 10% of J-Pod vocalizations in the 1960s, it was heard only twice in his 1978-1983 recordings, and not at all in the 2005-2006 recordings, demonstrating its extinction from the repertoire. As seen in Figure 6, all but one of the other lost call types made up a similarly small percentage (less than 5%) of J-Pod's vocalizations in 1979-1983, so may also have already been on the decline at that point in time. The true anomaly is S44, which made up a fairly large percentage of J-Pod's repertoire during that same time period and was not heard during this study. It was reported that S44 was a common call type when J-Pod was traveling (Ford 1989), making up 20% of their repertoire in that behavioral state (Ford 1991). For L-Pod, as seen Figure 7, a similar trend is shown with lost calls occurring, for the most part, in low frequencies. S13, a call type that was not heard in the 2005-2006 time period, occurred at just under 5% of the time in the 1978-1983 time period, the largest percentage of any call added or lost from L-Pod's repertoire. This indicates that calls that make up only a small proportion of a repertoire are the most likely to be lost. An analysis of the frequencies of calls lost from the K-Pod repertoire is not possible since call frequencies were not reported for this pod in the 1978-1983 time period.

For some of these call types that have apparently gone extinct, it is necessary to note that their absence may be a result of the small sample size in this study. When surveying a repertoire, a sample size of $10R^2$, where R is the number of call types, is ideal (Fagen and Young 1978). Using 24 as the total repertoire of the Southern Resident Community, an ideal sample size would be 5760 calls as compared to the 2765 calls that were categorized into call types in this study. Some scarce calls may not have been detected because not enough vocalizations were listened to. Due to their scarcity, rare vocalizations may only occur in certain similarly rare behavioral contexts not captured in the recordings of these studies. It would not be surprising to see these call types occur in small frequencies in future studies.

Also, it is possible that rare call types were not recognized by the author and were hence inadvertently categorized as “Unknown”, since no acoustic sample of the call types were available for comparison. This problem demonstrates one need for the establishment of an acoustic database where researchers can compare and share recordings and call type distinctions.

## Reasons for Call Shifts

There are several potential explanations for why pods are changing the calls that make up their repertoire. A repertoire may change as individuals in the population change, as population size changes, as pod association patterns vary, or in correlation with an external environmental factor. Each of these options is considered in turn.

Intuitively it makes sense that repertoires may shift due to drift at the population level as individuals are added to and lost from a population. Such a dramatic shift in the calls used by each of the Southern Resident pods is especially striking because, while individuals were certainly born into the population or lost from the population due to death, several individuals remained constant throughout the time period covered by this study. In J-Pod, eight whales that were alive in the 1978-1983 time period were still alive in the 2005-2006 time period. 11 whales that were alive in the earlier time period had died by the later time period, while 16 whales were added to the population between 1983 and 2005. For K-Pod, six whales remained constant between both time periods. 12 individuals were lost from the population while 16 individuals were added to the population between the two time periods. In L-Pod, the largest of the three pods, 17 whales were alive during both time periods, 34 whales were lost from the population, and 29 whales were added to the population (van Ginneken et al. 2005). This study demonstrated shifts in discrete call usage in a period of roughly twenty years, well under the life span of a resident killer whale.

It should be noted that the number of call types does not correlate with size of the pod (Yurk et al. 2002). J-Pod used the most call types, but only contains about half as many members as L-Pod. While every pod experienced some change in size between the two time periods, shifts in population size were marginal compared to shifts in repertoires. Since call types were added or lost from the repertoire while some individuals of the population remained constant, we can conclude that individuals are actually shifting their repertoires.

One possibility that could explain repertoire changes is pod association patterns. For instance, both J- and K-Pods both added call types that used to be unique to L-Pod. This could be due to them spending more time in the vicinity of L-Pod than they used to. While data on time spent with other pods were not available for this study, it is important to recall that all the recordings included in the present study were of isolated pods. This means that even if J-Pod picked up an L-Pod call type because they associate more with L-Pod, they would have integrated that vocalization into their communication even when L-Pod was not present.

Another likely cause for the changes observed in call type usage is environmental or behavioral change. The role that each call type plays within the social communication system may influence how often it was heard or whether or not it was heard at all. The real challenge is, of course, correlating a call type with an environmental or behavioral factor. Call types do not occur exclusively during certain behavioral contexts such as foraging or socializing, although different call types may occur with different frequencies in different behavioral activities (Ford 1989). In captivity, where there is a stable physical and social environment, all the call types of a whale's repertoire were still found to be used, and there was no one-to-one correlation between call type and behavior (Morton et al. 1986). Still, associations with other environmental patterns could be looked for. Is a certain call type only made in the presence of boats? In certain habitat types? In the presence of other species? In certain social contexts? Future exploratory studies could begin looking for such correlations, but as of now there is little indication of where to begin.

Repertoire changes due to shifts in population membership or pod size are not likely, shifts due to pod association patterns were untestable, and shifts due to environmental or behavioral factors are likely. While the exact reasons behind such dramatic repertoire shifts in all three pods remain unknown, the fact that they occurred at all is an extremely motivating finding. Rates of change in mammalian vocal systems have not often been studied (Janik and Slater 2003), and it was previously unknown how fast the discrete call communication system could change. This study has made it apparent that changes in call usage can occur within the matter of a couple of decades. This is a very short period of time when considering the evolution of a signal system.

## A Case for Cultural Evolution

Since we know individuals are changing their repertoires throughout the course of their lifetime, we can rule out that these changes are associated with genetic drift alone. At least some of the call changes must be associated with cultural evolution. Cultural evolution, which involves social learning, is favored when changes occur on the generational time scale (Bradbury and Vehrencamp 1998). Cultural behaviors are therefore population-level characteristics shared by members of a group and transmitted via social learning (Whiten et al. 1999; Laland and Janik 2006).

Non-directed cultural evolution occurs when errors in vocal learning result in gradual repertoire changes over time. In the case of the Southern Residents, the same individuals are involved in the repertoire shifts so there has been no opportunity for such cultural drift.

Directed cultural evolution requires that selection be acting on the socially transmitted cultural behaviors. One example of such directed cultural evolution involves specific foraging behaviors in killer whales. Some orcas beach themselves during foraging in order to prey on sea lions on the beach. This behavior undergoes selection as a successful foraging behavior and its social transmission has been documented via adults teaching and practicing this behavior with juveniles (Baird 2000). Directed cultural evolution must explain the changes observed in call usage because of the rapid rates of change; the question that remains is what is driving this cultural change.

It has been recognized that dialect shifts in killer whales are due to cultural evolution of some type, but it was assumed cultural drift was the most likely cause (Yurk et al. 2002). This study demonstrates that directed cultural selection at the pod level is playing a role in regulating how dialects are shifting. In the past, the appropriate time scale for assessing pod repertoire evolution was unknown (Ford 1991), but this study indicates that a period of several decades is adequate to witness substantial repertoire changes. The large shifts in the calls that make up each pod's repertoire are remarkable, especially given that they occurred over such a short time scale. Shifts in call types used, however, are only the first thing this study revealed about Southern Resident discrete call usage.

## Frequencies of Call Usage

Calls being gained and lost from a repertoire aren't the only way call usage can change. How all the call types in a pod's repertoire break down into their respective frequencies of occurrence can provide information on repertoire evolution; specifically, how frequencies change, call function, and basic structure of a pod's repertoire.

## Changes in Frequency of Call Usage

A comparison of frequency of each call type within a repertoire between the 1978-1983 and 2005-2006 time periods was only possible for J-Pod and L-Pod. The results of this comparison for J-Pod are seen in Figure 6. In addition to the call types added and lost from J-Pod's repertoire, it can be seen that many other call types experienced substantial shifts in their frequencies of occurrence. S1, while still the most frequent call type made by J-Pod, fell from approximately 38% of all calls in 1978-1983 to 25% of all calls in 2005-2006. Other calls that underwent sharp declines in occurrence include S2, S4, S7, and S42, whereas S3, S10, and S37i drastically increased in occurrence.

L-Pod also demonstrated shifts in frequency of occurrence for calls that remained constant in the repertoire across both time periods. S2iii showed the most drastic change, making up approximately 18% of the repertoire in the 1978-1983 time period and increasing to 33% of the repertoire in the 2005-2006 time period. S40 also showed a dramatic increase in usage, while S18 and S19 declined in overall frequency of use. While it is not possible at this point to conclude what these call shifts mean in terms of intrapod communication, it demonstrates that shifting frequencies of occurrence are not constant and hence are another way a repertoire evolves over the time period covered in this study.

It is important to note that in order to conduct this comparison for J- and L-Pods, 1978-1983 call frequencies had to be estimated from a bar graph figure (Ford 1991) and pooled across behavioral categories. Ford separated his results based on whether the pod was traveling or foraging, a distinction not made in the present study. Also, to statistically compare the differences in frequencies of call usage it is necessary to account for the non-independence of call occurrence. This can be accounted for via the transition matrices developed in this study, but such transition information is not available for the past data. Without further information of call sequences from the 1978-1983 data set, it is impossible to accurately test a statistically significant change in repertoire structure and frequency of call usage.

## Contact Calls

It is important to consider how often each call type is used by a pod in order to ask questions about call function and significant relationships among call types. When considering the frequency of call usage as shown in Figure 5, it is immediately apparent that each pod has one or two call types that make up the largest percentage of their repertoire. For J-Pod, it is the S1 vocalization; for K-Pod, the S16 vocalization; and for L-Pod, it is S2iii and S19.

The most-frequent call type used by each pod probably functions as a contact call through which members of a pod keep in contact while out of visual distance of one another. Contact calls, and in fact group specific dialects in general, are also important in maintaining group cohesion when pods spend a lot of time associating with other pods, as the Southern Residents do (Ford and Fisher 1983). Supporting the hypothesis of the most frequent call functioning as a contact call is the fact that all the proposed contact calls show significant patterns of being repeated (either by the same or different whales), as seen the highlighted cells of the transition matrices in Tables 3-5. One would expect these call types to be repeated as certain whales call and others answer with the contact call type. Additionally, at least for J-Pod and L-Pod, the proposed contact calls occurred in high frequencies over both time periods (as seen in Figures 6 and 7), suggesting that their dominant usage is a stable trait of the repertoire.

Another step would be to test whether the contact call is heard more often in cases where the whales are more spread out and hence in greater need of keeping in contact with one another. If occurrence of the dominant call type for each pod increased with pod spread out time (defined as the difference in time between when the first and last whale cross over the hydrophones), this would support the hypothesis that these calls are functioning as contact vocalizations. A similar study done in captivity with bottlenose dolphins demonstrated the function of signature whistles as group cohesion calls by recording their increased use when dolphins where in separate but connected pools and therefore out of sight of one another yet still within acoustic contact (Janik and Slater 1998). In the future, it would also be interesting to consider whether or not these hypothesized contact call types share any acoustic features that make them designed to function particularly well as contact calls over great distances.

It only requires one or two contact calls to maintain group cohesion (Ford 1989; Simmons 2003). The question of why resident killer whales have such a large repertoire still remains uncertain, but it is clear that the calls must be serving an additional social function.

While certain patterns in call usage have definitely changed with calls being added to and lost from a pod’s repertoire, it appears that the most common call used by a pod is relatively stable. J-Pod’s dominant call has been S1 since at least the 1970s (Ford and Fisher 1983). Interestingly enough, it is also one of the most variable discrete calls.

S16, K-Pod's dominant call type, is also extremely variable (personal observation). It is likely that there is more information being encoded into such vocalizations than we realize; perhaps S1 and S16 include and indicator of caller identity, which would aid in their functioning as contact calls.

Vocal similarity of discrete calls at the level of the pod does not preclude variation at the individual level. Chimpanzee pant hoots have certain features in common at the group level but different varying features at the individual level (Crockford et al. 2004). Bottlenose dolphin signature whistles remain distinct at the individual level but can show convergence with another dolphin in the case of paired male alliances (Watwood et al. 2004). In wild killer whales, it has been difficult to look for individual-level variation because of the difficulty in localizing vocalizations to specific whales. Recently, however, it has become possible to localize calls using a towed hydrophone array, resulting in the discovery of individual-level information in the contour shape of shared group call types in the Northern Resident killer whales (Nousek et al. 2006).

It is of special interest that L-Pod has two highly frequent call types, because in recent years a sub-group of L-Pod known as the L12s has been spending more time separate from the main L-Pod group, at least during the summer months (personal observation). Due to an already limited number of L-Pod recordings it was not possible to split the L12s into a separate category in this study, but in the future it would be extremely interesting to look at potential vocal divergence between the L12s and the rest of L-Pod. The S2iii vocalization is the primary call of the L12s, while S19 is possibly the primary call of the rest of L-Pod. Due to the larger group of L-Pod spending more and more time in the Strait of Juan de Fuca and in the open ocean during the summer, it has been especially difficult to get isolated recordings of the main group of L-Pod (personal observation). This should be an area of special attention when collecting recordings in the future years so that comparisons between the L12s and the rest of L-Pod can be made. When such a comparison becomes possible, calculating an index of acoustic similarity between the L12s and L-Pod would be a quantitative way to compare the vocal divergence of the L12s compared to the vocal divergence of L-Pod form both J- and K-Pods. It is possible that with the splitting off of the L12 subpod the formation of a new pod is being witnessed.

## <u>Overall Range and Density of Calls Used</u>

Call density (or number of vocalizations per minute) has been used as a basal measure of vocal activity. For the Southern Residents, call density has been reported to range from 7.9 calls/minute when traveling to 14.5 calls/minute when foraging to 22.4

calls/minute when milling or socializing (Hoelzel and Osborne 1986). When pooling data across all three pods, this study found a call density of 3.7 calls/minute. This value is artificially low, however, as in some recordings there were long distances between whales passing over the hydrophones and therefore long time gaps where no whales were present during periods of no vocalizations. This is also pooling call density across all behavioral states, including resting, a time when Southern Resident whales are silent. Different recordings also have a different number of whales present. A better measure for future studies may be calls/minute/whale.

Hoelzel and Osborne (1986) reported that the 10 most common calls made up 85% of the vocalizations recorded. When totaling the top 10 most common calls across all three pods in the present study, they make up a comparable percentage of all vocalizations at 82%. By considering the bar graph in Figure 5, it is apparent that J-Pod uses a wider variety of vocalizations more frequently than either K- or L-Pods. This trend will play a role in the analysis of significant two-call transitions. J-Pod's more frequent usage of more vocalization results in a very different state-transition diagram from the other two pods, as discussed below.

## Two-Call Sequences

By considering significant two-call sequences in each pod it is possible to begin to understand the structure of the repertoire in use. Transition matrices shows which two-call transitions are the most frequent. This establishes relationships of which call types are associated with one another. All three transition matrices showed vocal sequences that occurred with greater significance than would be expected by random as determined by a Poisson distribution. Each pod has at least some vocalizations that often follow themselves, resulting in significant transitions occurring along the diagonal of the transition matrices. This is not surprising since it has often been reported that discrete calls occur in repetitious bouts in both Northern and Southern Residents (Hoelzel and Osborne 1986; Ford 1989). Studies on captive whales have also yielded non-random transition matrices with a significant trend of calls following themselves (Bain 1986).

For all three pods, the most frequent vocalization, which may be acting as a contact call as discussed above, was the central "keystone" vocalization with the most associations to other call types. J-Pod had by far the greatest number of significant transitions: 25. The majority of these transitions are associated with the S1 call type or occur along the diagonal, representing the fact that a call type often follows itself. For K-Pod, S16 is the keystone vocalization as it occurs most frequently and is also associated with the other two most frequent calls: S17 and S36. It is remarkable that S36 plays such a central role in K-Pod's repertoire because it was not even a call type recognized to be in their repertoire in the 1978-1983 time period. L-Pod shows a similar transition structure to K-Pod, with S2iii being the keystone vocalization that is also associated with S19 and S40. The structure of J-Pod's repertoire is drastically different from that of either K-Pod or L-Pod, as can be seen by comparing Figures 8-10. This begs the question of why J-Pod is so different; for the present, the answer remains purely speculation.

Hoelzel and Osborne (1986) reported that repetitive sequences, defined as a call occurring repeatedly at least five times in a row, made up 87% of the vocalizations they recorded. 50% of the call types they heard were never heard in a repetitive sequence and only occurred sporadically. A similar percentage was found in this study, with 48% of call types (12 of 25) never occurring in repetitive sequence and only occurring sporadically. The call types that did occur in a repetitive sequence made up 85% of the total vocalizations, although not all occurrences of each call type were repetitive in nature.

Ford's study of two-call sequences also reported an association between S16 and S17 for both K- and L-Pods, a trend that was still seen in K-Pod in the present study but was no longer seen for L-Pod as S17 was not even recorded as part of L-Pod's current repertoire. Additional findings included an association between S22 and S18 for L-Pod, which was not seen in the present study. Remarkably, Ford concluded that there were no strong transitions in J-Pod's repertoire, whereas this study found 25 significant associations (Ford 1991). In his transition analysis, Ford also constructed frequency transition matrices but assessed significant deviation from a random model by creating 2 x 2 contingency tables for transitions of interest and testing using G-statistics (Ford 1989). G-statistics were not the applicable test for the transition matrices in this study because a large number of transitions did not occur and therefore had an observed frequency of zero. Ford did not present the transition matrix for the Southern Resident Community, so the number of zeroes in his matrix is not known.

At a minimum, the sample size for sequential analysis should be at least 4 or 5 times the number of cells in the transition matrix (Wickens 1989). In this study, the sample size for each pod was lower than ideal. For J-Pod, which had the largest sample size at 1801 calls, the 23x23 matrix of 529 cells would ideally involve at least 2116 calls. As a result of a small sample size, only particularly strong correlations will be apparent, and thus it is significant that even with the constraint of a reduced sample size, 25 significant transitions were found.

Variation between call types tells us there may be important information encoded between call types, but it is equally important to consider within-call type variation (Catchpole and Slater 1995). To do this, mean call durations were considered.

## Durations

Vocalizations can vary in one of three parameters: frequency, amplitude, or duration. In cetaceans, time variables such as duration are the most common parameters to show variation (Tyack and Miller 2002). It is possible that variation in any of these parameters is a method of encoding different information within a signal. For instance, if there are a wide variety of durations of a particular call type, perhaps what we are defining as a single call type is actually encoding more than a single type of message. Alternatively, these parameters may vary to adapt to specific environmental conditions.

Comparisons of the mean durations between 1978-1983 and 2005-2006 were possible for 21 call types. 16 of these call types showed a significant change in mean duration, and of these 16, 14 call types showed a significant increase in duration. This demonstrates a trend of many call types getting longer.

Increasing call duration is one method of overcoming background noise interference. Humpback whales increase the duration of their songs in the presence of LFA sonar playbacks (Miller et al. 2000). Similarly, beluga whales have been shown to alter the frequency of their calls in response to engine noise interference (Lesage et al. 1999), whereas bottlenose dolphins whistle more frequently in the presence of vessels (Buckstaff 2004). It has been demonstrated that underwater noise from boats can mask killer whale calls at distances up to 14 kilometers (Erbe 2002). The broadband interference of boat engine noise is demonstrated in the spectrogram of Figure 3.

The finding of increased discrete call durations in this study complements the results of a previous study. Foote et al. found an increase in duration for the main call type of each pod in the presence of boats in 2001-2003 as compared to the absence of boats in 2001-2003 or either condition in 1989-1992 and 1977-1981 (Foote et al. 2004). The researchers point out that the average number of commercial whale-watching vessels with the Southern Resident killer whales in the summer months increased five fold between 1990 and 2000, perhaps crossing a disturbance threshold in terms of underwater engine noise and leading to the increased length of discrete calls. The results found here of a broad increase in duration across many call types provided strong evidence for a biologically significant increase in underwater noise.

Of the two call types that significantly decreased in duration (S19 and S37i), an explanation for one of these declines is apparent. The S37i call is made up of two components: a buzz train followed by a tonal call. For many of the S37i calls observed in the present study, the buzz train component was absent. According to Ford (1987), the duration of the buzz train component is approximately 360 milliseconds, so the absence of this component could account for the observed shift in mean call duration.

## Zipf's Statistic and Cross-Species Comparisons

Zipf's statistic for the Southern Resident Community (using pooled data from all three pods) was found to be -1.47, substantially more negative than the -1.00 value found for human languages. When each pod was considered separately, the values were even more negative. A more negative Zipf's statistic indicates that the killer whale repertoire is more repetitive than human languages, an intuitive finding given how often calls occur in repetitive sequences. The killer whale repertoire did show a substantial difference from randomly generated data, which for McCowan et al. resulted in a Zipf's statistic of -0.09, as shown in Figure 13. This means that there is non-random structure to the repertoires of the Southern Resident killer whales, but the structure tends towards repetition rather than diversity.

It must be considered that the repertoires were, by some standards, undersampled, so interpretation of the results should be made with caution. The pooled data across all three pods had a sample size of 2765 calls, while the ideal size using the widely excepted $10R^2$ measure would be 10(24 signal types)^2 = 5760 calls. By contrast, McCowan et al (1999) reported that 10 times the number of signal types should be adequate, so the sample size of 2765 would be well over the required sample of 250 call types. Extreme undersampling has the effect of increasing the slope as the highest-ranking signals are over-represented in smaller samples (McCowan et al. 1999). An increased sample size would reveal the reliability of the Zipf's statistics reported here and may result in the leveling off the slope, hence making it closer to the -1.00 value of human languages.

While Zipf's statistic does not provide linguistic details about a communication system, it can begin to elucidate the structural complexity of a communication system, and this is especially useful in the case of killer whale discrete calls where repertoire function is still a mystery. Based on the Zipf's statistics presented here, which deviate from -1.00, this indicates that there may not be higher-order repertoire structure. This result is cast into doubt, however, by the number of significant two-call sequences found in the analysis of the transition matrices. To resolve this discrepancy, the next step is to increase sample size enough to calculate second-order entropies, which is another measure of two-call sequential structure.

## Future Directions

The results of this study, as in any good scientific endeavor, have led to even more questions. Future research into Southern Resident killer whale repertoire usage can be guided by the findings presented here.

### What Happens When Pods Get Together?

This study considered repertoire usage of individual pods in isolation from the other pods. Future studies looking at pod associations would provide another dimension to understanding repertoire usage of these pods. Now that the call repertoire of J-Pod and K-Pod have been established separately, what sort of repertoire do we see when the two pods are together? Is it simply a conglomeration of the pod's two independent repertoires, or are there new calls added into the mix? Do the frequencies of call usage add up to the cumulative frequencies of the call type between the two pods, or do different call types become more frequent when the two pods are together? Including a wider variety of recordings into a broader study will allow these questions to be answered, and such recordings of different pod associations are available from the same location during the same time period.

When all three pods associate together it is called a superpod. Superpod recordings often contain more vocalizations, more call types, and more variable and aberrant call types since the whales are in a more excited social state. Understanding the repertoires of each pod better will lead to being able to better understand the dynamics of a superpod and what is occurring at the vocal level during such complex and energized social interactions.

### Intervals Between Calls

This study demonstrated an increase in mean call duration found, and this leads to the question if a paralleled increase of intervals between calls would also follow. Additionally, it was found that some two-call sequences occur significantly often, and this raises the question of whether intervals between call types are also structured and contain information. In this study, call transitions were counted regardless of how much time elapsed between the two vocalizations. It has been suggested that timing between calls are important; for instance, in one matriline of W-Pod in the Northern Residents, 36% of vocalizations were produced within five seconds of the vocalization of another pod member (Miller et al. 2004).

Data for start and end time of every vocalization were collected for the present study, and from this it is possible to calculate the interval between every call that occurred by subtracting the start time of one vocalization from the end time of the previous vocalization. Analyses on call intervals could be conducted with the Southern Residents using the data already collected for this study.

## Higher-Order Entropies

This study considered the equivalent of a first-order entropy by using Zipf's statistic to assess the structural complexity of the killer whale discrete call repertoire. By adding more recordings to increase the sample size, there will be enough data to conduct higher-order analyses that look for sequential structure in call usage. Such analyses will compliment the original conclusions drawn here from Zipf's statistic and the transition frequency matrices.

## The Impact of Anthropogenic Noise

In November of 2005, the Southern Resident Community of killer whales was listed as an endangered population under the Endangered Species Act. The main issues facing the population have been identified as salmon declines, water pollutants, and vessel traffic around the whales. One of the main impacts of vessels around the whales is their underwater engine noise, and there is much interest in assessing the impact of this anthropogenic interference. If we want to determine the impact of engine noise on the killer whale communication system, we must first understand that communication system. Basic changes like increase in call duration can be analyzed based on our current knowledge, but changes in more complex aspects of call usage require a deeper understanding of killer whale repertoires that this study has begun to explore.

The next step of considering the impact of vessel noise on killer whale communication is to compare the mean durations of calls in recordings made both in the presence and absence of vessel noise. In the study done by Foote et al., vessel noise was scored as present or absent based on the acoustic detection of the listener. For recordings made at Lime Kiln Lighthouse over the past several years, however, exact vessel counts are available and could be used for a more in-depth analysis.

The difficulty is in obtaining recordings where no vessels are present, as during the majority of summer daylight hours the whales are accompanied by boats from the commercial whale watching fleet. One option is to increase effort at obtaining nighttime recordings where no boats are with the whales, since as of yet few such recordings are available. Another option is to deploy short-term suction tags with a hydrophone that could record vocal communication while attached to a whale.

## Development of an Acoustic Database

With an increasing number of recordings being made of the Southern Residents and of killer whales in general, the need for a shared database of calls and recordings is more important than ever. Currently, different researchers are using different techniques for making and archiving recordings. There is no acoustic sample database of call types, which would allow researchers to confirm that call type analysis is similar across studies. In this study, for instance, rare call types such as S44 may have been missed since the author did not have access to an acoustic sample of this call.

The SeaSound Project of The Whale Museum through which these recordings were made is a prime opportunity to begin assembling such a database. The author has begun an archival system for recordings over the past several years, and further standardization of this system would broadly benefit any future research. Making this archival database available to other researchers and allowing them to add their recordings to it would allow future research on killer whale communication to occur with more efficiency.

## Playback Studies

Exploratory studies such as this one are important in that they identify associations between signals that can be tested in future studies. Often, associations and theories about signal function are tested via playback experiments, which are recognized as a critical step in understanding a communication system. Playback experiments play acoustic signals back to the animals that have emitted them and record its effects on the individuals. They are useful in that they allow the experimenter to control stimuli presentation rather than observing the stimuli that naturally occur.

Playback experiments have been relatively rare in marine mammals despite being a common tool in terrestrial animals. The main reasons for this include logistical challenges of playback research underwater, the difficulty of quantifying underwater behavioral responses to playbacks, and the lack of sufficient background information to make playbacks informative with marine mammals (Deecke 2006). Necessary background information includes the basics of social interactions and of vocal system use in the study species of interest. When such information is available, field playback studies have been a useful tool in researching marine mammal communication. For instance, they have been used to determine that bottlenose dolphins use the individual recognition information in signature whistles (Sayigh et al. 1998) and to assess the mother grey seals respond to the vocalizations of their pup more than an unfamiliar pup (McCulloch and Boness 2000).

No playback experiments have been done with either captive or wild killer whales, although their importance in determining call function in killer whales has been expressed often (Simmons 2003; Miller et al. 2004; Deecke 2006). This study provides a lot of necessary baseline information on call usage in killer whales with which to compare results from playback studies, making field playback experiments a logical next step in understanding call function in the Southern Resident Community.

## Conclusions

This study set out with two main aims: to compare current call usage to past call usage and to assess the complexity and structure of the communication system. Both aims were successfully met. Comparisons with past data yielded details of many changes in killer whale discrete call usage. Call types used by each pod shifted and frequencies of call usage changed, which is evidence for cultural evolution occurring on a rapid time scale. Durations of individual call types lengthened, possibly due to increased vessel noise. This study has provided the first insights into more complex levels of Southern Resident discrete call repertoire structure such as two-call sequences. The results presented here have laid the foundation for studies of the impact of anthropogenic noise on the killer whale communication system as well as provided a baseline of data on call usage patterns that could be used in field-based playback experiments to further delve into the still-unknown function of this large repertoire of calls among extremely social whales.

# Appendix A: Recordings Included in this Study

**Table 6: Recordings Included in This Study**

Recordings included in this study. Pod indicates which of J-, K-, or L-Pods were present. Time analyzed was determined for each passby as being five minutes before the first whale crossed over the hydrophone(s) until five minutes after the last whale crossed over the hydrophone(s). # of Vocals refers to the total number of discrete calls heard during the time analyzed. Calls/Min is a ratio of # of Vocals : Time Analyzed.

| Date | Recording Start Time | Pod | Time Analyzed (Min) | # Vocals | Calls/Min |
|---|---|---|---|---|---|
| 5/30/05 | 12:55 | J | 32 | 70 | 2.19 |
| 6/3/05 | 10:29 | L | 10 | 0 | 0.00 |
| 6/9/05 | 8:20 | K | 38 | 319 | 8.39 |
| 6/10/05 | 15:43 | K | 28 | 117 | 4.18 |
| 6/17/05 | 12:34 | K | 12 | 22 | 1.83 |
| 6/19/05 | 14:47 | L | 60 | 87 | 1.45 |
| 6/19/05 | 18:04 | L | 18 | 0 | 0.00 |
| 6/20/05 | 9:20 | J | 34 | 183 | 5.38 |
| 6/22/05 | 9:04 | L | 17 | 8 | 0.47 |
| 6/28/05 | 14:09 | K | 17 | 57 | 3.35 |
| 7/2/05 | 16:33 | K | 48 | 197 | 4.10 |
| 7/4/05 | 17:05 | J | 64 | 297 | 4.64 |
| 7/5/05 | 12:53 | J | 40 | 117 | 2.93 |
| 7/8/05 | 14:51 | J | 29 | 179 | 6.17 |
| 7/14/05 | 10:11 | J | 39 | 75 | 1.92 |
| 6/7/06 | 11:52 | J | 37 | 42 | 1.14 |
| 6/7/06 | 13:15 | J | 18 | 278 | 15.44 |
| 6/9/06 | 10:53 | J | 71 | 155 | 2.18 |
| 6/19/06 | 13:40 | J | 40 | 51 | 1.28 |
| 6/21/06 | 12:59 | K | 34 | 134 | 3.94 |
| 7/4/06 | 13:22 | L | 29 | 48 | 1.66 |
| 7/4/06 | 15:59 | L | 10 | 0 | 0.00 |
| 7/6/06 | 16:03 | K | 33 | 132 | 4.00 |
| 7/8/06 | 13:56 | K | 14 | 37 | 2.64 |
| 7/10/06 | 18:31 | K | 66 | 149 | 2.26 |
| 7/13/06 | 13:06 | K | 16 | 19 | 1.19 |
| 7/24/06 | 20:37 | K | 30 | 107 | 3.57 |
| 7/27/06 | 14:23 | J | 26 | 190 | 7.31 |
| 8/1/06 | 17:19 | J | 17 | 164 | 9.65 |
| 8/5/06 | 14:00 | L | 21 | 234 | 11.14 |
| 8/19/06 | 17:18 | L | 10 | 3 | 0.30 |
|  |  | **Totals** | 958 | 3471 |  |

# Appendix B: R Functions

## The “Read” Function

(Imports data into R)

```
> Read=function(filename){ # Creates a function named "Read" with a variable "filename"
+ data=read.table(filename, stringsAsFactors=FALSE, header=TRUE) # “data” will be the table imported from the file. The entries under the column heading not to be read as numeric, and headers as names of the columns will be kept
+ data$Call=factor(data$Call, CallTypes) # Take the Call column from the imported data and make it a factor based on Call Types, a stored list of all call type classifications used in the file
+ data} # Display the data table

> dataset=Read("/Users/monika/Desktop/0506200920Copy.txt") # Runs the “Read” function on the specified file and stores it into a vector named “dataset”
```

## The “CreateTM” Function

(Creates a transition matrix from the imported data)

```
> CreateTM=function(calls){ # Creates a function named "CreateTM" with a variable "calls", which is the dataset from which the function will create a matrix
nc = length(attributes(calls$Call)$levels) # nc (number of call types) refers to the length (number) of call types in the Call column of the dataset
M=matrix(0,nrow=nc, ncol=nc) # Creates a matrix with dimensions nc x nc (a square a matrix with a row and column for every call type used in the data set)
Call=as.numeric(calls$Call) # Makes “Call” a numeric version of the “Call” column in the data set
n=length(Call) # “n” refers to the total number of calls in the data set
C1=Call[-n]
C2=Call[-1] # Creates two columns made up of a list of all the calls in the data set, one without the first call and one without the last call, since those calls have no preceding or following transitions, respectively
```

```
n=n-1   # “n” now equals n-1 since one call was removed from each list
for(i in 1:n) M[C1[i],C2[i]]=M[C1[i],C2[i]]+1   # For every value from 1 to n, add +1 to
the corresponding cell in the matrix for every transition from ith value in C1 to the ith
value in C2
M}   # Displays the contents of the transition matrix

> TransitionMatrix=CreateTM(datatset) # Runs the “CreateTM” function on the imported
“dataset” and saves it to a vector called “TransitionMatrix”
```

## The “qpois” Function

(Used to analyze the transition matrices)

```
> 1801/23^2 # J-Pod data contains 1801 vocalizations in a 23 x 23 matrix. The expected
number of observations per cell is calculated by dividing the total number of observations
by the number of cells.
[1] 3.404537 # For a chi-squared test to be applicable, the expected number of
observations per cell should be at least 5. Since it is only 3.4, a chi-squared test cannot be
used.
> 1- (.05)/23^2 # The Bonferroni correction to determine the appropriate alpha value to
input into the qpois function. 0.05 is the desired level of significant, but it is corrected for
the number of cells in the matrix.
[1] 0.9999055 # The probability of getting a significant result given the Bonferroni
correction.
> qpois(0.9999055, 3.402647) # The input values for the qpois function are the
probability of getting a significant result and the expected number of observations per
cell.
[1] 12 # The output of the qpois function indicates that any value in the matrix of J-Pod
data that is 12 or higher has less than a .0001 chance of occurring by chance.
```

# Bibliography

Bain, David E. (1986), 'Acoustic Behavior of *Orcinus*: Sequences, Periodicity, Behavioral Correlates and an Automated Technique for Call Classification', in Kirkevold, Barbara C. and Joan S. Lockard (eds.), *Behavioral Biology of Killer Whales* (New York: Alan R. Liss, Inc.), 335-371.

Baird, Robin W. (2000), 'The Killer Whale: Foraging Specializations and Group Hunting', in Mann, Janet, et al. (eds.), *Cetacean Societies* (Chicago: The University of Chicago Press), 127-153.

——— (2002), *Killer Whales of the World: Natural History and Conservation*, (Stillwater: Voyageur Press).

Bakeman, Roger and John M. Gottman (1997), *Observing Interaction*, (Cambridge: Cambridge University Press).

Baker, Myron Charles and Michael A. Cunningham (1985), "The Biology of Bird-Song Dialects", *Behavioral and Brain Sciences*, 8 (1):85-100.

Barrett-Lennard, Lance G., John K.B. Ford, and Kathy A. Heise (1996), "The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales", *Animal Behaviour*, 51:553-565.

Boughman, Janette Wenrick and Cynthia F. Moss (2003), 'Social Sounds: Vocal Learning and Development of Mammal and Bird Calls', in Simmons, Andrea Megela, Arthur N. Popper, and Richard R. Fay (eds.), *Acoustic Communication* (New York: Springer), 138-224.

Bradbury, Jack W. and Sandra L. Vehrencamp (1998), *Principles of Animal Communication*, (Sunderland: Sinauer Associations, Inc.).

Buckstaff, Kara C. (2004), "Effects of Watercraft Noise on the Acoustic Behavior of Bottlenose Dolphins, *Tursiops truncatus*, in Saratosa Bay, Florida", *Marine Mammal Science*, 20 (4):709-725.

Catchpole, C.K. and Peter J.B. Slater (1995), *Bird Song: Biological Themes and Variations*, (Cambridge: Cambridge University Press).

"Center for Whale Research" (2006). [http://www.whaleresearch.com/thecenter/research.html] Center for Whale Research. Accessed January 2007.

Conner, Douglas A. (1982), "Dialects Versus Geographic Variation in Mammalian Vocalizations", *Animal Behaviour*, 30:297-298.

Crockford, Catherine, et al. (2004), "Wild Chimpanzees Produce Group-Specifc Calls: a Case for Vocal Learning?", *Ethology*, 110:221-243.

da Silva, ML, JRC Piqueira, and JME Vielliard (2000), "Using Shannon entropy on measuring the individual variability in the Rufous-bellied thrush Turdus rufiventris vocal communication", *Journal of Theoretical Biology*, 207 (1):57-64.

Deecke, Volker B., John K.B. Ford, and Paul Spong (2000), "Dialect change in resident killer whales: implications for vocal learning and cultural transmission", *Animal Behaviour*, 60:629-638.

Deecke, Volker B. (2006), "Studying Marine Mammal Cognition in the Wild: A Review of Four Decades of Playback Experiments", *Aquatic Mammals*, 32 (4):461-482.

Erbe, C. (2002), "Underwater noise of whale-watching boats and potential effects on killer whales (Orcinus orca), based on an acoustic impact model", *Marine Mammal Science*, 18 (2):394-418.

Fagen, Robert M. and Donald Y. Young (1978), 'Temporal Patterns of Behaviors: Durations, Intervals, Latencies, and Sequences', in Colgan, Patrick W. (eds.), *Quantitative Ethology* (New York: John Wiley & Sons, Inc.), 79-114.

Fernando, Prithiviraj and Russell Lande (2000), "Molecular genetic and behavioral analysis of social organization in the Asian elephant (*Elephas maximus*)", *Behavioral Ecology and Sociobiology*, 48:84-91.

Foote, Andrew D., et al. (2006), "Killer whales are capable of vocal learning", *Biology Letters*, 2 (4):509-512.

Foote, Andrew D., Richard W. Osborne, and A. Rus Hoelzel (2004), "Whale-call response to masking boat noise", *Nature*, 428:910.

Ford, John K.B. and H. Dean Fisher (1983), 'Group Specific Dialects of Killer Whales (Orcinus orca) in British Columbia', in Roger, Payne (ed.), *Communication and Behavior of Whales* (Boulder: Westview Press, Inc.), 129-161.

Ford, John K.B. and Graeme M. Ellis (1999), *Transients: Mammal-Hunting Killer Whales*, (Vancouver: UBC Press).

Ford, John K.B., Graeme M. Ellis, and Kenneth C. Balcomb (1999), *Killer Whales*, (Vancouver: UBC Press).

Ford, John K.B. (1987), "A Catalogue of Underwater Calls Produced By Killer Whales (*Orcinus orca*) in British Columbia", *Canadian Data Report of Fisheries and Aquatic Sciences*, No. 633

——— (1989), "Acoustic Behaviour of Resident Killer Whales (*Orcinus orca*) Off Vancouver Island, British Columbia", *Canadian Journal of Zoology*, 67 (3):727-745.

——— (1991), "Vocal Traditions Among Resident Killer Whales (*Orcinus orca*) in Coastal Waters of British Columbia", *Canadian Journal of Zoology*, 69 (6):1454-1483.

Hailman, Jack P. (1977), *Optical Signals: Animal Communication and Light*, (Bloomington: Indiana University Press)

Hailman, Jack P. and Millicent Sigler Ficken (1996), 'Comparative Analysis of Vocal Repertoires, With Reference to Chickadees', in Kroodsma, Donald and Edward H. Miller (eds.), *Ecology and Evolution of Acoustic Communication in Birds* (Ithaca: Cornell University Press), 136-159.

——— (1986), "Combinatorial Animal Communication with Computable Syntax: Chick-a-dee Calling Qualifies as a 'Language' by Structural Linguistics", *Animal Behaviour*, 34:1899-1901.

Hoelzel, A. Rus and Richard W. Osborne (1986), 'Killer Whale Call Characteristics: Implications for Cooperative Foraging Strategies', in Kirkevold, Barbara C. and Joan S. Lockard (eds.), *Behavioral Biology of Killer Whales* (New York: Alan R. Liss, Inc.), 373-403.

Hoelzel, A. Rus and Gabriel A. Dover (1991), "Genetic differentiation between sympatric killer whale populations", *Heredity*, 66:191-195.

Janik, Vincent M. and Peter J.B. Slater (1998), "Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls", *Animal Behaviour*, 56:829-838.

——— (2003), 'Traditions in Mammalian and Avian Vocal Communication', in Fragaszy, Dorothy M. and Susan Perry (eds.), *The Biology of Traditions: Models and Evidence* (Cambridge: Cambridge University Press), 213-235.

Janik, Vincent M. (2005), 'Underwater Acoustic Communication Networks in Marine Mammals', in McGregor, Peter (eds.), *Animal Communication Networks* (Cambridge: Cambridge University Press), 390-415.

Krebs, J.R. and N.B. Davies (1993), *An Introduction to Behavioral Ecology*, (Third edn., Oxford: Blackwell Publishing).

Laland, Kevin N. and Vincent M. Janik (2006), "The animal cultures debate", *Trends in Ecology & Evolution*, 21 (10):542-547.

Lesage, V., et al. (1999), "The effect of vessel noise on the vocal behavior of Belugas in the St. Lawrence River estuary, Canada", *Marine Mammal Science*, 15 (1):65-84.

Lindburg, Donald G. and H. Fitchsnyder (1994), "Use of behavior to evaluate reproductive problems in captive mammals", *Zoo Biology*, 13 (5):433-445.

Mann, Janet (2000), 'Unraveling the Dynamics of Social Life: Long-Term Studies and Observational Methods', in Mann, Janet, et al. (eds.), *Cetacean Societies* (Chicago: University of Chicago Press), 45-64.

Martin, Paul and Patrick Bateson (1993), 'The reliability and validity of measures', in *Measuring Behavior* (Cambridge: Cambridge University Press), 114-124.

McComb, K. and S. Semple (2005), "Coevolution of vocal communication and sociality in primates", *Biology Letters*, 1 (4):381-385.

McCowan, B., S.F. Hanser, and L.R. Doyle (1999), "Quantitative tools for comparing animal communication systems: information theory applied to bottlenose dolphin whistle repertoires", *Animal Behaviour*, 57:409-419.

McCowan, B., L.R. Doyle, and S.F. Hanser (2002), "Using information theory to assess the diversity, complexity, and development of communicative repertoires", *Journal of Comparative Psychology*, 116 (2):166-172.

McCulloch, S. and D.J. Boness (2000), "Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada", *Journal of Zoology*, 251:449-455.

Miller, Patrick J. O. and David E. Bain (2000), "Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*", *Animal Behaviour*, 60:617-628.

Miller, Patrick J. O., et al. (2000), "Whale songs lengthen in response to sonar", *Nature*, 405:903.

Miller, Patrick J.O., et al. (2004), "Call-type matching in vocal exchanges of free-ranging resident killer whales, Orcinus orca", *Animal Behaviour*, 67:1099-1107.

Morton, Alexandra, John Gale, and Renee Prince (1986), 'Sounds and Behavioral Correlations in Captive *Orcinus orca*', in Kirkevold, Barbara C. and Joan S. Lockard (eds.), *Behavioral Biology of Killer Whales* (New York: Alan R. Liss, Inc.), 303-333.

Mundinger, Paul C. (1982), 'Microgeographic and Macrogeographic Variation in the Acquired Vocalizations of Birds', in Kroodsma, Donald E., Edward H. Miller, and Henri Ouellet (eds.), *Acoustic Communication in Birds, Vol. 2* Communication and Behavior, (New York: Academic Press), 147-208.

Noad, Michael J., et al. (2000), "Cultural revolution in whale song", *Nature*, 408:537.

Nousek, Anna E., et al. (2006), "The influence of social affiliation on vocal signatures of northern resident killer whales (*Orcinus orca*)", *Biology Letters*, 2:481-484.

Owings, Donald H. and Eugene S. Morton (1998), *Animal Vocal Communication: A New Approach*, (Cambridge: Cambridge University Press).

Rendell, Luke and Hal Whitehead (2001), "Culture in whales and dolphins", *Behavioural and Brain Sciences*, 24 (2):309.

——— (2005), "Spatial and temporal variation in sperm whale coda vocalizations: stable usage and local dialects", *Animal Behaviour*, 70:191-198.

Sayigh, Laela S., et al. (1998), "Individual recognition in wild bottlenose dolphins: a field test using playback experiments", *Animal Behaviour*, 57:41-50.

Shannon, Claude E. and Warren Weaver (1949), *The Mathematical Theory of Communication*, (Chicago: University of Illinois Press).

Simmons, Andrea Megela (2003), 'Perspectives and Progress in Animal Acoustic Communication', in Simmons, Andrea Megela, Arthur N. Popper, and Richard R. Fay (eds.), *Acoustic Communication* (New York: Springer), 1-14.

Stenersen, John and Tiu Simila (2004), *Norwegian Killer Whales*, (Henningsvaer: Tringa Forlag).

Suggs, Dianne N. and Andrea Megela Simmons (2005), "Information theory analysis patterns of modulation in the advertisement call of the male bullfrog, *Rana catesbeiana*", *Journal of the Acoustical Society of America*, 117 (4):2330-2337.

Suzuki, Ryuji, John R. Buck, and Peter L. Tyack (2006), "Information entropy of humpback whale songs", *Journal of the Acoustical Society of America*, 119 (3):1849-1866.

Swaisgood, Ronald R., Donald G. Lindburg, and Xiaoping Zhou (1999), "Giant pandas discriminate individual differences in conspecific scent", *Animal Behaviour*, 57:1045-1053.

Tyack, Peter L. (2000), 'Functional Aspects of Cetacean Communication', in Mann, Janet, et al. (eds.), *Cetacean Societies* (Chicago: University of Chicago Press), 270-307.

Tyack, Peter L. and Edward H. Miller (2002), 'Vocal Anatomy, Acoustic Communication and Echolcation', in Hoelzel, A. Rus (eds.), *Marine Mammal Biology: An Evolutionary Approach* (Oxford: Blackwell Science Ltd), 142-184.

van Ginneken, Astrid M., David K. Ellifrit, and Kenneth C. Balcomb (2005), *Official Orca Survey: Photo-Identification Guide to Orca Whales of the Southern Resident Community*, (Spring 2005 Edition; Friday Harbor, WA: Center for Whale Research).

Watwood, Stephanie L., Peter L. Tyack, and Randall S. Wells (2004), "Whistle sharing in in paired male bottlenose dolphins, *Tursiops truncatus*", *Behavioral Ecology and Sociobiology*, 55:531-543.

Whiten, A., et al. (1999), "Cultures in chimpanzees", *Nature*, 399:682-685.

Wickens, Thomas D. (1989), *Multiway Contingency Tables Analysis for the Social Sciences*, (Hillsdale: Lawrence Erlbaum Associates).

Yurk, H., et al. (2002), "Cultural transmission within matrilineal lineages: vocal clans in resident killer whales in southern Alaska", *Animal Behaviour*, 63:1103-1119.

Zipf, George K. (1949), *Human Behaviour and the Principle of Least Effort*, (Cambridge: Addison-Wesley).