Call Types and Acoustic Features Associated with Aggressive Chase in the Killer Whale (*Orcinus orca*)

Melissa A. Graham and Michael Noonan

Animal Behavior, Ecology, and Conservation, Canisius College, 2001 Main Street, Buffalo, NY 14208, USA;
E-mail: noonan@canisius.edu

Abstract

Instances of aggressive chase over a 5-mo period were investigated in captive killer whales (*Orcinus orca*). Such episodes were found to be quite rare, occurring only eight times in 1,872 h of observation. A consistent vocal pattern was found to be associated with agonistic episodes that differed markedly from the pattern recorded during non-aggressive, time-matched control periods. In general, vocalizations associated with aggressive chase were characterized by amplitude and frequency modulated pulses of approximately 190 ms in duration. In addition, three specific call types were found to occur only during chase events. As a whole, these particular call types and associated features are offered as an acoustic signature of agonism in the killer whale. It is hoped that these sounds might aid researchers in interpreting heretofore enigmatic killer whale vocalizations recorded from wild populations.

Key Words: agonistic, aggression, cetacean, acoustic behavior, vocalizations, killer whale, *Orcinus orca*

Introduction

Attempts to decode the functional significance of animal sounds often depend upon establishing correlations of those sounds with behaviors observed visually (Hurd, 1996; Crockford & Boesch, 2003). However, the efficacy of this approach depends on the availability of both visual and auditory channels for observation. This proves to be a particular challenge when studying cetaceans because much behavior occurs at depths where direct visual observations are not possible. Consequently, whale and dolphin studies conducted in the wild are usually limited to relating vocalizations to surface behaviors only (Weilgart & Whitehead, 1990; Henderson et al., 2009), and vocalizations often cannot be confidently linked to specific behaviors below the surface.

For example, in cataloging the vocal repertoire of killer whales (*Orcinus orca*) in the eastern Pacific, Ford (1989) described call features that were usually associated with excited behavioral states—that is, occasions in which fast erratic movements were observed. Ford speculated that some of these events might have been aggressive in nature, but it was impossible for him to be certain. This is unfortunate because agonistic interactions are among the most consequential of all behaviors, and understanding such events should be a high priority when investigating the social dynamics of any species.

Studies focusing on cetaceans in captivity have the potential to combine acoustic recordings with visual observations made through underwater viewing windows (Vergara & Barrett-Lennard, 2008). However, studies of this type have only rarely focused on agonistic events, and the few that have investigated such interactions have primarily concentrated on bottlenose dolphins (*Tursiops truncatus*) (Overstrom, 1983; McCowan & Reiss, 1995; Janik & Slater, 1998; Blomqvist & Amundin, 2004). To date, vocalizations positively associated directly with killer whale agonism have not been reported. In an effort to address this paucity of information, vocalizations made during aggressive chase episodes between two captive killer whales are described and discussed here.

Materials and Methods

The subjects of this investigation were a 20-y-old male and a 22-y-old female killer whale held in captivity at Marineland of Canada (Niagara Falls, Ontario). Both individuals had been wild-caught decades earlier in Icelandic waters (D. Perri, pers. comm., 1997). During the period of study, both animals were housed together in an 8 million liter pool, along with a 1-y-old juvenile male, who was their offspring.

Over a 5-mo period, simultaneous video and audio were recorded on a 24 h/d basis via underwater viewing windows and two in-pool hydrophones (Offshore Acoustics Model 97B). The daylight hours of these video recordings were subsequently screened for agonistic episodes

between the two adult orcas. Periods of aggression were defined by the occurrence of high-speed chase and rapid open-mouth approaches at the tail flukes and genital region of the killer whale being pursued (*cf.* Psarakos et al., 2003). The extreme speed of these events, combined with the dramatic evasive maneuvers and forceful tail fluke swipes by the pursued individual allowed for confident attributions of genuine aggression as opposed to a playful state.

All vocalizations (excluding clicks) during each period of aggressive chase and during 1-h "control" periods centered around the same times on days prior to the aggressive episodes were subjected to the same two-stage analysis. First, each vocalization was classified into one of 12 vocal categories/call-types (Figure 1). Second, each vocalization was assessed according to 13 acoustic dimensions (Table 1).

Results

Over the course of 1,872 screened hours, a total of eight instances of aggression were detected. These agonistic episodes lasted an average of 12.1 min. The episodes were separated by an average of 9 d (range: 0.5 to 28) during which the two animals returned to an apparently amicable coexistence. In all eight instances, it was the adult female that aggressively chased the adult male.

Each of the episodes was characterized by two distinct alternating behavioral patterns: brief periods of intense aggressive chase (AC), separated by less intense inter-chase intervals (ICI). AC periods were characterized by apparent bite attempts, very rapid swimming, and unmistakable evasive maneuvers on the part of the male. ICI periods were characterized by less intense swimming and apparent mutual avoidance. There were on average 10.5 AC periods per agonistic episode (range: 6 to 20), and the AC periods lasted an average of 7 s (range: 1 to 44). The ICI periods averaged 62 s (range: 1 to 642).

No aggressive behavior was observed during any of the time-matched control periods. In general, the killer whales' behavior on these days was characterized by low intensity socializing (e.g., swimming together) and/or ordinary pool exploration (e.g., interactions with enrichment toys). The differences between the agonistic days and the time-matched control days are summarized below.

Vocalization Rate
In total, 986 vocalizations were recorded during the 56.1 min derived from the agonistic episodes, and 2,839 vocalizations were recorded during the 480 min of time-matched, non-agonistic control periods. Thus, during times of aggression, the

whales vocalized an average of 0.32 calls/s compared to 0.10 calls/s during the non-aggression periods ($F(1,7) = 10.05$, $p < 0.01$) (Figure 2).

Call Type
Table 2 presents the proportion of each vocalization that occurred in the chase versus non-chase periods (as a function of all vocalizations in those same periods). In all, there were six calls (Call Types 01 to 06) that were recorded more frequently during chase episodes, and six vocalizations (Call Types 07 to 11 and Whistles) that occurred more frequently during the time-matched, non-chase periods (Chi-square tests, $p < .05$).

Acoustic Features
When pooled across call types, 12 of 13 acoustic features showed significant differences between chase and non-chase periods (Table 3). In general, the agonistic episodes were characterized by modulations in amplitude and frequency approximately every 190 ms that were not observed during the non-chase, time-matched control periods. They were also characterized by sidebands that had greater bandwidth. In addition, the agonistic periods were associated with greater variation on those same parameters within calls.

Table 4a & b present those same acoustic features as a function of chase/non-chase for each call type separately. Since three of the 11 call types occurred only during chase periods, and some features were not applicable to every call type, approximately 34% of the feature-by-call-type cells in this table did not yield comparisons. Among the 95 call-type/feature combinations that were applicable and recorded under both conditions, 43% showed significant differences between the chase and non-chase conditions. The specific direction and extent of these differences varied from feature to feature across call types, but the preponderance and degree of rhythmic frequency modulation were the features that most consistently differentiated the two conditions. Figure 3 provides illustrative examples for Call Type 08.

Discussion

It is undoubtedly adaptive for animals to employ unambiguous signals during highly consequential events like agonistic interactions. This was first articulated by Darwin (1872) when he described the Principle of Antithesis by which opposing signals come to take divergent forms. The acoustic patterns documented in the present study for agonism in killer whales appear to conform to that expectation in that they are highly distinctive in at least three ways. First, vocalizations were found to be more frequent during agonistic episodes. Second,
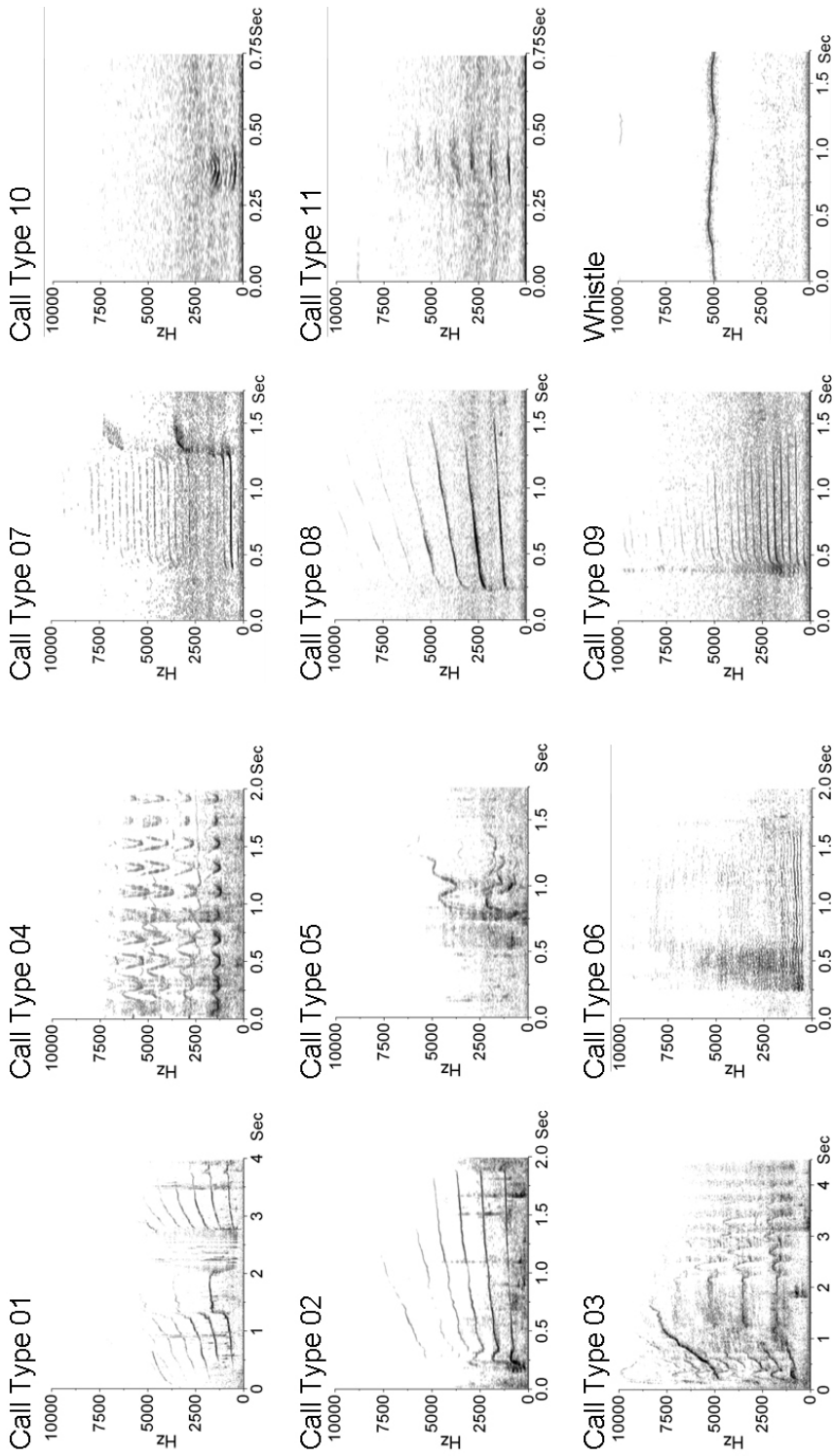
Figure 1. Vocalizations recorded at Marineland of Canada during agonistic and non-agonistic episodes

Table 1. Description of acoustic features used to analyze pulsed calls

	Feature	Defined as	Measured by
Time-dependent features	Length	Overall call length	In ms
	Number of segments	Number of portions separated by distinct inflection points	Manually counted from spectrogram
	Overall amplitude variation	Extent of amplitude variation from lowest value to highest value	Subjectively scaled 0-5 (5 = max)
	Rhythmic amplitude modulation	Extent of successive amplitude bursts across 50-250 ms time scale	Subjectively scaled 0-5 (5 = max)
	Average slope	Average line slope of lower ½ of all visible bands	Calculated from spectrogram
	Preponderance of Rhythmic Frequency Modulation (RFM)	Extent of successive frequency fluctuations across 50-250 ms time scale	Subjectively scaled 0-5 (5 = max)
	Variation in RFM	Extent of RFM variation from lowest value to highest value over time	Subjectively scaled 0-4 (4 = max)
Frequency-dependent features	Number of harmonics and sidebands	Number of visible bands	Manually counted from spectrogram
	Average distance between 2nd and 3rd sidebands	Average vertical distance between 2nd and 3rd visible bands	Calculated from spectrogram, in Hz
	Degree of RFM	Overall size of RFM	Subjectively scaled 0-5 (5 = max)
	Slope differences among sidebands	Average slope of top ½ of visible bands minus average slope of bottom ½ of visible bands	Calculated from spectrogram
	RFM differences among sidebands	Difference in RFM between top ½ of visible bands and bottom ½ of visible bands	Subjectively scaled 0-4 (4 = max)
	Frequency range within sidebands	Characteristic bandwidth in lower ½ of visible bands	Subjectively scaled 0-5 (5 = max)
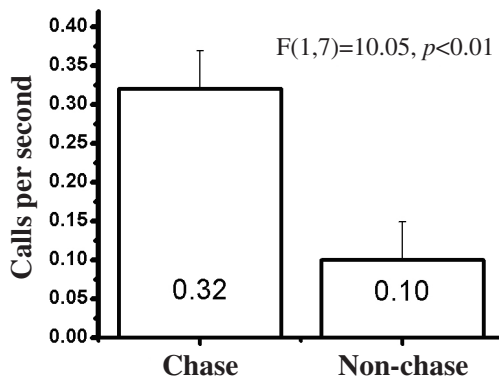
Figure 2. Vocalization rate—chase vs non-chase periods ± standard error

$F(1,7)=10.05$, $p<0.01$

the overall proportion with which each call type was produced differed dramatically between the aggressive and control periods. Third, the average acoustic features were markedly different during times of aggression. Together, these differences make the calls associated with killer whale agonism readily recognizable when compared to those made during non-agonistic periods.

Upon examination of the calls, it can be asked whether the vocal differences between chase and non-chase stemmed from features which were added onto vocalizations that were already in the normal-state behavioral repertoire of these animals or whether they derived from categorically different call types that were uniquely produced during agonistic exchanges. The evidence suggests that both occurred.

On the one hand, the juxtaposition of calls depicted in Figure 3 suggest that one is merely a modified version of the other—that is, the same harmonics and sidebands with additional frequency and amplitude modulations in the case of agonism. Thus, for at least some call types, the vocalizations during chase did appear to be modified versions of otherwise similar, non-chase calls (amplitude and frequency modulations being superimposed upon them). Ford (1989) previously reported that similar modifications of familiar calls also occasionally occur in the wild, referring to them as aberrant calls. An analogy to tone of voice in humans might be appropriate here. In humans, vocal features can signal changes in emotional content even in conditions when the same specific words are produced (Wurm et al., 2001). Perhaps such variations in frequency and amplitude will prove to be universal characteristics of agonism in killer whales in the same way that tone-of-voice

Table 2. Proportion of call types produced by killer whales at Marineland of Canada during chase (C) and non-chase (NC) periods

Call type/ Vocal category	Proportion		Chi square
	C	NC	
Call Type 01	0.01	0.003	$\chi^2(1) = 19.2$ $p < 0.001$
Call Type 02	0.09	0.00	$\chi^2(1) = 279.8$ $p < 0.001$
Call Type 03	0.13	0.004	$\chi^2(1) = 371.7$ $p < 0.001$
Call Type 04	0.08	0.00	$\chi^2(1) = 256.2$ $p < 0.001$
Call Type 05	0.05	0.00	$\chi^2(1) = 154.9$ $p < 0.001$
Call Type 06	0.15	0.12	$\chi^2(1) = 7.6$ $p < 0.01$
Call Type 07	0.02	0.16	$\chi^2(1) = 165.3$ $p < 0.001$
Call Type 08	0.02	0.18	$\chi^2(1) = 179.4$ $p < 0.001$
Call Type 09	0.04	0.05	$\chi^2(1) = 6.0$ $p < 0.05$
Call Type 10	0.01	0.03	$\chi^2(1) = 9.0$ $p < 0.001$
Call Type 11	0.03	0.08	$\chi^2(1) = 32.3$ $p < 0.001$
Whistle	0.01	0.14	$\chi^2(1) = 172.2$ $p < 0.001$

Table 3. Acoustic features of killer whale vocalizations during chase (C) and non-chase (NC) periods

	Feature	C	NC
Time-dependent features	Length	0.81	0.93 *
	Number of segments	2.17	2.72 **
	Overall amplitude variation	1.06	0.44 **
	Rhythmic amplitude modulation	1.97	0.08 **
	Average slope	0.73	0.39 **
	Preponderance of Rhythmic Frequency Modulation (RFM)	3.03	0.48 **
	Variation in RFM	0.65	0.04 **
Frequency-dependent features	Number of harmonics and sidebands	5.70	8.77 **
	Average distance between 2nd and 3rd sidebands	911	786 **
	Degree of RFM	2.38	0.33 **
	Slope differences among sidebands	1.46	1.41 ns
	RFM differences among sidebands	1.35	0.33 **
	Frequency range within sideband	2.04	1.41 **

ANOVAs *$p < 0.01$; **$p < 0.001$

connections with emotions are rather universal in humans. In 1989, Ford appeared to anticipate that possibility by noting that what he described as the excitement call was heard across a number of killer whale pods.

However, in other instances, the findings of this study appear to provide evidence that killer whales also produce some categorically different calls during agonism. For three call types in particular (Call Types 02, 04, and 05), there was not a single instance of them being recorded during any of the time-matched, non-aggression control periods. Thus, at least those call types might be functionally associated with aggressive events specifically.

In past studies of wild orca vocalizations, very few call types show features similar to those documented here during chase events (i.e., modulations occurring approximately every 190 ms). In addition to Ford's (1989) description of such features in excitement calls, Rehn et al. (2007) described a V4 category of vocalizations that (1) had similar acoustic features and (2) were also associated with close-range socializing that was speculatively agonistic or playful in nature. If

frequency and amplitude variations of the type reported here and by Ford and Rehn et al. are truly characteristic of agonistic behavior, the low rate of occurrence of aggression for the pair of adult killer whales in the present study is compatible with a view that inter-animal aggression is generally rare in this species. Their rate of agonism was certainly lower than that which has been recorded for captive bottlenose dolphins (Overstrom, 1983; Samuels & Gifford, 1997; Weaver, 2003). A similar observation regarding the rarity of intraspecific aggression in killer whales was made by Wiles (2003). Jacobsen (1986) presented the alternative point of view that killer whale aggression must be somewhat common based on the number of rake mark scars observed on wild orcas. However, rake marks are at best only an indirect index of aggressiveness, and even the number of rake marks observed on killer whales is far fewer than those observed on some other cetacean species (e.g., Rizzo's dolphin, *Grampus grisseus*) (Würsig & Jefferson, 1990). As more data are collected, it will be interesting to determine whether the rarity

Table 4a. Acoustic features by call type—chase (C) vs non-chase (NC) periods for call types produced in greater proportion during chase. Comparisons that were not significantly different are denoted with "ns."

Feature	Call Type 01 C	Call Type 01 NC	sig	Call Type 02 C	Call Type 02 NC	Call Type 03 C	Call Type 03 NC	sig	Call Type 04 C	Call Type 04 NC	Call Type 05 C	Call Type 05 NC	Call Type 06 C	Call Type 06 NC	sig
Time-dependent features															
Length	2.67	2.28	ns	1.16	--	1.99	1.68	ns	0.84	--	0.50	--	0.82	1.21	***
Number of segments	6.41	8.13	ns	3.19	--	3.61	4.15	ns	1.21	--	1.73	--	1.13	9.33	**
Overall amplitude variation	1.47	0.88	ns	0.98	--	1.72	1.46	ns	1.20	--	1.11	--	0.30	1.00	ns
Rhythmic amplitude modulation	1.18	0.13	ns	0.86	--	2.87	0.00	***	4.16	--	3.66	--	0.40	5.00	**
Average slope	0.44	0.81	*	1.06	--	0.92	0.89	ns	0.34	--	0.61	--	0.00	-0.25	*
Preponderance of Rhythmic Frequency Modulation (RFM)	2.76	0.38	**	3.08	--	3.83	1.69	***	4.93	--	3.14	--	--	2.50	--
Variation in RFM	0.76	0.13	ns	0.41	--	1.35	0.23	**	0.90	--	0.20	--	--	0.00	--
Frequency-dependent features															
Number of harmonics and sidebands	6.59	9.75	***	5.99	--	5.40	7.54	**	5.82	--	3.98	--	--	45.00	--
Average Distance between 2nd and 3rd sidebands	947	1,113	*	1,050	--	1,105	1,230	ns	848	--	927	--	--	100	--
Degree of RFM	1.94	0.13	**	1.76	--	3.29	1.46	***	4.35	--	3.05	--	--	0.50	--
Slope differences among sidebands	1.59	2.25	*	1.74	--	1.87	2.00	ns	1.02	--	0.73	--	--	1.00	--
RFM differences among sidebands	1.59	0.63	ns	1.30	--	1.79	0.77	**	2.34	--	1.00	--	--	0.00	--
Frequency range within sideband	2.47	1.75	ns	1.79	--	2.88	2.69	ns	2.14	--	2.55	--	--	2.00	--

ANOVAs $*p < 0.05$; $**p < 0.01$; $***p < 0.001$

Table 4b. Acoustic features by call type—chase (C) vs non-chase (NC) periods for call types produced in greater proportion during non-chase. Comparisons that were not significantly different are denoted with "ns."

Feature	CT07 C	sig	CT07 NC	CT08 C	sig	CT08 NC	CT09 C	sig	CT09 NC	CT10 C	sig	CT10 NC	CT11 C	sig	CT11 NC
Time-dependent features															
Length	0.59	ns	0.65	0.85	ns	0.98	0.67	***	1.05	0.22	*	0.29	0.13	ns	0.12
Number of segments	2.53	ns	2.74	1.71	***	2.83	2.44	ns	2.62	1.56	ns	1.62	1.12	ns	1.06
Overall amplitude variation	0.47	ns	0.35	0.46	ns	0.52	0.56	*	0.32	0.44	**	0.14	0.08	ns	0.20
Rhythmic amplitude modulation	0.05	ns	0.02	0.60	***	0.08	0.03	ns	0.03	0.00	ns	0.00	0.00	ns	0.00
Average slope	-0.25	ns	-0.12	0.99	ns	0.88	0.61	***	0.25	0.40	**	-0.16	0.70	ns	0.22
Preponderance of Rhythmic Frequency Modulation	0.68	*	0.19	1.60	***	0.64	0.85	*	0.28	0.13	*	0.06	0.50	*	0.00
Variation in RFM	0.00	ns	0.00	0.09	ns	0.04	0.00	ns	0.01	0.00	ns	0.00	0.00	ns	0.00
Frequency-dependent features															
Number of harmonics and sidebands	7.32	*	12.00	3.63	***	5.62	9.47	*	11.85	5.88	ns	9.65	4.20	ns	5.10
Average distance between 2nd and 3rd sidebands	317	ns	331	1,156	*	1,341	447	***	365	319	*	261	611	ns	737
Degree of RFM	0.42	*	0.11	1.14	***	0.46	0.56	**	0.17	0.06	ns	0.01	0.10	*	0.00
Slope differences among sidebands	1.28	ns	1.35	1.42	ns	1.50	1.15	ns	1.05	0.88	ns	1.28	0.78	ns	0.68
RFM differences among sidebands	0.33	ns	0.17	0.67	ns	0.40	0.56	ns	0.42	0.00	ns	0.06	0.00	ns	0.00
Frequency range within sideband	0.95	ns	1.07	0.89	***	1.64	0.24	ns	0.37	2.06	*	0.96	3.18	ns	2.87

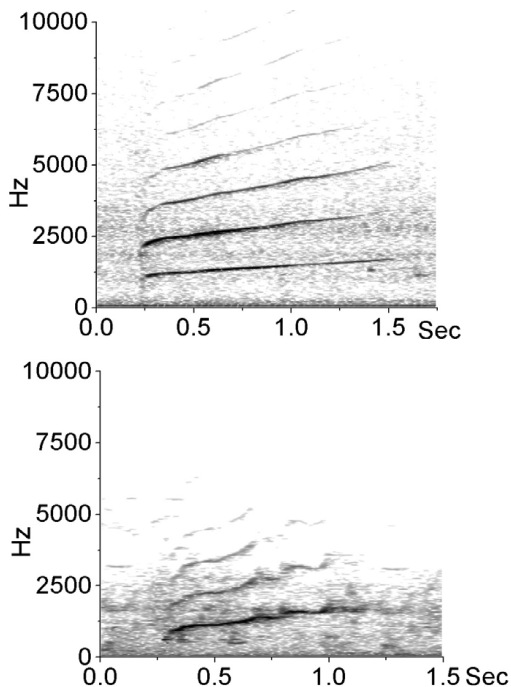ANOVAs *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Figure 3. Spectrogram of Call Type 08 during non-chase period (upper) and during chase period (lower)

of aggression documented in the present study is characteristic of this species generally and where killer whales rank on aggressive tendencies when compared to other species of cetacean (MacLeod, 1998).

It is certainly noteworthy that in all eight episodes of aggression investigated here, it was the adult female who chased the adult male rather than the reverse. This gender difference was particularly striking since the male was approximately twice the weight of the female. Whether a sex difference in aggressiveness proves to be merely unique to this pair or more generally characteristic of this species will be an important question to address in future investigations. Killer whales have been reported to have a matrilineal social structure (Bigg et al., 1990; Baird, 2000). If they can also be said to be matriarchal, the sex difference in this pair of animals could be viewed as compatible with the expectation that females would have dominance.

Independent of that question, it should not be implied here that the unique acoustic features associated with the agonistic exchanges between these two killer whales were specifically or uniquely associated with the aggressor per se. It is important to note that sounds associated with any given agonistic exchange are likely to include vocalizations emanating from both of the two

antagonists. Thus, they might well reflect a variety of motivational states, including antagonism, submission, distress, and so on (Scott, 1966).

During aggressive chase episodes, the two animals in the present study were usually in such close proximity that it was rarely possible to confidently discern the identity of the vocalizing whale. However, in some cases, the release of bubble streams from the male's blowhole occurred with such perfect simultaneity with the production of vocalizations that attribution of those calls to the male seems reasonable. Call Types 02, 03, and 04 (Figure 1) are examples of vocalizations that were associated with the male in this way. Thus, it is highly likely that at least some of the calls reported here were produced by the non-aggressor, and, if so, they might have been signaling either subordination or distress.

Morton (1977) argued that animals showing fear or appeasement often emit calls characterized by rising frequencies. In this light, it is worth noting that the average spectrographic slope of calls recorded during chase was significantly greater than that calculated for non-chase (see row five in Table 3). This is consistent with a view that at least some of the calls were reflective of distress or subordination. However, the following two anecdotal accounts suggest an alternative explanation. First, on occasions when the seaquarium pools were drained in order to "beach" the whales for veterinary examinations/procedures, the animals did not characteristically produce Call Types 02, 03, or 04 despite the fact that they did vocalize frequently at such times and that they were presumably under distress. Second, there have been occasions in which the male was housed in a pool alone and was observed to engage in a mock attack of an enrichment toy (i.e., occasions in which he vigorously bit at a large plastic object while rapidly twisting his body to deliver repeated head, pectoral fin, and fluke blows to the object); at such times, he always produced Call Type 04. In other words, each time he engaged in what looked like aggression targeted at an inanimate object, the male was observed to produce the identical calls that he made during episodes in which he was being chased by the adult female.

Since the present report is based upon only two animals and derives from observations made in captivity, the extent to which these findings can be generalized to free-ranging whales remains to be determined. Nevertheless, the calls and acoustic features reported here are tentatively offered as comprising the acoustic signature of agonism in the killer whale. As such, these findings supplement and support those of Morton et al. (1986), Ford (1989), and Rehn et al. (2007) in documenting the ways in which killer whales modify their

vocalizations to reflect their emotional state. It is hoped that these findings will aid future researchers when interpreting potentially enigmatic vocalizations from acoustic recordings of killer whales in the wild. If similar calls can be confirmed for other populations, perhaps it will be possible to assess the frequency and duration of aggression in wild populations primarily by monitoring recordings for the calls and acoustic features described here.

Acknowledgments

Literature Cited

Baird, R. W. (2000). The killer whale foraging specializations and group hunting. In J. Mann, R. C. Connor, P. L. Tyack, & H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 127-153). Chicago: University of Chicago Press.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission*, *12*, 383-405.

Blomqvist, C., & Amundin, M. (2004). High-frequency burst-pulsed sounds in agonistic/aggressive interactions in bottlenose dolphins, *Tursiops truncatus*. In J. A. Thomas, C. F. Moss, & M. Vater (Eds.), *Echolocation in bats and dolphins* (pp. 425-431). Chicago: University of Chicago Press.

Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: Analysis of barks. *Animal Behaviour*, *66*, 115-125.

Darwin, C. (1872). *The expression of emotions in man and animals.* London: John Murray.

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, *67*, 727-745.

Henderson, E. E., Hilbrand, J. A., & Wiggins, S. M. (2009, July). Behavior and vocalizations of Pacific white-sided dolphins *Lagenorhynchus obliquidens*. Proceedings of the 46th Annual Meeting of the Animal Behavior Society, Pirenopolis, Brazil.

Hurd, C. R. (1996). Interspecific attraction to the mobbing calls of Black-capped Chickadees (*Parus atricapillus*). *Behavioral Ecology and Sociobiology*, *38*, 287-292.

Jacobsen, J. K. (1986). The behavior of *Orcinus orca* in the Johnstone Strait, British Columbia. In B. C. Kirkevold

& J. S. Lockard (Eds.), *Behavioural biology of killer whales* (pp. 135-185). New York: Alan R. Liss.

Janik, V., & Slater, P. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, *56*, 829-838.

MacLeod, C. D. (1998). Intraspecific scarring in odontocete cetaceans: An indicator of male "quality" in aggressive social interactions? *Journal of Zoology*, *244*, 71-77.

McCowan, B., & Reiss, D. (1995). Maternal aggressive contact vocalizations in captive bottlenose dolphins (*Tursiops truncatus*): Wide-band, low-frequency signals during mother/aunt-infant interactions. *Zoo Biology*, *14*, 293-309.

Morton, A. B., Gale, J. C., & Prince, R. C. (1986). Sound and behavioural correlations in captive *Orcinus orca*. In B. C. Kirkevold & J. S. Lockard (Eds.), *Behavioural biology of killer whales* (pp. 303-333). New York: Alan R. Liss.

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *The American Naturalist*, *111*, 855-869.

Overstrom, N. A. (1983). Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (*Tursiops truncatus*). *Zoo Biology*, *2*, 93-103.

Psarakos, S., Herzing, D. L., & Marten, K. (2003). Mixed-species associations between Pantropical spotted dolphins (*Stenella attenuata*) and Hawaiian spinner dolphins (*Stenella longirostris*) off Oahu, Hawaii. *Aquatic Mammals*, *29*(3), 390-395.

Rehn, N., Teichert, S., & Thomsen, F. (2007). Structural and temporal emission patterns of variable pulsed calls in free-ranging killer whales (*Orcinus orca*). *Behaviour*, *144*, 307-329.

Samuels, A., & Gifford, T. (1997). A quantitative assessment of dominance relations among bottlenose dolphins. *Marine Mammal Science*, *13*, 70-99.

Scott, J. P. (1966). Agonistic behavior of mice and rats: A review. *American Zoologist*, *6*, 683-701.

Vergara, V., & Barrett-Lennard, L. G. (2008). Vocal development in a beluga calf (*Delphinapterus leucas*). *Aquatic Mammals*, *34*(1), 123-143.

Weaver, A. (2003). Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, *19*, 836-846.

Weilgart, L. S., & Whitehead, H. (1990). Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. *Behavioral Ecology and Sociobiology*, *26*, 399-402.

Wiles, G. J. (2003). *Draft Washington State status report for the killer whale.* Olympia: Washington Department of Fish and Wildlife.

Wurm, L. H., Vakoch, D. A., Strasser, M. R., Calin-Jageman, R., & Ross, S. E. (2001). Speech perception and vocal expression of emotion. *Cognition & Emotion*, *15*, 831-852.

Würsig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. In P. S. Hammond, S. A. Mizroch, & G. P. Donovan (Eds.), *Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters* (pp. 43-45). Cambridge, UK: International Whaling Commission.