An acoustic measurement of the leadership role/s of the matriarchs in the SRKW population of the Salish Sea

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Final proposal

Three distinct ecotypes of Orcinus orca, commonly known as killer whales, inhabit the Northeastern Pacific: resident, transients and offshores. Specifically, the coastal waters of British Columbia, the state of Washington and southern Alaska are populated by resident and transient types. This separation is based on the long and detailed record of surface-behavior observations, prey preferences, group associations and genetic tracing obtained by researchers over the last 3 decades (Bigg et al. 1987; Ford et al. 1998; Hoelzel 1998.) Resident populations have been defined as such by their prey-specialization on fish, specifically salmonids (at least during their observed foraging in these waters from spring-fall), by the long stability and exclusive membership of their social aggregations as well as by their distinct vocal dialects. Extensive research since the 1970's has established two resident populations, fish-specialists, with stable social structures in which center lies the matrifocal unit or matriline. Matrilines are the smallest and most cohesive social unit in resident orcas. They are comprised of a matriarch, the oldest female in the group, and all of her direct descendants, both females and males. Matrilines may contain anywhere from 2 to 4 or 5 generations depending on the age of the matriarch (Ford, 1989.) These matrilines in SRKWs (southern resident killer whales) and NRKWs (northern resident killer whales) exhibit high philopatry from both sexes throughout their lives, a very rare occurrence in nature. Individuals from a matriline rarely break off from the group for significantly prolonged periods. Matrilines with a higher average of males have been observed to be slightly more independent in their travels than the ones with a more equal sex ratio or more females to males ratio. This is to be expected as males will most likely try to breed with females from other pods to prevent inbreeding (Ford, 1989.) This study will concentrate on the SRKWs whose home range encompasses the waters off the southern half of Vancouver Island and along the Puget Sound.

The physical conditions of the marine environment have made odontocetes primarily acoustic mammals. Particular properties of sound in the aquatic medium such as increased speed of propagation, the attenuation patterns and different absorption rates from lower to higher frequencies, the transoceanic 'SOFAR channel' formed by pressure and temperature differentials, which can carry a signal for possibly tens or hundreds of kilometers, make the evolution and structure of the acoustic world of whales a very fascinating mystery. The role of vocal communication and sound in all aspects of the lives of orcas, from echolocation for prey and navigation to social interactions, identification and localization of conspecifics, etc., is an absolutely essential tool in any attempt at understanding their societies and general ecology. Therefore, establishing whether a leadership role exists for the matriarchs within the matriline unit and/or among matrilines within a pod or even clan, requires the careful study of the vocal activity and context of the vocalization during a specific behavior by the identified matriarchs. Due to the inherent difficulties linking consequent underwater behavior to surface-observations and association to a particular acoustic signal or sequence of signals, positive identification of the signaler and the signal immediately prior to or during the change-event between behaviors is a must.

The vocal repertoire of resident killer whales is comprised of whistles, clicks-believed to be primarily used for echolocation but suspected to have a strong social component in more recent studies, and pulsed calls. Pulsed calls are the most frequently emitted type of sound and are themselves divided into several categories that are still under intense study: a)Discrete calls: these are pulsed calls that are steady or unchanged through time and specific to the pods. B) Aberrant calls: these are by definition mutated or varied forms from the discrete call types and c)Variable calls: which are signals that cannot be classified in the same manner as the previous two categories but are related by human listeners to the equivalent of "squeaks, trills and squawks" (Ford, 1989) This last class, the variable calls, are characterized by very fast alterations in frequency and could be attributed, as their parallels in human speech, the fast and unambiguous communication of emotion or serving the function of a "redundant" indicator of the emitter's affective state. In fact, a study by (Thomsen et al. in 2001a cited within Rehn et al., 2007), identified 6 classes of variable calls, naming them from V1 to V6. Among these classes they identified what Ford described in 1989 as the "chatter call", which they labeled under the V4 class. Teichert and Thomsen's study in 2001 classified over 2,000 calls defining them by their contours (frequency vs. time graphs) and the fundamental frequency of each. They also found that more than 70% of these variable calls were used in sequences of analogous fundamental frequencies. They contemplated the possibility that these variable calls were a ranking system to indicate emotional states or "motivational variables". However, the study found no strong correlation between the size of the group and the amount of variable calls within a sequence and did not observe any behavioral preference for the use of these types of calls. If variable calls were indeed found to express instant and clear affective states, the lack of correlation between activity and timing for the use of this communication tool could indicate a relaxed social system that nurtures self expression and/or is highly receptive to the emotional states of its members (personal observation.)

Calls emitted by orcas seem to contain dual frequency elements, a low frequency named (LFC for low frequency component) and a higher frequency element or (HFC). The HFC seems to be more directional than the LFC (Watkins 1967, Ford and Fischer 1982) In "within-pod variation" studies of the calls emitted by different matrilineal units which Miller et al. abbreviated as MUs in 1999, the length of the terminal note at the end of the LFC of each call was found to carry most of the difference between the shared calls of a given pod. However, this study did not account for specific behavior during the sampling of the calls and did not mention a unification of the sampling for a specific behavioral activity across the pod. This study concluded that the particularities of the vocal repertoires of different pods of resident killer whales arise from the gradual divergence from the matrifocal unit over time.

Comparing the resident orca society to that of the transients that overlap with their home range but have discrete differences, both in their social fluidity and vocal activity, sheds some light into the possible reasons behind the evolution of these very stable matrifocal units and the relative difference in the matriarch's role in both societies as the cohesive element throughout generations. The radical difference in the prey choice between resident and transient communities dictate to a great extent the social fluidity, optimal group size and vocal activity level of each ecotype. Transient communities are smaller and more flexible or variable in their composition as they feed on marine mammals who are permanent residents of the coast. This means that they do not have to follow migration routes and adjust their prey choice by season, and, it also requires a different tactic for location of prey. Given the fact that marine mammals can detect/hear the echolocation clicks of their predator, transients rely on passive sonar techniques to locate their prey and stage a 'sneak attack'. Their social units have been observed to have variable compositions, from a mother and her offspring, to aggregations of adult females with no particular maternal relatedness; even adult males who generally travel alone have been observed joining other foraging groups on a temporal basis (Ford et al., 1998.) Contrastingly, residents' prey of choice, salmon, can only hear frequencies below400 Hz and is therefore 'deaf' to the sound of the orca's clicks. (Whitlow et al., 2004) The different foraging and hunting techniques specific to each prey choice could have a very strong effect in the stability of the resident orcas. Knowledge on the timing of the migrations, the location of the rivers and the coordination of the hunt itself for individual salmon or schools of fish carry specific demands on a group. Throughout the world, sophisticated hunting strategies that involve careful observation, progressive improvement of techniques (such as the ray-hunting technique of New Zealand Killer whales) fine group coordination and teaching to youngsters have been observed in killer whale societies who feed on marine mammals. No less sophistication or teaching traditions can be expected of fish-eating orcas, especially given the fact that salmon species have the capacity to reach burst/darting speeds of up to 22ft/sec (Design For Fish Passage at Roadway - Stream Crossings: Synthesis Report) and the fact that the highly evolved lateral line system in fish allows them to detect not only small water disturbances produced by their prey but movement in general (Coombs and Netten, 2006.) It is then expected that this highly sensitive system would allow them to detect, even with more accuracy, the much greater disturbance wave produced by a large orca in direct pursuit or "sneak" attack.

The amount of accrued knowledge required to live in highly unpredictable environments with seasonal and changeable food resources, coupled with the cognitive and emotional demands of living within and maintaining lifelong complex social bonds, make the niche for an individual or individuals as the receptacle of experiential and trans-generational knowledge a most needed role. The readily available bank of knowledge and reference the matriarchs and older whales in the matriline may provide for the group at a moment's notice may be invaluable. Navigating effectively and safely in increasingly noisier zones with high boat traffic to avoid collisions and loss of communication are also pressures and challenges that could possibly demand the rapid decision and moment to moment coordination of a leader in the group. Playback studies on African elephant societies (*Loxodonta Africana)* have shown that the presence of older individuals with highly developed skills and accumulated knowledge to discriminate between social companions and or hazardous conditions or individuals may benefit the fitness of the group overall (McComb et al., 2001.) McComb's study also showed a decreased clustering tendency of the group as the age of the matriarch increased, which was interpreted as a greater vocal recognition network or greater group confidence in general for groups with older leaders. No direct agonistic behavior, at least from surface activities has been reported on resident killer whale societies; therefore, the immediate detection of danger or threat discrimination during an encounter that could be forewarned by a matriarch is not really an obvious advantage for these societies. However, the packed, army like formation and incredible coordination of the J2 matriline observed during their encounter with the L pod on October of 2005, reveals an enormous amount of information regarding the importance of the family unit and the presentation of a "cohesive front" in the presence of a strange or unfamiliar competitor. Even though J's and L's are often spotted nearby each other and some males frequent different pods, the fact that they often socialize does not exclude the fact that each pod, and matrilines within a pod, directly compete with each other for the same resource. Extraordinary events such as this one open a window into the importance of a coordinating/organizing leader in resident killer whale societies and validate the importance of detailed studies into the social dynamics and hierarchy of matrilines, groups and pods.

Killer whales exhibit one of the longest life-spans in the animal world. While no clear support for the evolutionary advantage of post-reproductive or menopausal females in a group has been established so far, Ward et al., in 2009 demonstrated an increased calf survival for older mothers equivalent to 10% and a direct benefit in recently weaned-off calves derived from 'grandmother care." This finding indirectly supports the "The Helpful Grandmother Hypothesis", which supposes that the presence of older grandmothers directly improve the group's inclusive fitness by aiding mothers, who, in turn, increase their fecundity rates, decrease birth intervals and possibly extend their life-expectancy. Even though resident killer whale matrilines have been identified by the oldest known female with direct descendants in the group, the "matriarch leader role" of the female in the lead may not be necessarily performed by the oldest living "grandmother" in the group. As the ratio between age and knowledge/fitness increases, or, in other words, as the leader gets "too old and slow" to lead the role may be passed on to the next female in the chain.

The benefits and energetic costs of social aggregations determine the size of the group in fission-fusion societies. Decreasing the effects of resource-competition within a unit in fission-fusion societies is accomplished by temporal divisions during periods of resource scarcity while the opposite is observed when the benefits of aggregation and sociality are high and the energetic costs of such aggregations are low (Devore & Washburn 1963, Kummer 1968, Dunbar 1992 and Kummer 1995.) However, resident killer whale societies do not seem to exhibit any unit split of the matriline group at any moment throughout their life, with the exception of temporary elapses here and there. This phenomenon poses very interesting questions regarding the benefits of their group foraging habits and the great value and adaptive advantage they derive from the protection, learning, cooperative hunting and social interactions of their group system.

Observation and analysis of the footage and audio files of the "Ceremony" meeting between J2 matriline and the L pod, (Beam Reach, 2005) mentioned above, reveal fascinating clues to the importance of group cohesiveness and coordination in the face of unknown or potentially dangerous conditions. During this event, the J2s are observed travelling tightly packed in an army-like formation with the youngest calf in the center, without submerging their dorsal fins for several minutes. After a highly vocal introduction filled with S2 type calls, one of the females in the group performs a sudden tail slap and the formation breaks down to start a vocal frenzy with a different call/sound composition than the period prior to the slap event. The same coordinated behavior was observed when boats crowded over a tightly traveling group in the northern part of the Haro Strait. This behavior was observed in two occasions, in which the whole group went underwater for several minutes to emerge later at an unexpected location with the males segregated to the sides over 50 meters in distance to the central group (personal observation.) These findings have prompted my attention to the possible role of "percussive" -tail slaps in particular, in the coordination of behavioral changes or responses, and the further possibility of relating these behaviors to the matriarchs. Considering tail slaps as active communication tools requires the consideration of the following premise: the active space of a slap used for communication and/or to incite a behavioral change/warning, etc. must be wide enough and distinct enough to be effective. Tail slaps and "percussives" in general are energetically expensive but they cover an enormous frequency range instantaneously. Examples from a few selected slaps have shown frequency ranges from 13 kHz to 1.9 kHz, 14.9 kHz to 2.18 KHZ, and from 24 kHz to 5.6 kHz.

Other studies on cetaceans suggest that "percussives" may have the capacity to transmit motivation or intention as well as directional information on travel or location of an individual. It is also thought that non-vocal percussive signals are useful in communicating information within a smaller active space than a call which can be a useful tool when transmitting specific info to group members in the vicinity but not to other conspecifics present in the area, who could directly compete for prey (Lusseau, D., 2006.) It has also been shown that females and male killer whales have slightly different strategies to avoid crowding vessels, both genders becoming less predictable in their paths and increasing their angle of deviation. Females, in particular, tend to increase their swimming speed by 25% and their angle of deviation, making their paths more erratic, while males tend to increase their swimming speed when boats are closer but to decrease it when then number of vessels is increased. It was also observed that the rate of surface behaviors, "percussives" included, increased as the number of vessels increased and that vessel avoidance behaviors by killer whales resembled prey-predator avoidance strategies observed in other species (Williams, R. et all, 2001.) This is consistent with the observed "percussives"/vessel number and distance, and also with the idea that under noisy, heavy traffic and close vessel conditions, instantaneous, wide range signals may well be an active tool to coordinate behavior or to "gather everyone else's attention."

Examination on highly cognitive social functions such as grieving (Rose, 2000a), observed in killer whales along with the apparent differential importance of certain matrilines within the pod or clans following targeted removals from the population (Williams et al., 2006) need to be examined further, as they may reflect important affective behaviors within the group in relation to the loss of a matriarch, thus elucidating some cues into the relevance of their role in the lives of resident killer whales.

This study would aim to answer or give an initial understanding to the following questions: Are matriarchs playing an active leadership role in the matriline and is this reflected in their vocalizations and/or "percussives"? Are matriarchs coordinating collective or coordinated behavioral changes with some type of vocal lead or percussive? Is there an optimal age range in which the physical fitness/experience ratio determines the maximum time or age during which a matriarch is an active leader or decision maker? If the matriarch is indeed an essential leader in resident killer whale societies and her survival or prolonged presence directly increases the group's fitness and survival in general, then strategies to protect these individuals from selective removal and efforts to reduce stress or risk to these females may be implemented. Establishing their importance as leaders can also shed a light into the transcendence of trans-generational knowledge transmission, the value of such an evolved strategy in the cementation of a species as a top predator, and, the direct impact of central leadership in the longevity and general success of a species.

For this study, opportunistic focal follows of identified matriarchs will be performed. Detailed records for the group composition will be recorded. Acoustic focal follows and pin-point observations of surface-behavior prior to and during the initial period of the new behavior will be recorded carefully to be able to determine the extent of the participation of the matriarch in initializing and/or coordinating rapid behavioral changes. Her choice of calls, sequence structure and/or other sounds must be then compared to those recorded for the general population prior to and post the behavior change event. The context and characteristics of percussives performed by older males and other individuals will also be recorded and analyzed. Special attention will be paid to any event involving encounters between 2 or more matrilines by carefully observing the roles or behaviors of the matriarchs involved, especially during the initial period following the encounters.

Experimental Design and Methods

This study expects to find a distinct difference in the behavior, vocal repertoire and/or communication tools used by the matriarchs to lead or coordinate behavioral change bouts. These leading behaviors are expected to be more pronounced or observable under stressful or hazardous conditions (e.g.: heavy boat traffic and/or approaching vessels presence) and under unexpected or unusual conditions such (e.g.: approaching different pods or groups in the area).

General Procedure:

Initial Data Collection:

a) Acoustic Recordings: To record the vocalizations and percussive signals of the tail slaps, a composite of 5 hydrophones will be used. A first set of 4 LabCore Hydrophones with a peak frequency sensitivity of 5kHz (1,3,4 actively recording) organized in a linear array with fixed and measured distances (see table 1), will be deployed from the starboard-aft corner of the boat to troll behind the catamaran. A 5^{th} high frequency hydrophone, known as the CRT (Cetacean Research Technology), with sampling size of 194kHz-downsampled to 48khz for this experiment and a flat frequency sensitivity peak from 1kHz to 30kHz, will be trolled behind the boat off the port-aft corner. This 5 (4 active) hydrophone array with set distances across the y and x axis will maximize our possibilities for localization of the vocals as well as wide frequency coverage, ranging from calls to clicks, and covering the large frequency range of 'percussive" signals in the meantime. Hydrophones from the linear array are connected to two Sound Devices Recording units, ARJ and Cecil, organized in a master-slave configuration, where ARJ is the top and master unit that controls the recordings. The hydrophones will be connected to each channel in the following manner and with the following gain settings: H1-channel 1 (gain 43.5dB), CRT-channel 2 (gain 37.3dB), H3-channel 3 (43.5 dB) and H4-channel 4 (43.5 dB).

b) Relative location and distance estimation of whales to boat. (Note: the stern of the boat will be used as the reference point): On a separate data sheet, the location of the individual whales and/or groups will be noted in a clock-wise fashion, using the boat as the center, the bow sprit as 12 clock and the center of the stern as 6 clock. Notes on types of vocals heard such as clicks and calls will be noted along with general behavior. Occurrence of aerial displays and "percussives" will be recorded as they occur along the recording. The distance to the focal animals and/or groups will be estimated both visually, with the aid of a range finder (Newcon Optikc x9; LRM 2000PRC) when possible and/or with calculations derived from the focal length measurements of each photograph, using the information provided on each image file. This will be done in the following manner: Firstly, a photograph of an object of known dimensions at a known distance will be taken to calculate a scale factor between actual size and image pixel size for a particular focal length. Secondly, estimating the dorsal fin size of the whale in question (aided by available size data/individual), we will proceed to count the height in pixels of the dorsal fin in the photo. Once this is measured, an equivalent in meters will be obtained from the height in pixels by multiplying by the H meters/h pixels factor calculated in the previous step. All the information will be then entered into a simple equation to calculate the distance to the target (dorsal fin): *R (distance)=(H fin/h meters camera)x (focal length)*

c) Specific behavior of focal individuals and group in general will be recorded in 5 minute intervals on a separate data sheet. Special behaviors and group spread will be recorded for later analysis.

d) Identification of individuals: Photo Id of each focal individual and the general group composition will be performed when distance and weather conditions allow. For this study, a Canon EOS with a zoom lens of 70-300mm (macro 1.5m/4.9ft) and image stabilizer technology will be used to perform the photo-identification. The camera will be time-synchronized with the recording units to accurately document the events in time and to later aid in the adjudication of an Id to the focal animal. Correlations between vocal localizations and documented images will be then performed to validate the results obtained from Ishmael.

Data Processing and Analysis:

a) The physical characteristics of the acoustic recordings will be initially analyzed using Audacity 1.3-Beta Unicode software. This program will be used to observe the spectrum of each signal (vocals and percussives), to determine their received levels, the SNR (sound to noise ratio) and to estimate the active space of each signal. Once this information is calculated for each signal of interest, a localization of each signal will be performed using Ishmael 2.0 software. Processing the data through these two programs will allow to quantify the acoustic environment pre and post the signal or the percussive event and to determine its importance and/or role, if any, in behavioral modulations. By identifying each individual who performs the behavior or emits the signal, a determination of whether matriarchs, and/or senescent females are at all leaders and/or leading this behavior or behavioral change under various conditions will be possible. Response to percussive events both in visible surface-behaviors and/or in vocalizations will be localized and analyzed as well. "Percussives" performed by males and juveniles will also be quantified and analyzed for comparison and to establish a possible distinction in context or in function, if existent.

b) Statistical analysis will be performed to establish the validity of the data and to determine relationship between variables. Possibly, a Chi Square test will be necessary since most of the variables measured are categorical in nature. For the measurement of the acoustic environment prior to a "signaling percussive" and the responses to such an event, a T-test or Anova test will be performed since the amount of noise or calls surrounding the behavior and the distance between the "slapper' and the "responder" will be considered.

Further examination of the experimental data upon acquisition will be needed to establish the best fitting statistical tests.

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