

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, which 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). In the Pacific Northwest, the resident killer whale population includes two communities composed of pods that regularly associate with one another (Ford et al. 2000). The southern residents' range extends from Puget Sound to the southern half of Vancouver Island, and northern residents are found from the northern half of Vancouver Island to southeastern Alaska (Ford et al. 2000). As of 1999, the combined resident population was comprised of approximately 300 whales (Ford et al. 2000). The southern resident community, on which this proposal focuses, has only one clan (J), which is composed of three pods (J, K, and L).

There are three types of killer whale vocalizations: clicks, whistles, and pulses (Ford 1989). Ford (1987) found that pulsed calls, the most common type of vocalizations, are often distinctive and repetitive, lending themselves to categorization. These sounds have a tonal quality and 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). Of the

44 southern resident discrete calls identified by Ford (1987), only four are used by all three pods; however, most discrete calls are used by at least two of the three pods. Some calls are more plastic than others and require sub-categorizations because of their subtle variations (Ford 1987; 1989).

Ford (1991) suggested that discrete calls are context-independent because they occur regardless of the activity in which the whales are engaged. However, nuanced variations within a specific discrete call can perhaps be attributed to an individual whale's emotional state (Ford 1991). 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 (Gouzoules and Gouzoules 2000). According to Morton's motivation-structural (MS) rules, animals use harsh, low frequency sounds in hostile situations and tonal, high frequency sounds in frightening, appeasing, or friendly situations. This primarily applies to sounds made when animals are close to one another (Morton 1977). While the MS rules hypothesis appears to make sweeping generalizations, Morton insists that the idea's value lies in its potential for cross-taxon applicability.

August and Anderson (1987) tested the MS rules hypothesis to

find out whether or not Morton's acoustic classifications would hold up to scrupulous investigation. Data from existing scientific papers was used to test Morton's MS rules. Analysis showed a correlation between harsh, low frequency sounds and hostile behavior with regards to frequency. However, sounds associated with fear, appeasement, and/or friendliness were randomly distributed in terms of both frequency and bandwidth (August and Anderson 1987). Overall, the investigators conceded that the acoustic design of close contact social vocalizations was loosely consistent with the MS rule hypothesis but highlighted the fact that further testing was necessary. The MS rule hypothesis has not yet been proven to apply to wild killer whales. The southern residents' tight-knight social structure and stable vocal repertoire make the population ideal for testing the application of Morton's hypothesis.

The discrete calls of the resident killer whale communities of Washington and British Columbia can be categorized into three groups: discrete, variable, and aberrant (Ford 1989). Discrete calls, as already mentioned, are fairly static in their structure but do sometimes exhibit subtle variations. Variable calls cannot be categorized and are not repetitive. Aberrant calls occur when a discrete call becomes modulated or distorted in structure (Ford 1989). It is possible that call distortion results from a conflict of behavioral states. If an animal has yet to reach a behavioral endpoint (hostility or

fear/appeasement/friendliness), its motives might not yet be clear enough to articulate (Morton 1977). There is evidence that killer whale calls reflect behavioral and emotional states of individual animals. Ford (1989) found that, when northern residents were engaged in behavior that could be interpreted as rough play or antagonism, their vocalizations became shortened and higher-pitched, accompanied by distinctive series of signals with rapid up-and-down pitch modulation. Similar calls were also recorded in the southern resident community (Ford 1989). Likewise, agonistic calls in aggressive situations have been recorded in captive studies (Graham and Noonan 2010), but these observations have not yet occurred in the wild.

In order to test Morton's MS rules hypothesis in the southern resident community, I propose to analyze individual variations in the most common southern resident vocalization, S1, within different behavioral contexts. I aim to categorize each S1 call or train according to its corresponding surface activity in the hopes of assigning meaning to slight variations in a single call type. If seemingly "friendly" or "appeasing" behavior coincides with a tonal, higher frequency S1 call and "hostile" behavior accompanies a harsher, lower frequency S1 call, then the MS rule hypothesis is correct.

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