Testing the Motivation-Structural Rules Hypothesis in Southern Resident Killer Whales (*Orcinus orca*)

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Killer whales (*Orcinus orca*) are the most widely distributed marine mammals in the world (Bigg et al. 1987; National Marine Fisheries Service 2008). They are the largest members of the *Delphinidae* family with males weighing 10-11 tons and growing up to 32 feet in length (Bigg et al. 1987). Killer whales exhibit extreme sexual dimorphism – males are nearly twice the size of females and sprout dorsal fins that can grow to be six feet tall (Ford et al. 2000). The most basic social unit in killer whale society is the matriline, which is composed of a matriarch and her male and female descendents (Ford et al. 2000). Pods are made up of related matrilines that spend at least 50% of their time together (Bigg et al. 1990 *in* Baird and Whitehead 2000), and clans are defined as groups of pods that share calls in their vocal repertoires (Bigg et al. 1987; Ford et al. 2000).

The Eastern Pacific killer whale population, which is native to Washington and British Columbia, consists of three ecotypes: residents, transients, and off-shores (Ford et al. 2000; National Marine Fisheries Service 2008). Each ecotype is distinct in terms of behavior, social organization, and ecology (Ford et al. 2000). The most striking difference between resident and transient killer whales involves prey preference: residents eat salmon and other fish, while transients dine exclusively on marine mammals (Ford et al. 2000; National Marine Fisheries Service 2008). Although the ranges of all three ecotypes overlap, there is no evidence of interbreeding (Ford et al. 2000; Morton 2002; National Marine Fisheries Service 2008). This reproductive isolation suggests that these ecotypes may diverge into different species in the future (Ford et al. 2000). The resident killer whale population includes two communities, each composed of pods that regularly associate with one another (Ford et al. 2000). As of 1999, the resident population was comprised of approximately 300 whales (Ford et al. 2000). The Southern Resident community, on which this paper focuses, has one clan (J), which is composed of three pods (J, K, and L) (Bigg et al. 1987; Ford et al. 2000).

There are three types of killer whale vocalizations: clicks, whistles, and pulsed calls (Ford 1989). Clicks are used for echolocation whereas pulsed calls and whistles are used for communicative purposes (Ford 1989). Ford (1987) found that pulsed calls are often distinctive and repetitive, lending themselves to categorization. These sounds are referred to as “discrete calls” (Ford 1987; 1989; 1991). In both the Northern and Southern communities, discrete calls dominate vocal exchanges during periods of activity and appear to serve the purpose of maintaining group cohesion (Ford 1991). Whistles are tonal, non-pulsed sounds that are structurally distinct from pulsed calls (Ford 1989; Riesch et al. 2006). In the Northern Resident killer whale community, whistles are mostly used during close-range interactions (Ford 1989; Thomsen et al. 2002). However, it has been suggested that Southern Residents use whistle signals for long-distance communication (Colleen Barry 2006; Riesch et al. 2006).

Morton (1977) hypothesized that there is a relationship between the physical structures of sounds and the motivation underlying their use. This idea is based on Darwin's principle of antithesis, which suggests that it is evolutionarily advantageous for disparate signals to minimize ambiguity by taking antithetical forms (Collias 1963 *in* Morton 1977; Gouzoules and Gouzoules 2000). According to the motivation-structural (MS) rules, animals use harsh, low frequency sounds in aggressive or hostile situations and tonal, high frequency sounds in appeasing or friendly situations. This primarily applies to sounds made when animals are close to one another (Morton 1977). August and Anderson (1987) tested the MS rules hypothesis across a number of taxa using data from existing scientific papers. Analysis showed a correlation between harsh, low frequency sounds and hostile behavior with regards to frequency but not bandwidth. Sounds associated with appeasement and/or friendliness were randomly distributed in terms of both frequency and bandwidth (August and Anderson 1987). Overall, the investigators concluded that the acoustic design of analyzed close-contact vocalizations was loosely consistent with the MS rule hypothesis but highlighted the fact that further testing was necessary. This study aims to take preliminary steps towards discerning the motivational and emotional content of killer whale calls. The Southern Residents' tight-knight social structure and dynamic vocal repertoire make the population ideal for testing the application of Morton's hypothesis in cetaceans.

Neither friendly nor agonistic vocalizations have been identified in Southern Resident killer whales. However, some vocalizations appear to align with the prediction that a conflict of motivational states is represented acoustically as rapid frequency modulation (Morton 1977). Pulsed calls that are non-repetitive and cannot be easily classified are called variable calls (Ford 1989). No calls in this category have been correlated with a specific behavior or surface activity, leading researchers to believe that they may convey information about the vocalizing whale's emotional state (Ford 1989; Rehn et al. 2007). Graham and Noonan (2010) concluded that calls made by captive killer whales during aggressive chase periods were characterized by 190 ms-long frequency modulation pulses. Ford (1989) found that in the Northern Resident community, periods of intense excitement were accompanied by shortened and higher-pitched vocalizations and by distinctive series of signals with rapid up-and-down pitch modulation.

Similar “excitement calls” were also recorded in the Southern Resident community (Ford 1989).

A recent study re-classified these “excitement” vocalizations as V4 calls, which are thought to be the most commonly occurring class of variable calls in Northern Residents (Rehn et al. 2007). Ford (1989) found that variable calls were used by Northern Residents more frequently during socializing than during other behavior states, with rates reaching close to 100% during brief periods of particularly intense socializing. Variable calls have not been categorized in the Southern Resident community, but it seems reasonable to suggest that they, along with other frequency-modulated calls, could be used to gauge motivational states on the gradient between excitement and aggression during close-contact scenarios.

In order to test Morton’s MS-rules hypothesis in the Southern Resident community, I analyzed rates of harsh, tonal, and frequency-modulated pulsed calls during active and non-active behavior states. I hypothesized that there would be higher rates of harsh sounds during active states (when aggression is more likely to occur) than during non-active states. I also hypothesized that there would be higher rates of tonal sound during non-active states than during active states, assuming that less active behavior corresponds with lower stress and agitation. I expected to see high rates of distinctly harsh, tonal, and frequency modulated sounds during close-contact scenarios, when clear communication of motivational state is most important and the consequences of misinterpretation are most severe.

Methods

Due to the whales’ inconsistent presence, historical acoustic and behavioral data was analyzed in addition to data collected in the field.

2010 Beam Reach Data

Data was collected aboard the 42-foot catamaran *Gato Verde*. Acoustic recordings were made using a LabCore four hydrophone array (peak sensitivity = 5 kHz) and two SoundDevices 702 solid state audio recorders (sampling rate = 44.1 kHz, bit depth = 16, file format = wav). Categorical behavioral data was recorded by hand using custom-made data sheets. Data collection was carried out in accordance with the Be Whale Wise guidelines. Distance from whales, side of boat, number of whales, group spread, and behavior state were observed and recorded throughout each recording session. Behavior state categories and definitions were adapted from NOAA’s 2004 Southern Resident killer whale behavior classification workshop.

Monika Wieland Data

Acoustic and behavioral data were collected by Monika Wieland during the summer of 2007 at Lime Kiln State Park (N48’30.954, W123’09.143). Recording began whenever whales entered the study area (eg were within one mile of the recording equipment at Lime Kin Lighthouse) and were terminated when whales were ½ to 1 mile past the lighthouse (Wieland 2007). Behavioral data recorded included pod, surface-active behaviors observed, number of whales entering study area, and individual whales identified. Whales were counted as entering the study area when they crossed an invisible line extending from Lime Kiln lighthouse to Mt. Douglas on Vancouver Island (Wieland 2007). Dr. Robert Otis, a professor at Ripon University, and his students took behavioral data using the same parameters. Hydrophones used to make acoustic recordings varied throughout the field season but had adequate frequency response to record killer whale calls.

Greeting Ceremony Data

Six minutes of a greeting ceremony between J and L pods was recorded (audio and video) on October 4, 2005. A single, stationary hydrophone was used to record the event, and the video and audio were later synched by Dr. Scott Veirs and Dr. Val Veirs. The audio recordings were spliced into six one-minute segments.

In this study, harsh calls are defined as calls that cover a wide-frequency band, and tonal calls are defined as pure calls with narrow frequency bands (Morton 1977). Because harsh and tonal calls have not been explicitly defined for the Southern Resident killer whales' vocal repertoire, one discrete pulsed call, S37 (Figure 1), was used as the exemplar for "harsh" in this study, and another discrete pulsed call, S19 (Figure 2), was used as the exemplar for "tonal." The V4 (Figure 3) class of variable calls, which has been identified as the most common variable call type in the Northern Resident community, has recently been identified in the Southern community and was used to represent intermediate calls with frequency modulation (Foote, pers. comm.).

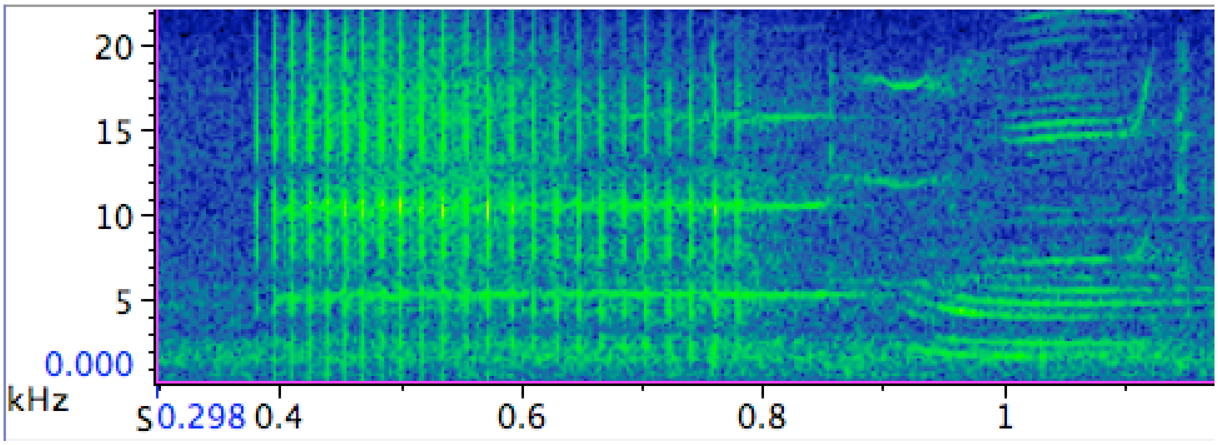

Figure 1. Spectrogram of an S37 discrete pulsed call (x axis=time, y axis=frequency, sampling rate = 44.1 kHz, FFT rate = 512)

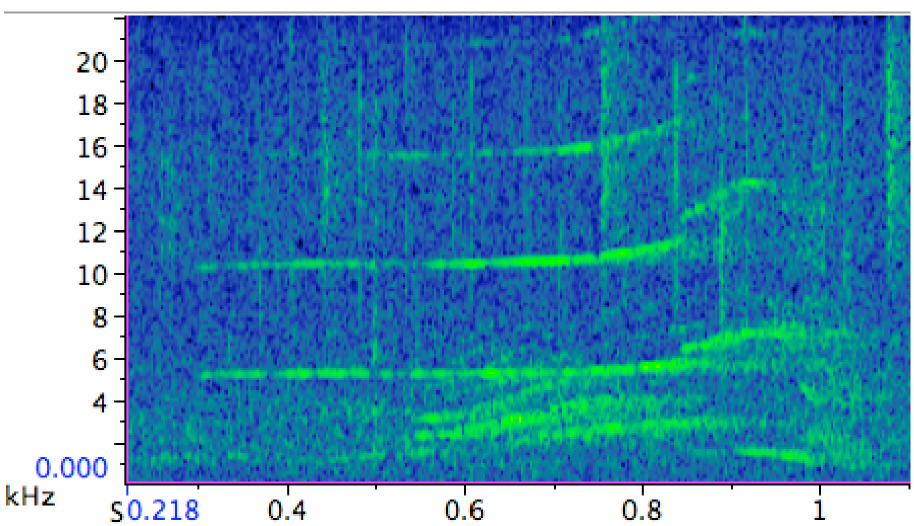

Figure 2. Spectrogram of an S19 discrete pulsed call (sampling rate = 44.1 kHz, FFT rate = 512)

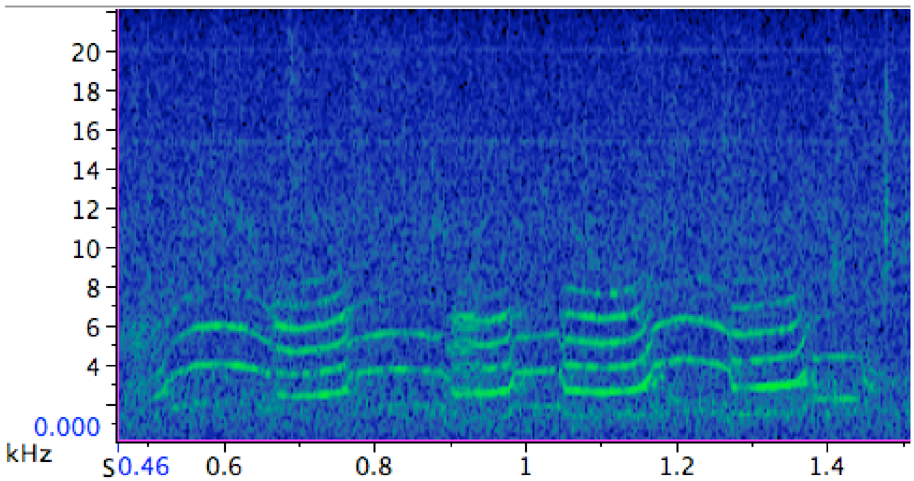

Figure 3. Spectrogram of a V4 variable pulsed call (sampling rate = 44.1 kHz, FFT rate = 512)

In this study, all sounds were analyzed using Audacity (sampling rate = 44.1 kHz, bit depth = 16, FFT rate = 512). Rates of tonal (S19), harsh (S37), and frequency modulated (V4) calls were calculated for each uninterrupted behavioral bout and were analyzed in two different dimensions: active vs non-active behavior states and close vs loose group spread. A behavioral bout is defined as a period of un-interrupted observation time during which a group of whales is in one of five behavior states (foraging, traveling, socializing, milling, or resting). In this study, foraging, traveling, and socializing were grouped in the "active" category, and milling and resting were grouped in the "non-active" category. Close is defined as 0-10 m between animals, and loose is defined as 11or more m between animals. Behavior states were categorized as either "active" or "non-active" rather than "aggressive" or "appeasing/friendly" because it is nearly impossible to distinguish aggression from excitement or playfulness in killer whales without witnessing aggressive behavior (eg biting and/or chasing followed by an obviously evasive maneuver).

For the Lime Kiln data set, behavioral descriptions corresponding with Monika's recordings were used to determine the whales' behavior state. Observation periods where surface active behaviors occurred were categorized as "active" and those without surface active behaviors were categorized as "non-active." Number of whales and group spread data were taken from Dr. Otis' 2007 Excel spreadsheets that corresponded with the times and dates of Monika's recordings. Group spread was recorded by Dr. Otis as "spread out time," which was calculated by noting the elapsed time between the first whale and last whale crossing the line marking the beginning of the study area. I calculated the average spread out time for the entire 2007 summer field season and defined "close" as any number below the average and "loose" as any number above the average. Greeting ceremony recordings were also analyzed using Audacity, and call rates were calculated in a separate Excel spreadsheet. All recordings used in this study were made on days observing L pod.

Results

In total, 176 minutes of historical data, 6 minutes of greeting ceremony data, and 272 minutes of field recordings from the Beam Reach Spring 2010 program were analyzed in this study. Rates (calls/whale/minute) of S37, S19, and V4 were calculated for all behavioral bouts during each observation period. Rates from Monika Wieland's 2007 data and rates from Beam Reach 2010 data were combined for statistical analysis. Using StatPlus, two non-parametric tests (Kruskal-Wallis) were run to compare call rates during active (n=11) vs non-active (n=3) behavior states and during close (n=4) vs loose (n=10) group spread. The average rate (±SEM) of S19 calls during active behavior states was 0.257 (± 0.186 calls/whale/minute), as opposed to 0.010 (± 0.010 calls/whale/minute) during non-active behavior states. The rate of S19 calls was significantly higher (H=11.859, p=0.037) during active states than rates of S37 or V4 during active states and rates of all three calls during non-active states. S37 calls were present during active behavior states (0.003 ± 0.003 calls/whale/minute), as were V4 calls (0.001 ± 0.000 calls/whale/minute), but neither were recorded during non-active behavior states (*Figure 1)*[1]. These rates were also analyzed in the close vs loose group spread dimension. The rate of S19 during loose group spread was significantly higher (H=14.132, p=0.015) than the rate of S19 during close group spread and the rates of S37 and V4 during both close and loose group spread bouts. S37 calls were recorded during loose group spread bouts (0.004 ± 0.004 calls/whale/minute) but not during close group spread bouts. Conversely, V4 calls were present during close group spread bouts (0.001 ± 0.001 calls/whale/minute) but not during loose group spread bouts (*Figure 2*).

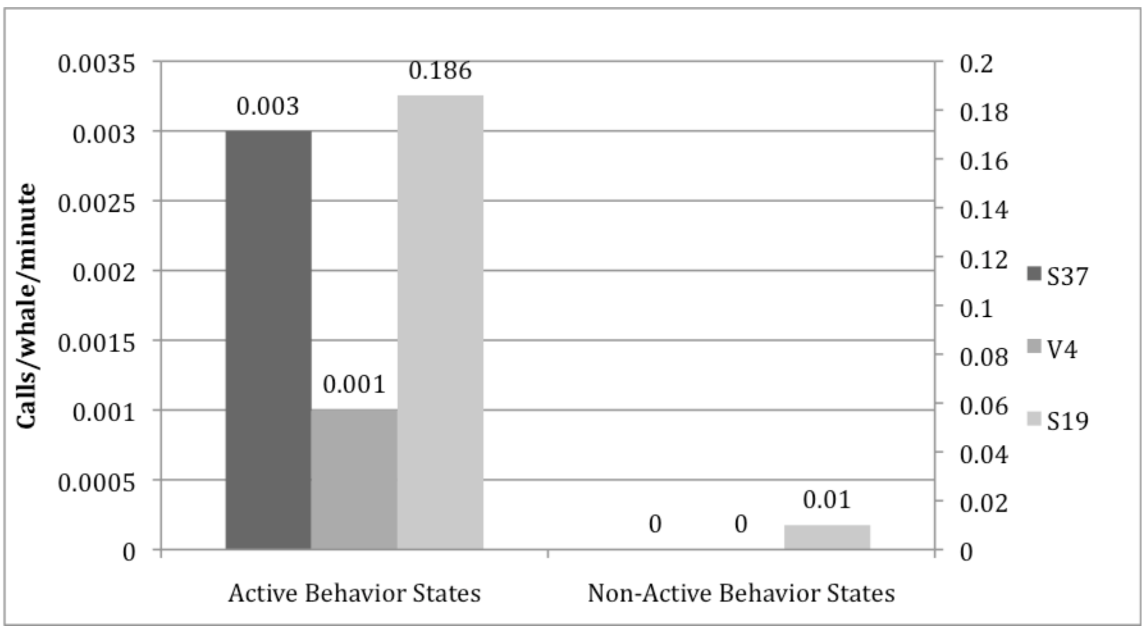

Figure 1. Rates of S37, S19, and V4 calls during active and non-active behavior states (n=42, H=11.859, p=0.037)

[1] Note that in Figure 1 and Figure 2, S19 call rates are represented on the secondary axis. Also note that SEMs are noted in text but are not represented as error bars on graphs.

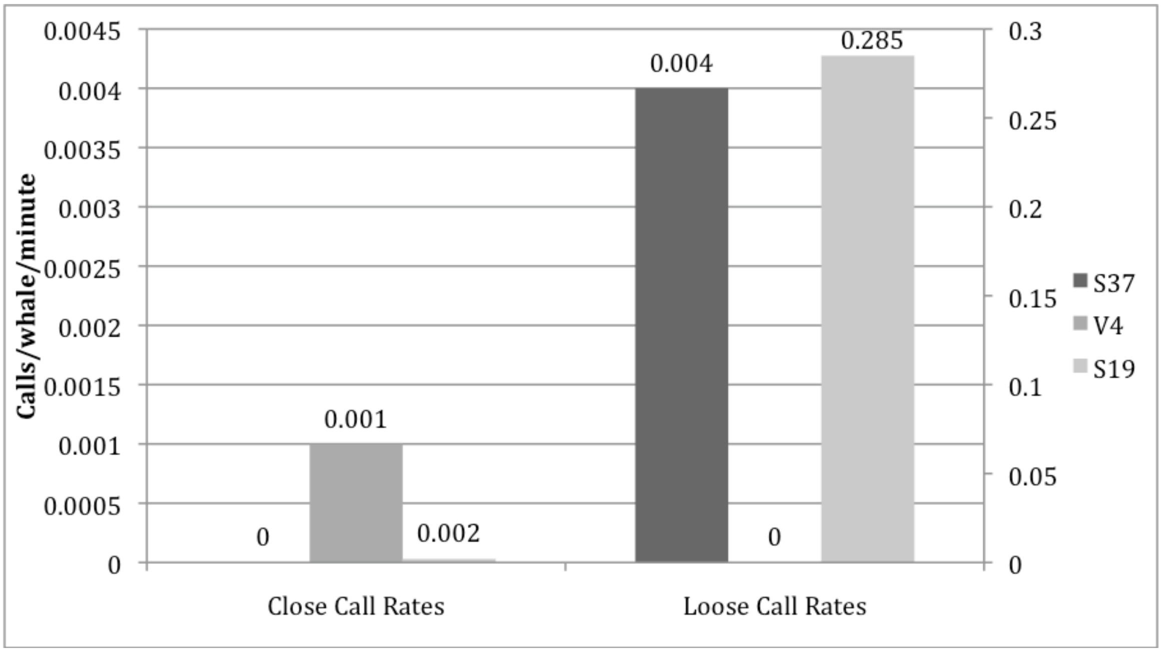

Figure 2. Rates of S37, S19, and V4 calls during close and loose group spread periods (n=42, H=14.132, p=0.015)

The means of all S37, S19, and V4 (Beam Reach/Lime Kiln combined, n=42) rates were compared to mean rates of the same calls during the 2005 greeting ceremony (n=6) using a Wilcoxon Signed Rank Test. All three calls occurred at higher rates during the greeting ceremony than during Beam Reach/Lime Kiln observations (*Figure 3*). S37 occurred at the highest rate (0.280 calls/whale/minute)(p=0.000) during the greeting ceremony, followed by S19 (0.195 calls/whale/minute) (p=0.033) and V4 (0.010 calls/whale/minute)(p=0.000).

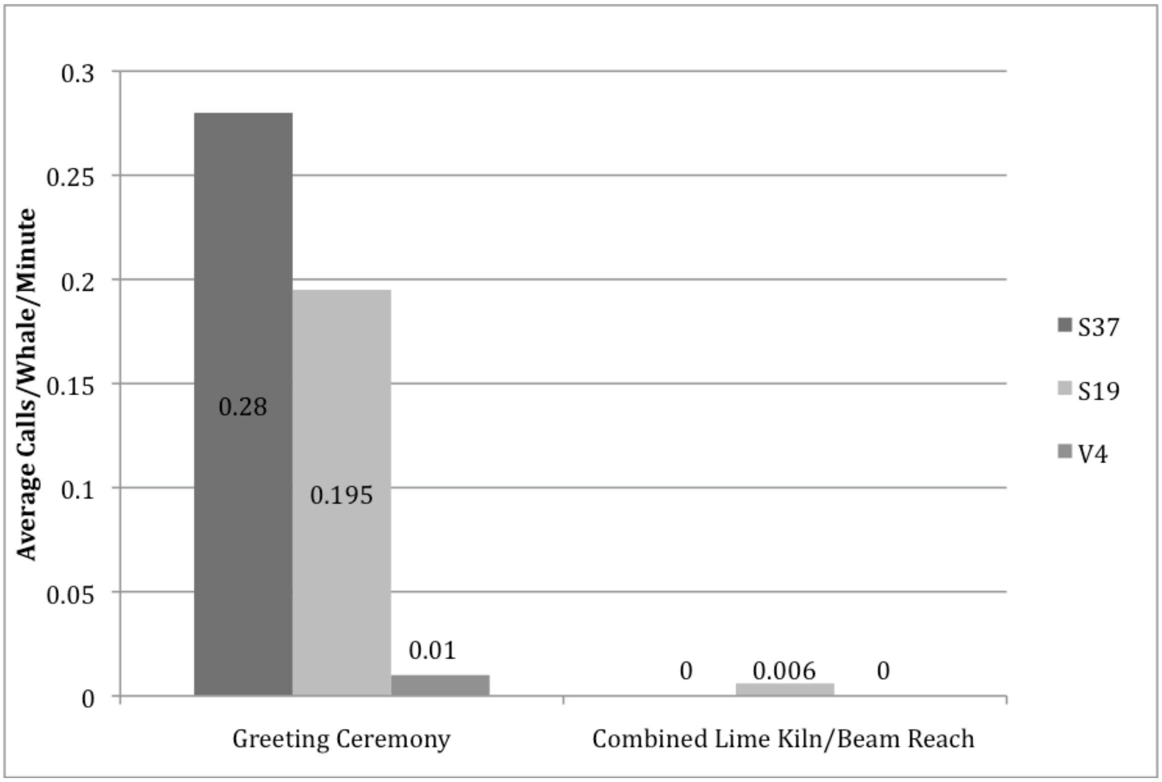

Figure 3. Rates of S37, S19, and V4 calls during greeting ceremony vs combined Lime Kiln/Beam Reach ($p<0.030$)

Discussion

It is impossible to know what an animal is thinking when it emits a sound, which makes it extremely difficult to interpret animal vocalizations as an outsider. Field scientists who study terrestrial animals can use visual cues to make connections between an animal's behavior and vocalizations. Cetacean researchers must base observations and conclusions on information collected during the short time their study subjects come to the surface to breathe – a difficult and, at times, frustrating endeavor. Scientists have attempted to assign meaning to killer whale vocalizations by examining links between specific behaviors and specific calls, but this strategy simply unearths correlations; it does not necessarily bring us closer to understanding what calls mean. By studying the emotional content of killer whale phonations, we can learn about meanings of calls beyond the level of functionality.

The motivation-structural rules hypothesis suggests that sound structure reflects motivation in two dimensions: sound frequency and bandwidth. In general, these two characteristics vary together in mammals and birds (Morton 1977, 1983). The hypothesis states that if an animal is in a friendly, frightened, or appeasing state, the sounds it emits will be relatively high-frequency and tonal in quality. Likewise, if an animal is in an aggressive or hostile state, its vocalizations will be low-frequency and harsh (Morton 1977, 1982). This hypothesis has been tested in terrestrial mammals (Sieber 1984, August and Anderson 1987, Compton et al. 2001 Gouzoules and Gouzoules 2002) but has yet to be applied to marine mammal sounds. Most studies testing the MS-rules hypothesis in terrestrial animals use study subjects with stereotyped calls. Compton *et al.* (2001) tested the hypothesis in the white-nosed coati (*Nasua narica*) by analyzing two distinct call types (chips, which are tonal sounds used as contact calls, and squawks, which are harsh sounds used in agonistic situations) in aggressive and non-aggressive contexts. Such a study is not possible with killer whales for two reasons: first, because no single killer whale call is used exclusively in one behavioral context, and second, because open aggression is so rarely witnessed during field observations. For these reasons, a different approach was used in this study.

Three calls that are used across behavioral contexts (S37, S19, and V4) were used to test the MS-rules hypothesis in one pod (L) of the Southern Resident killer whale community. The rate of S19 calls was higher than that of S37 and V4 calls in all four categories analyzed (active, non-active, close group spread, and loose group spread).   In terms of the behavior state dimension, the high rate of S19 calls during active behavior states would not necessarily be expected based on the MS-rules, if we assume that aggression is most likely to occur when whales are active. However, when looking at the group spread dimension, the high rate of S19 calls during loose group spread bouts does conform to the MS-rules, if we assume that the whales are in a more relaxed state when they are far apart and less interactive. Rates of S37 and V4 calls were higher during active behavior states, which also conforms to the MS-rules, but this result is based on a very small sample size. V4 calls were noted during close group spread events, which would be expected based on the MS-rules, but S37 calls were not noted. Several factors could have contributed to the results shown in this study. Firstly, data grouped into the “active” category was collected during periods when whales were foraging or traveling – never during socializing, the behavior state where the MS-rules would be expected to apply most. In addition, rates for all three calls examined were low during non-active behavior states because most data in this category came from an instance where whales were resting and did not vocalize.

The 2005 greeting ceremony between J and L pod provided the best data for analysis in this study. Because the ceremony was an intense socializing period, it served as an extreme against which to compare the field and historical data collected during less intense observation periods. A greeting ceremony between two pods is an ideal scenario for testing the MS-rules hypothesis because the whales are close together and are highly active, during which time animals’ motivational states oscillate subtly and frequently. Rates of all three examined calls, especially S37, were significantly higher during the greeting ceremony than during Beam Reach 2010 and Lime Kiln data collection periods. The high rate of S37 calls could be due to the whales’ extreme excitement (possibly bordering on aggression), or could simply be due to the increase in overall call rate that occurred during the greeting ceremony. During periods of high energy and close group spread, there is selective pressure for unambiguous calls because the consequences of misinterpretation are immediate and potentially lethal. This may help explain the high rates of both distinctly harsh and tonal calls made during the greeting ceremony. The presence of V4 calls during the greeting ceremony could be explained by the subtle shifts in emotional states that likely occur during socializing, or, as Morton predicts, by conflicting motivational states.

CONCLUSION

Spending hours listening to killer whale recordings has made it abundantly clear that Southern Residents' phonations are extremely complex and depend heavily on context. It is insufficient to test the MS-rules using only three discrete pulsed calls when killer whales use so many other types of calls in their vocal repertoire. Acoustic parameters such as frequency, amplitude, and bandwidth should be used to quantify harshness and tonality so that the MS-rules can be tested using all call types. Using active and non-active behavior states instead of aggression and non-aggression proved to be a useful means of analysis in this study but should not be used in future studies. Active and non-active are not equal to aggression and non-aggression in terms of behavior, and thus do not provide meaningful categorization of observed behavior. Thus, efforts should be made to define and classify aggression in wild killer whales. Being able to quantify intra-specific surface aggression will make future studies testing the MS-rules in killer whales more elegant and straightforward. The results of this study suggest that killer whale calls can be classified using harsh and tonal categorizations, but the conclusions reached here are not sufficient for proving that Southern Resident killer whale calls conform to the MS-rules.

ACKNOWLEDGEMENTS

I am very grateful to the institutions and individuals who helped make this project a reality. Special thanks to Dr. Jason Wood for his patient guidance and assistance with data analysis, Dr. Val Veirs for his infectious enthusiasm for science and for pushing me to always think critically, and Dr. Scott Veirs for providing me with the opportunity to participate in Beam Reach and for giving me the tools to pursue my deep curiosity about killer whale communication. I thank the University of Washington and Friday Harbor Labs for providing us with a home base while on land and Captain Todd Shuster for giving me a phenomenal sailing experience while at sea. I am also grateful to Dr. Robert Otis and to Monika Wieland for allowing me the use of their data and to Ken Balcomb for providing me with my first up-close-and-personal Southern Resident killer whale experience.

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