Structural and temporal emission patterns of variable pulsed calls in free-ranging killer whales (*Orcinus orca*)

Nicola Rehn, **Stefanie Teichert & Frank Thomsen**[1)]
(Biozentrum Grindel, Universität Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany)

(Accepted: 5 February 2007)

Summary

Resident killer whales off Vancouver Island, British Columbia, produce variable burst pulsed calls most commonly during close-range interactions such as socialising or social-travelling. Earlier studies indicated that variable calls are graded and can be arranged into a scale from low-frequency calls to high-frequency ones. These graded calls are often emitted in sequences, were call-classes of similar frequency follow one another more often than different classes. However, a detailed analysis of sequences was lacking to date. Therefore, our understanding of the function of variable calls during interactions among killer whales is rather limited. Simultaneous recordings of underwater vocalizations and behavioural observations from resident killer whales were collected off Vancouver Island, British Columbia during 1996-2001. Socialising activities were divided into four categories: male-female, male-male, female-juvenile and juvenile-juvenile. Variable call sequences were analysed with RTS and SIGNAL acoustic-software. We found no positive correlation between group-size and number of used calls or the duration of sequences, indicating that only one or a few animals were involved in the production of each sequence. Furthermore, sequences were present in all four behaviour categories and the composition of the group had no influence on the duration of calls and used call-classes. One particular call class (V4) could be further separated into structurally distinct sub-classes. These sub-classes often formed rather stereotyped sequences. The results of our study indicate that sequences of variable calls emit broad motivational information that is not age or sex-related. Sequences of distinct sub-classes might encode more subtle information on emotional states during socialising. Therefore, variable calls might posses different functions, depending on the nature of the interaction. Thus, variable calls might be of great importance for close-range communication in wild killer whales.

---

1) Corresponding author's e-mail address: frank.thomsen@cefas.co.uk

Behaviour 144, 307-329
Also available online - www.brill.nl/beh

Introduction

Many social terrestrial mammals use acoustic signals to coordinate close-range interactions such as play, fight or mating. Most of these signals are designed to convey information about the affective state of the signaller, for example on its motivation or emotional state (review by Hauser, 1997; Owings & Morton, 1998). Studies on hoofed animals, terrestrial carnivores and primates have shown that many affective signals used in close-range signalling are graded (e.g., Green, 1975; Fox & Cohen, 1977; Gautier & Gautier, 1977; Marler & Tenaza, 1977; Goodall, 1986; Estes, 1991; Peters & Tonkin-Leyhausen, 1999; Robbins, 2000; Fischer & Hammerschmidt, 2002; Yin & McCowan, 2004). A graded signal system is characterised by continuous acoustic variation between and within related signal classes, with no obvious boundaries that allow a listener to discriminate easily between one signal type and another. Graded signals are thought to reflect gradual changes of motivation or emotion and therefore allow a subtle communication relating to the relatively high degree of behavioural complexity during friendly, but also during agonistic interactions (Marler, 1967, 1976, 1977).

Different from terrestrial mammals, the study of close-range signalling in cetaceans is still very much in its infancy. It has been noted that in several species signalling during social interactions is highly variable and perhaps graded. However, efforts to define structural categories in detail were limited (Caldwell & Caldwell, 1968; Ford & Fisher, 1978; Hermann & Tavolga, 1980; Clark, 1982; Overstrom, 1983; Sjare & Smith, 1986; Ford, 1989; Weilgart & Whitehead, 1990; Dawson, 1991; Brownlee & Norris, 1994). Recent studies on bottlenose dolphins (*Tursiops truncatus*; McCowan & Reiss, 1994; Connor & Smolker, 1996; Herzing, 1996, 2000; Blomqvist & Amundin, 2004; Blomqvist et al., 2005) and spotted dolphins (*Stenella frontalis*; Herzing, 1996, 2000) reported rather distinct vocal signals used in agonistic and affiliate contexts, some of them resembling affective signals used in primates.

Killer whales (*Orcinus orca*) off Vancouver Island, British Columbia produce whistles and burst pulsed calls in underwater communication. Calls can either be discrete or variable. Variable burst pulsed calls comprise a great variety of non-repetitive forms and are most commonly used during close-range interactions such as socialising or social-travelling (Ford, 1989; Thomsen et al., 2002). Ford (1989) described distinctive series of rather intense 'excitement-calls' with rapid up and down pitch modulation. He proposed that these and other variable calls are graded signals used to coordinate the various interactions of the whales during close-ranges. In a first systematic attempt to bring order into the many forms of variable calls in wild killer whales, Teichert (see Appendix) and Thomsen et al. (2001a) categorised more than 2000 variable calls into six structurally related classes that could be distinguished by contour characteristics and carrier frequency. These classes could be arranged into a graded scale from low-frequency calls to high-frequency ones. Over 70% of all variable calls were emitted in sequences, where those of similar carrier-frequency followed one another more often than different classes (see Appendix; Thomsen et al., 2001a). The results of the study indicate that variable calls in wild killer whales represent a graded system with the different call-classes probably indicating subtle variations in motivation. However, no study described the structural and temporal emission patterns of variable call sequences in more detail. For example, it was unknown how many senders contribute to the sequences. It was also not clear, if the emission of sequences is depending on group-composition. Finally, a structural classification of calls with the use of additional observers to replicate the results was lacking to date. Therefore, the function of variable pulsed calls in underwater communication among free-ranging killer whales was rather unknown.

In the present study, we are going to define structural and temporal emission patterns of variable pulsed calls in free-ranging killer whales. The analysis was based on recordings of underwater vocalisations and behavioural observations from resident killer whales collected off Vancouver Island, British Columbia during 1996, 1997 and 2001. We will define age and sex related correlates of call sequences and will look at the temporal pattern of specific call-classes in more detail. Based on the results, the possible function of variable pulsed calls for underwater communication in free-ranging killer whales will be discussed.

Materials and methods

Data collection and study population

The studied animals belong to the community of northern resident killer whales, which comprised at the time of the study about 220 animals in

33 matrilines (Ford et al., 2000). Simultaneous behaviour observations and underwater recordings were collected in 1996, 1997 and 2001. The field trips were undertaken with two commercial whale-watching companies based in Port McNeill and Telegraph Cove at the northern tip of Vancouver Island. We collected data from July 1st to October 13th 1996, from July 11th to October 13th 1997 and from July 18th to September 19th 2001. Free-ranging killer whales were observed on 245 field trips with a duration of 3-9 h. The individual whales were identified by their natural markings for example the shape of the dorsal fin and/or natural markings like scars and pigmentation of the saddle patch. Identifications were made with a binocular and confirmed by other whale watching companies and two land-based observation and monitoring stations. Identification pictures were also taken with a single lens reflex camera. After sighting and identifying the whales, the vessel was stopped at least 500 m ahead of them for the sound recordings and behaviour observations. The sounds were recorded with various equipment (hydrophone: Bruel and Kjaer 8101 in 1996, Offshore Acoustics in 1997 and a DEEPSEA Powerlight SM 1000 S/N 153 hydrophone in 2001; tape-recorder: Sony TCD-D8-DAT in 1996, Sony TCD-7-DAT in 1997, Sony audio cassette recorder (WM-D6C) in 2001; responses of the systems: 20 Hz to 18/20 kHz). During the recordings, the weather conditions, the number of animals, their position, their swimming direction and their behaviour were reported using the second channel of the recorder. A total of 283 sound recordings with a total duration of approx. 67 h were collected.

Behavioural classification

Since in northern resident killer whales, variable calls are mostly associated with close-range behaviours (Ford, 1989; Thomsen et al., 2002), only recordings of two behavioural categories, social-travelling and socialising (defined after Ford, 1989; Thomsen et al., 2002; Riesch et al., 2006), were analysed. While social-travelling the whales usually swim with a speed of 3-6 km/h. Some of the animals exhibit body contact and the distance between the animals is less than a body length (Thomsen et al., 2002). Often interactions like spy hopping, flipper and fluke slapping on the surface can be observed. During socialising the whales slow down, group up in clusters while engaged in various interactions (see Ford, 1989; Thomsen et al., 2002 for a detailed description). We additionally divided the close-range recordings into four categories depending on the predominant age and sex class involved: 1) juvenile-juvenile, 2) female-juvenile 3) female-male and 4) male-male interactions. Only such recordings were used where the behaviour of the majority of the observed animals could be placed clearly into one of the categories mentioned above. We also omitted recordings where more than one group was within the range of the hydrophone.

Initial identification of variable call-classes

The killer whale sounds were classified refering to Ford (1989) and Thomsen et al. (2001b, 2002) into whistles and pulsed calls using RTS Version RTSD-software (Engineering Design, Belmont, MA, USA; 150 kHz 16 bit A/D converter sample rate = 50 kHz, frequency range = 0-20 kHz, dynamic range = 42 dB, FFT size = 512 points, DT = 10.2 ms, DF = 98 Hz, overlap = 50%). Pulsed calls were divided after Ford (1989) in discrete, aberrant and variable ones. Discrete pulsed calls are stable over years and pod specific (Ford 1989, 1991). Aberrant calls include signals that are based on a discrete format, but are highly modified or distorted in structure. Variable calls cannot be separated into clearly defined structural categories. They comprise a great variety of forms like squeaks, trills and squawks (Ford, 1989). Based on real-time analysis of more than 2300 variable calls recorded during 1996-1999 six classes of variable calls – termed V1-V6 – were defined (Teichert, see appendix; Thomsen et al., 2001a). These classes could be separated by contour characteristics and parameters such as duration and bandwidth. However, call-classes were best distinguished by their carrier frequency with significant differences across classes (see Appendix).

Analysis of variable call sequences

As variable call sequences, a time-series of variable calls, separated by another by less than 10 s, was defined. The sequence should also not have been interrupted by discrete and aberrant calls, only when they were assumed to be given by other animals in the background. We selected 20 recordings from the years 1996, 1997 and 2001 with sequences of variable calls, which were not masked by boat noise and where we could clearly classify the behaviour in one of the four subcategories of close-range behaviour. A total of 98 sequences were printed on paper. For each sequence the number of calls was counted and each call was classified into the classes V1-V6 (see

Appendix). The duration of the sequences was measured on-screen and the number of animals present during the recording was also noted in regard to the simultaneous behavioural observations (see above). The correlation between duration of the sequence, the number of calls within a sequence, as well as the number of animals present in recording range (=500 m; see Miller, 2006 for active space of variable calls) were tested with a Spearman rank-order procedure (Zar, 1996). The duration of sequences and number of calls in a sequence across the four group compositions was tested using a one way ANOVA on ranks (H-test, Kruskal-Wallis). If means differed, a multiple comparison (Dunn's method) was performed (Zar, 1996). Very early in the study, we noticed that two main classes of sequences existed: regular sequences in which structurally similar or nearly identical calls followed one another and random sequences composed of structurally different classes of variable calls (see Appendix; Thomsen et al., 2001a). Each of the 98 sequences was assigned to either one of these categories.

Analysis of the V4 call

For a detailed structural analysis, we chose the 'chatter' call or V4 (see Appendix; Thomsen et al., 2001a) since this was the predominant call-class in the sequences. This call described previously by Ford (1989) as 'excitement call' is characterised by rapid frequency modulations (see Appendix). Sequences containing the V4 call-class were inspected and sub-classes were visually classified depending on differences in spectrographic contour. A subset of 20 calls of each class was selected and following parameters were measured on-screen: start frequency of sideband interval end frequency of sideband interval minimum frequency, maximum frequency (kHz), duration (s) and number of frequency modulations. We used a subset of 63 chosen sub-classes of the V4 call to confirm our initial classification of the categories after a method developed by Janik (1999; see also Riesch et al., 2006 for further details). Spectrograms of the variable V4 calls were calculated using Raven Lite Version 1.0 (DF = 48.8 kHz, DT = 20.5 ms, FFT = 1024 points). All calls were printed on separate sheets of 14.8 × 21 cm in size. Six additional observers were asked to classify the calls independently by their shape. Spectrograms were presented in a random order and the observers were asked to categorise the calls in as many categories as appropriate to them. We then used Kappa statistic to test for interobserver reliability

(Siegel & Castellan, 1988). Finally, we classified each V4 call and developed a transition frequency matrix to analyse transitions of calls within the sequences.

Results

Variable call sequences in northern resident killer whales

A total of 642 variable calls were found in the 98 sequences that could be classified as follows: V1, 28 (4.4%); V2, 55 (8.6%); V3, 42 (6.5%); V4, 325 (50.6%); V5, 147 (22.9%); and V6, 45 (7.0%). The V4 call was the predominant call in these recordings. The mean duration of the sequences was 7.61 s (± 6.99 SD, range = 1.01-37.25 s). Per sequence the animals emitted a mean of 6.16 ± 4.62 calls. The number of calls in the sequences varied between 2 and 28. We found no positive correlation between group size and the duration of sequences (Spearman rank-order correlation, $R = 0.0613$, $p = 0.548$, $N = 98$). We also found no positive correlation between group size and the number of used calls within the sequences (Spearman rank-order correlation, $R = 0.0306$, $p = 0.765$, $N = 98$; Figure 1). We found sequences of variable calls in all four different socialising behavioural interactions. The durations of sequences didn't differ significantly across group-compositions (female-juvenile: 9.22 ± 8.49 s ($N = 15$), male-female interactions: 8.06 ± 7.21 s ($N = 57$), male-male: 5.73 ± 5.92 s ($N = 20$), juvenile-juvenile:

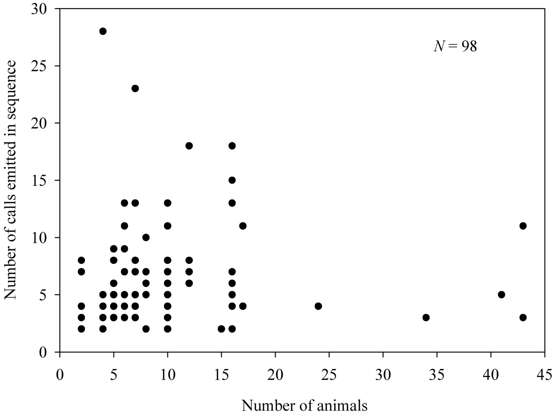


Figure 1. Number of emitted calls in the sequences of variable calls by different number of animals.

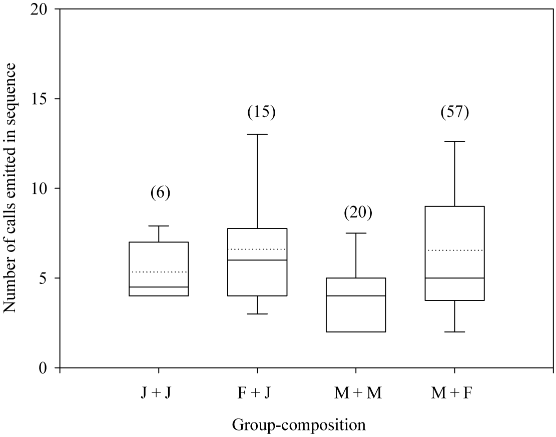


Figure 2. Number of calls within the sequences during juvenile-juvenile interactions (J + J), female-juvenile interactions (F + J), male-male interactions (M + M) and male-female interactions (M + F). Solid horizontal lines represent the medians. The dotted lines represent the means.

5.17 ± 2.03 s ($N = 6$); H-test, Kruskal-Wallis, df = 3, $H = 5.36$, $p = 0.147$). More calls were emitted in sequences of female-juvenile and male-female interactions. However, these differences were not significant (juvenile-juvenile: 5.33 ± 1.76, female-juvenile: 6.60 ± 4.15, male-male interactions: 5.00 ± 5.68, male-female: 6.54 ± 4.27; H-test, Kruskal-Wallis, df = 3, $H = 7.11$, $p = 0.068$; Figure 2). Of all sequences 64.29% were regular and 35.71% were random (Figure 3). Regular sequences were predominant in all group compositions, except juvenile-juvenile interactions (Figure 4).

Sub-classes of the V4 call

Six sub-classes of this call could be classified. Examples of the sub-classes of the V4 calls recorded in the years from 1996, 1997 and 2001 are shown in Figure 5. As can be seen, sub-classes varied in their duration and number of frequency modulations. Parameters of the six sub-classes of the V4 call are shown in Table 1. The visual inspection method revealed that the observers tended to split calls that we expected to belong to one class into separate classes, resulting in a total of 48 different classes. However most of the calls were placed into the same categories by each observer, as we have found earlier, and there was also a highly significant similarity among observer-judgement (Kappa statistic: $\kappa = 0.50$, $z = 38.17$, $p < 0.0001$;

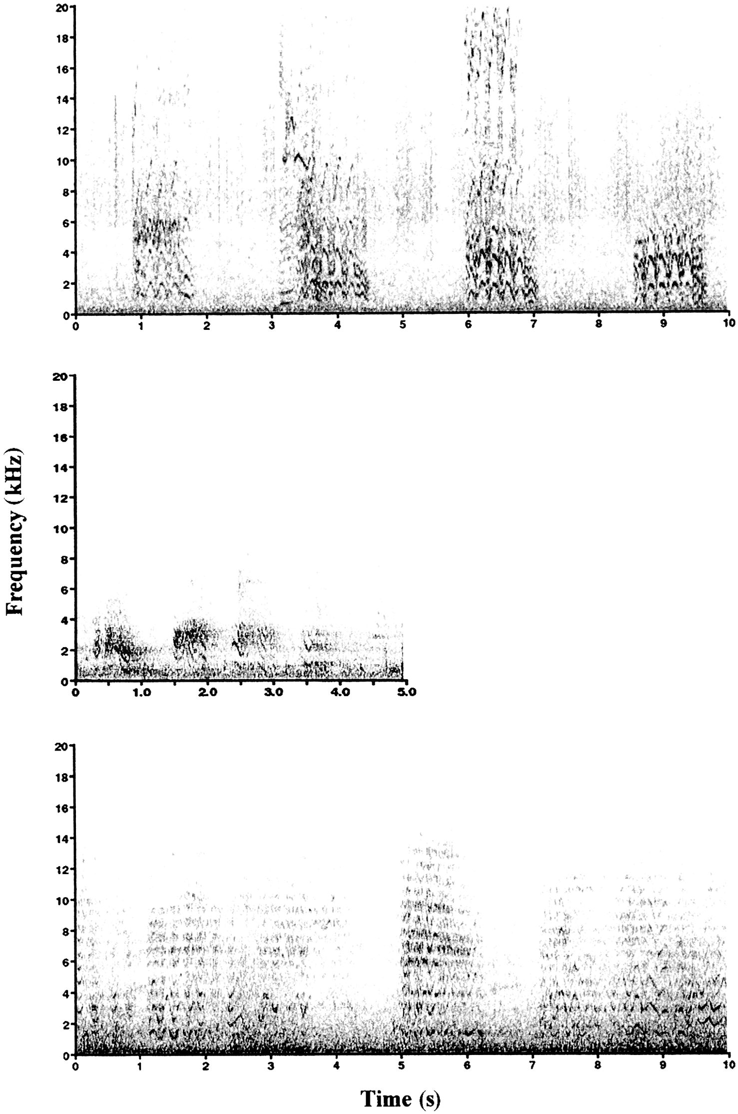


Figure 3. Three examples of a regular sequence of variable calls with the V4-a,d,f sub-class of the V4 call. DF = 98 Hz, DT = 10.2 ms, FFT = 512 points.

Table 2). Table 2 shows that agreement differed between sub-classes with lower values for V4b and c compared to the remaining sub-classes. There was also considerable variation in the classification of single calls. The transitions between the different sub-classes are registered in Table 3. As can be

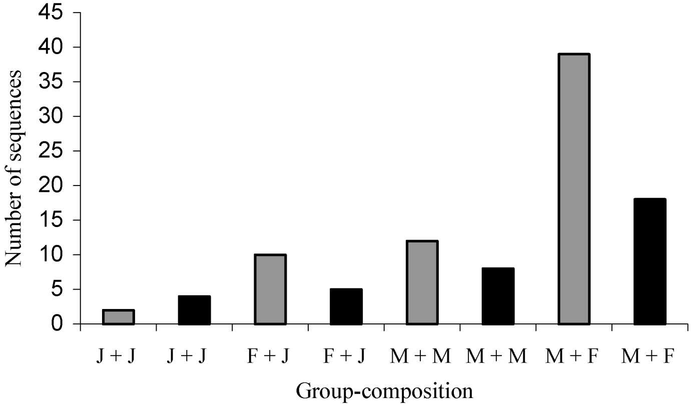


Figure 4. Number of regular and random sequences of variable calls while juvenile-juvenile (J + J), female-juvenile (F + J), male-male (M + M) and male-female (M + F) interactions (grey = regular, black = random).

seen in Table 3, preferably the same sub-classes of the V4 call followed each other.

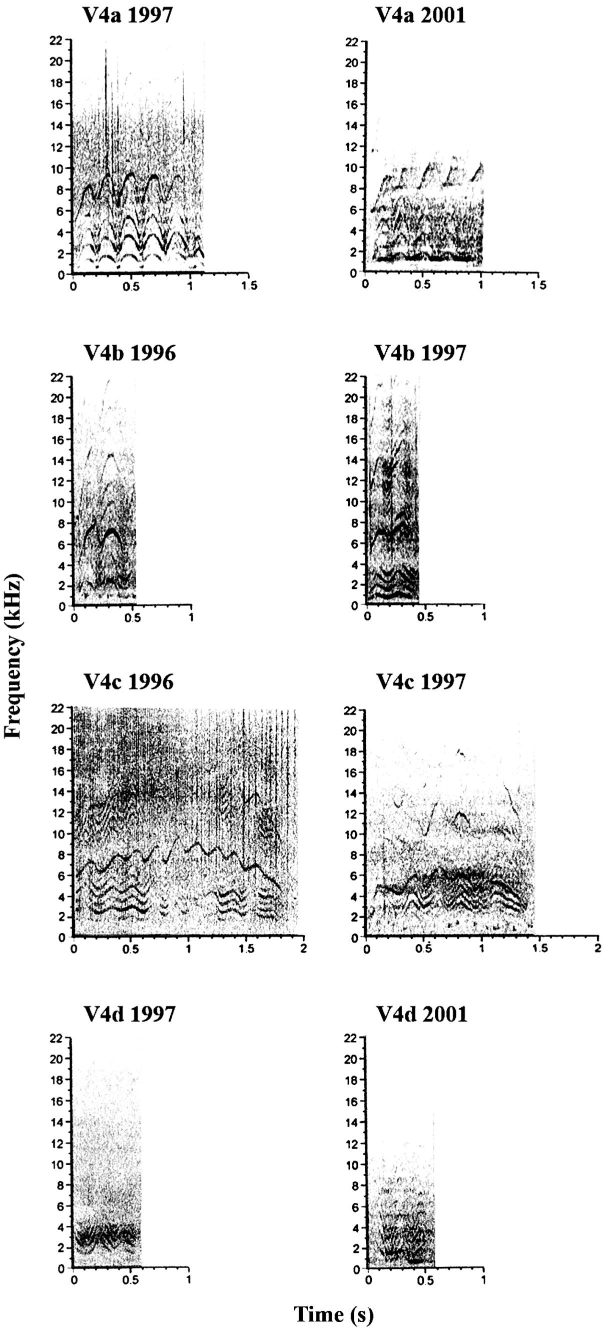
Discussion

Variable calls as graded signals in wild killer whales

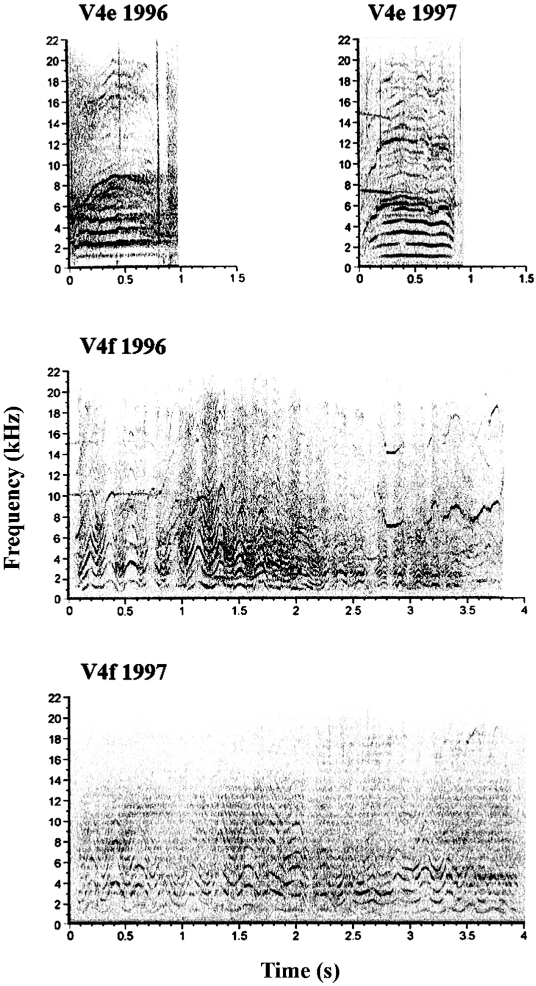
Our study shows that variable calls in free-ranging killer whales are not as variable as their name might suggest as they can be categorised into rather distinct classes that were confirmed by additional observers. However, we also found that the observers more loosely classified some sub-classes than others, most notably the V4c call. This result matches our expectation, as the V4c category was the one we initially found to be most variable in structure, duration and frequency modulations. We also noted that the human observers tended to place calls, which we considered to be only slightly different, in separate classes, resulting in many more categories than we expected. It is, therefore, quite likely that our division of the V4 category into only six sub-classes might have been too broad and that future investigations will find much more categories. However, caution should be taken into splitting categories too much as most mammalian sound types, including signature whistles of bottlenose dolphins, show considerable within-category variation (Theberge & Falls, 1967; Marler, 1973; Waser, 1975; Gautier & Gautier, 1977; Byrne, 1981, 1982; Ford, 1989; Caldwell et al., 1990; Janik et al., 1994; Tyack & Sayigh, 1997). On the other hand, a rather high number of extra categories – as indicated by the observer classification – might suggest that the V4 sub-classes do not represent a discrete division with clearly defined categories, but rather a graded system with related 'basic' categories and rather fluid transitions between them (Marler, 1976). Our study, therefore, confirms earlier qualitative observations by Ford (1989), who proposed that variable calls in wild killer whales are graded.

Function of sequences of variable calls

The results of this study indicate that only one or two animals contribute to sequences of variable calls in free-ranging killer whales. Towed hydrophone arrays used to identify which animal in a group is signalling have recently been applied in studies on killer whales (Miller, 2006). However, even with this method it would be barely possible to locate the sender during socialising interactions since distances between animals are usually short and positions are ever-changing. Digital acoustic recording tags, used in studies on sperm whales (*Physeter macrocephalus*) and northern right whales (*Eubalaena glacialis*) (Johnson & Tyack, 2003) would be an alternative and might hold great promise for future studies on killer whales. But it is so far untested if killer whales would accept those devices and if so, how the behaviour of individuals would be altered by them. Therefore, we have to use other, more indirect methods to describe at least the approximate number of animals that are involved in the production of sequences. Would several individuals be involved in the production of sequences, we could expect that the duration of sequences and the number of calls increase with group size. In this study we could not find a positive correlation between group size and number of used calls or the duration of sequences, which indicates that only one or two animals are involved in the production of each sequence. Miller et al. (2004) analysed series of discrete pulsed calls with hydrophone arrays and found that calling by individual whales is closely synchronised to calling by other group members. This call-type matching might be important in the coordination of group members that are out of sight (Miller et al., 2004). However, it is unlikely that this model applies also to variable calls. Variable calls are generally more complex than discrete calls and their source levels are lower than the ones of most discrete calls (Miller, 2006). They are, therefore, not suited as contact signals for long-range communication where call-type


V4a 1997
V4a 2001
V4b 1996
V4b 1997
V4c 1996
V4c 1997
V4d 1997
V4d 2001
Frequency (kHz)
Time (s)
0
2
4
6
8
10
12
14
16
18
20
22
0.5
1
1.5
2

(a)


V4e 1996

V4e 1997

V4f 1996

V4f 1997

(b)

Figure 5. Exemplary spectrograms of the sub-classes a-f of the V4 call used in the test of interobserver reliability. DF = 48.4 Hz, DT = 20.5 ms, FFT = 1024 points.

matching would make sense. Further, most sequences of variable calls are composed of rather short and intense bouts of calls of very similar energy (see Figure 3). This emission pattern appears to be quite different from the relatively long sequences of discrete calling, with calls from distant animals much quieter than the ones of individuals nearby (Ford, 1989; see Miller et al., 2004, Figure 3).

Table 1. Parameters (mean ± SD) of variable call sub-classes V4a-V4f of northern resident killer whales recorded 1996, 1997 and 2001.

Parameter/ sub-class	1st SBI start (kHz)	1st SBI end (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Duration (s)	Number of frequency modulations
V4a	1.04 ± 0.82	0.77 ± 0.76	0.63 ± 0.63	13.73 ± 2.72	1.27 ± 0.33	11.90 ± 1.59
V4b	0.85 ± 0.32	0.93 ± 0.24	0.81 ± 0.36	13.06 ± 2.90	0.45 ± 0.17	4.40 ± 1.47
V4c	0.89 ± 0.38	0.80 ± 0.31	0.61 ± 0.35	10.20 ± 3.86	1.17 ± 0.69	8.90 ± 2.57
V4d	0.95 ± 0.33	1.05 ± 0.37	0.90 ± 0.41	3.71 ± 1.46	0.45 ± 0.17	3.45 ± 0.69
V4e	0.89 ± 0.24	0.91 ± 0.29	0.82 ± 0.15	13.58 ± 2.61	0.85 ± 0.22	7.80 ± 1.15
V4f	0.81 ± 0.22	1.29 ± 1.80	0.75 ± 0.13	12.74 ± 2.89	3.50 ± 1.21	28.15 ± 8.43
Mean	0.93 ± 0.43	0.96 ± 0.83	0.75 ± 0.39	11.17 ± 4.50	1.28 ± 1.20	10.77 ± 9.07

Table 2. Classification of sub-classes of the V4 call by human observers. Numbers correspond to the identification number of the variable call sub-class while numbers in parentheses show how many of the six observers put the corresponding subtype into one class. Bold = Calls classified by the investigators F.T. and N.R. into one class.

Variable sub-class					
V4a	V4b	V4c	V4d	V4e	V4f
1 (3)	**15 (4)**	**25 (1)**	**34 (5)**	**46 (5)**	**53 (5)**
2 (2)	**16 (4)**	**26 (2)**	**35 (4)**	**47 (6)**	**54 (5)**
3 (6)	**17 (4)**	**27 (5)**	**36 (1)**	**48 (6)**	**55 (1)**
4 (3)	**18 (2)**	**28 (5)**	**37 (2)**	**49 (3)**	**56 (6)**
5 (6)	**19 (4)**	**29 (1)**	**38 (3)**	**50 (2)**	**57 (2)**
6 (2)	**20 (3)**	**30 (1)**	**39 (4)**	**51 (5)**	**58 (2)**
7 (4)	**21 (3)**	**31 (3)**	**40 (4)**	**52 (5)**	**59 (6)**
8 (5)	**22 (4)**	**32 (2)**	**41 (3)**	17 (1)	**60 (6)**
9 (5)	**23 (1)**	**33 (0)**	**42 (6)**	25 (1)	**61 (6)**
10 (5)	**24 (5)**	6 (1)	**43 (6)**		**62 (6)**
11 (6)	43 (3)	38 (1)	**44 (3)**		**63 (5)**
12 (6)			**45 (6)**		26 (1)
13 (6)			23 (2)		
14 (4)			33 (1)		
28 (1)					
29 (2)					

We propose that sequences of variable calls are general indicators of the affective state of single animals that are emitted spontaneously during all kinds of socialising activities, irrespective of age and sex. Consequently, we could not find significant differences in the duration of the sequences and the number of emitted calls within the sequences during the four socialising interactions. The duration and the number of calls within the sequences probably depend only on the affective state of the sender (Ford, 1989). The finding that most sequences are composed of series of similar calls supports this idea further. Blomqvist et al. (2005) described sequences of 'pulsed whistles' used in play-fights among juveniles and subadults. Adult bottlenose dolphins that are involved in more aggressive interactions emitted series of very different burst-pulsed sounds (Blomqvist & Amundin, 2004; Blomqvist et al., 2005). Some primates emit bouts of similar call-classes with the affective state of the signaller encoded in the call type used, the duration of the vo-

Table 3. Transition frequency matrix for 168 transitions of the sub-classes of the V4 call. Horizontal row = successor call. Vertical row = predecessor call. Thick framed are the fields in which the same sub-class of the V4 call followed each other.

	Successor						
Predecessor	V4a	V4b	V4c	V4d	V4e	V4f	Different variable call
V4a	18	–	–	–	–	–	3
V4b	–	44	3	–	2	1	4
V4c	–	1	33	1	1	–	2
V4d	–	2	–	10	–	–	1
V4e	–	–	–	–	7	–	–
V4f	–	–	4	–	–	11	1
Different variable call	1	4	2	–	–	1	11

cal sequence and fine-scale structural changes between calls (Goodall, 1986; Fischer & Hammerschmidt, 2002).

Vocal plasticity in juveniles

We found that regular sequences were predominant in all group compositions during close-ranges, except juvenile-juvenile interactions. Because of the small sample-size of juvenile-juvenile recordings, this might be just a random phenomon and it is difficult to draw final conclusions. However, it might be possible that the more random sequences of variable calls in juvenile-juvenile interactions reflect the vocal plasticity of the very young. Vocal learning in bottlenose dolphins has been studied intensively (Tyack, 1986; Reiss & McCowan, 1993; McCowan & Reiss, 1995; Janik & Slater, 1997, 2000; Tyack & Sayigh, 1997) and for killer whales it appears highly likely (Ford, 1991; Deecke et al., 2000; Yurk, 2003; Foote et al., 2006). It is, therefore, possible that a learning process governs the use of variable calls in close-range contacts. Juvenile killer whales might not be able to coordinate their communication signals as adults do and it is likely, that they have yet to learn how to effectively transmit their motivational status to other animals.

Possible function of the V4 call

That sequences of variable call-classes are emitted by animals of either sex and probably all age classes does not mean that they are unspecific. The information conveyed probably depends on the class of call used. We found the V4 call to be the most frequent call in all sequences. The V4 call-class is particularly qualified to transmit motivational information since it usually comprises many frequency modulations (see Appendix). After Morton (1977), abrupt motivational changes – for example, conflicts between retreat and approach – are directly encoded in more or less regular up-and-down shifts in frequency. The V4 call-class would be most effective as socialising activities among killer whales usually involve rapid changes in behaviour, for example role-reversals during play (Jacobsen, 1986; personal observation). It is, therefore, quite possible that this particular call is neither purely friendly nor agonistic but rather represents rapid shifts in affective states that are very common in play situation (Fagen, 1981). This interpretation is supported by other studies, since in bottlenose dolphins, aggressive calls comprise not much frequency modulation, whereas, general excitement or 'play-fight' signals are heavily or partly frequency modulated (McCowan & Reiss, 1994; Herzing, 1996, 2000; Blomqvist & Amundin, 2004; Blomqvist et al., 2005). In this regard the V4 also resembles the excitement 'twitters' and 'chatters' of chimpanzees (Goodall, 1994). Since in wild killer whales, not only juveniles but also adults of both sexes are frequently involved in playing, the V4 call-class could be found in recordings were both sexes and all age classes were present. Subtle variations of the call might represent underlying small-scale changes in motivation. Masataka (1989) found similar variations in 'girneys' in Japanese monkeys (*Macaca fuscata*). He postulates that the variation of the basic call format depends on individual differences and different arousal levels. On the basis of spectrograms, Green (1975) described seven forms of a call of *M. fuscata* which the human ear couldn't distinguish. These seven calls got used in different behaviour contexts. It is possible that this model applies to the V4 call-class too. The sub-classes of the V4 would then transmit fine-scale changes of affective states. Then, slight variations within the sub-classes in a sequence could be the result from individual arousal levels of the animals as described by Masataka (1989) in primates. Repetitions of sub-classes within a sequence (see Table 3) would then aid to amplify the message.

Acknowledgements

We are very grateful to John Ford for his logistical and theoretical support of the study. Thanks to Bill and Donna Mackay, Jim and Mary Borrowman, Robert Butler, Wayne Garton, Bob Mollett, Jackie Hildering, Dave Tyre, Rolf Hicker, Paul Spong, Anna Spong and Helena Symonds for their help during fieldwork. Jakob Parzefall, Ralf Wanker and Cord Crasselt helped during the analysis of the data at the University of Hamburg. We thank Hannah Spitzhorn, Georgine Szipl, Stefan Nessler, Petra Ziemer, Sabine Holst and Kristiani Lesmono for their help in call classification. We are grateful to Roger Mundry for statistical advice. The study was partly funded by a scholarship of the German Academic Exchange Fund, the Steffens Memorial Fund and the Hansische Universitätsstiftung.

References

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

Blomqvist, C., Mello, I. & Amundin, M. (2005). An acoustic play-fight signal in bottlenose dolphins (*Tursiops truncatus*) in human care. — Aquat. Mamm. 31(2): 187-194

Brownlee, S.M. & Norris, K.S. (1994). The acoustic domain. — In: The Hawaiian spinner dolphin (Norris, K.S., ed.). University of California Press Press, Santa Cruz, CA, p. 161-183.

Byrne, R.W. (1981). Distance vocalisations of Guinea baboons (*Papio papio*) in Senegal: an analysis of function. — Behaviour 80: 283-312.

Byrne, R.W. (1982). Primate vocalisations: structural and functional approaches to understanding. — Behaviour 80: 241-258.

Caldwell, M.C. & Caldwell, D.K. (1968). Vocalizations of naive captive dolphins in small groups. — Science 159: 1121-1123.

Caldwell, M.C., Caldwell, D.K. & Tyack, P.L. (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. — In: The Bottlenose Dolphin (Leatherwood, S. & Reeves, R.R., eds). Academic Press, San Diego, CA, p. 199-234.

Clark, C.W. (1982). The acoustic repertoire of the southern right whale: a quantitative analysis. — Anim. Behav. 30: 1060-1071.

Connor, R.C. & Smolker, R.A. (1996). 'Pop' goes the dolphin: a vocalization male bottlenose dolphins produce during consort ships. — Behaviour 133: 643-662.

Dawson, S.M. (1991). Clicks and communication: the behavioral and social contexts of Hector's dolphin vocalizations. — Ethology 88: 265-276.

Deecke, V.B., Ford, J.K.B. & Spong, P. (2000). Dialect change in resident killer whales: implications for vocal learning and cultural transmission. — Anim. Behav. 60: 629-638.

Estes, R.D. (1991). The behavior guide to African mammals: including hoofed mammals, carnivors, primates. — University of California Press, Santa Cruz, CA, p. 660.

Fagen, R. (1981). Animal play behavior. — Oxford University Press, New York, NY.

Fischer, J. & Hammerschmidt, K. (2002). An overview of the Barbary Macaque, *Macaca sylvanus*, vocal repertoire. — Folia Primatol. 73: 32-45.

Foote, A.D., Griffin, R.M., Howitt, D., Larsson, L., Miller, P.J.O. & Hoelzel, A.R. (2006). Killer whales are capable of vocal learning. — Biol. Lett. Doi: 10.1098/ rsbl.2006.0525 (published online).

Ford, J.K.B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. — Can. J. Zool. 67: 727-745.

Ford, J.K.B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. — Can. J. Zool. 69: 1454-1483.

Ford, J.K.B. & Fisher, H.D. (1978). Underwater acoustic signals of the narwhal (*Monodon monocerus*). — Can. J. Zool. 56: 552-560.

Ford, J.K.B., Ellis, G.E. & Balcomb, K.C. (2000). Killer whales, second edition. The natural history and genealogy of *Orcinus orca* in British Columbia and Washington State. — UBC Press, Vancouver, BC.

Fox, M.W. & Cohen, J.A. (1977). Canid communication. — In: How animals communicate (Sebeok, T.A., ed.). Indiana University Press, Bloomington, IN, p. 729-747.

Gautier, J.-P. & Gautier, A. (1977). Communication in old world monkeys. — In: How animals communicate (Sebeok, T.A., ed.). Indiana University Press, Bloomington, IN, p. 890-964.

Goodall, J. (1986). The chimpanzees of Gombe. Patterns of behavior. — The Belknap Press of Harvard University Press, Cambridge, MA.

Goodall, J. (1994). Wilde Schimpansen: Verhaltensforschung am Gombe-Strom. — Rowohlt, Reinbek.

Green, S. (1975). Variation of social pattern with social situation in the Japanese Monkey (*Macaca fuscata*): a fiel study. — In: Primate behavior: developments in field and laboratory reserach (Rosenblum, L.A., ed.), Vol. 4. Academic Press, New York, NY, p. 1-102.

Hauser, M.D. (1997). The evolution of communication. — MIT Press, Cambridge, MA.

Hermann, L.M. & Tavolga, W.N. (1980). The communication systems of cetaceans. — In: Cetacean behavior: mechanisms and functions (Hermann, L.M., ed.). Wiley, New York, NY, p. 149-209.

Herzing, D. (1996). Vocalizations and associated underwater behaviour of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*). — Aquat. Mamm. 22(2): 61-79.

Herzing, D. (2000). Acoustic and social behaviour of wild dolphins: implication for a sound society. — In: Hearing by whales and dolphins (Au, W.W.L., Popper, A.N. & Fay, R.R., eds). Springer, Berlin, p. 225-273.

Jacobsen, J.K. (1986). The behavior of *Orcinus orca* in Johnstone Strait, British Columbia. — In: Behavioural biology of killer whales (Kirkevold, B.C. & Lockard, J.S., eds). Alan R. Liss, New York, NY, p. 135-187.

Janik, V.M. (1999). Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. — Anim. Behav. 57: 133-143.

Janik, V.M. & Slater, P.J.B. (1997). Vocal learning in mammals. — Adv. Study Behav. 26: 59-99.

Janik, V.M. & Slater, P.J.B. (2000). The different roles of social learning in vocal communication. — Anim. Behav. 60: 1-11.

Janik, V.M., Dehnhardt, G. & Todt, D. (1994). Signature whistles variations in a bottlenose dolphin, *Tursiops truncatus*. — Behav. Ecol. Sociobiol. 35: 243-248.

Johnson, M.P. & Tyack, P.L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. — IEEE J. Oceanic Eng. 28(1): 3-12.

Marler, P. (1967). Animal communication signals. — Science 157: 769-774.

Marler, P. (1973). A comparison of vocalizations of red-tailed monkeys and blue monkeys, *Cercopithecus ascanius and C. mitis*, in Uganda. Z. Tierpsychol. 33: 223-247.

Marler, P. (1976). Social organisation, communication and graded signals: the chimpanzee and the gorilla. — In: Growing points in ethology (Bateson, P.P.G. & Hinde, R.A., eds). Cambridge University Press, Cambridge.

Marler, P. (1977). The evolution of communication. — In: How animals communicate (Sebeok, T.A., ed.). Indiana University Press, Bloomington, IN, p. 45-70.

Marler, P. & Tenaza, R. (1977). Signalling behavior of apes with special references of vocalization. — In: How animals communicate (Sebeok, T.A., ed.). Indiana University Press, Bloomington, IN, p. 965-1033.

Masataka, N. (1989). Motivational referents of contact calls in Japanese monkeys. — Ethology 80: 265-273.

McCowan, B. & Reiss, D. (1994). Maternal aggressive contact vocalizations in captive bottlenose dolphins (*Tursiops truncatus*): wide-band, low-frequency signals during mother/aunt-infant interactions. — Zool. Biol. 14: 293-309.

McCowan, B. & Reiss, D. (1995). Whistle contour development in captive-born infant bottlenose dolphins (*Tursiops truncatus*): Role of learning. — J. Comp. Psychol. 109: 242-260.

Miller, P.J.O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. — J. Comp. Physiol. A. 192: 449-459.

Miller, P.J.O., Shapiro, A.D., Tyack, P.L. & Solow, A.R. (2004). Call-type matching in vocal exchanges of free ranging resident killer whales, *Orcinus orca*. — Anim. Behav. 67: 1099-1107.

Morton, E.S. (1977). On the occurrence and significance of motivation-structural rules in some birds and mammal sounds. — Am. Nat. 111: 855-869.

Owings, H.O. & Morton, E.S. (1998). Animal vocal communication: a new approach. — Cambridge University Press, Cambridge.

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

Peters, G. & Tonkin-Leyhausen, B.A. (1999). Evolution of acoustic communication signals of mammals: friendly close-range vocalizations in felidae (Carnivora). — J. Mamm. Evol. 6: 129-159.

Reiss, D. & McCowan, B. (1993). Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. — J. Comp. Psychol. 107: 301-312.

Riesch, R., Ford, J.K.B. & Thomsen, F. (2006). Stability and group specificity of stereotyped whistles in wild killer whales, *Orcinus orca*, off British Columbia. — Anim. Behav. 71: 79-91.

Robbins, R.L. (2000). Vocal communication in free-ranging African wild dogs (*Lyacon pictus*). — Behaviour 137: 1271-1298.

Siegel, S. & Castellan, N.J., Jr. (1988). Nonparametic Statistics for the Behavioral Science, 2nd edition. — McGraw-Hill, New York, NY.

Sjare, B.L. & Smith, T.G. (1986). The acoustic repertoire of white whales (*Delphinapteras leucas*) summering in Cunningham Inlet. — Can. J. Zool. 64: 2824-2831.

Theberge, J.B. & Falls, J.B. (1967). Howling as a means of communication in timber wolves. — Am. Zool. 7: 331-338.

Thomsen, F., Teichert, S., Franck, D. & Ford, J.K.B. (2001a). Variable calls as graded close-range signals in wild killer whales (*Orcinus orca*). — In: Abstracts of the 14th Bienial Conference on the Biology of Marine Mammals, Nov. 28-Dec. 3 2001, Vancouver. Society for Marine Mammalogy, p. 213.

Thomsen, F., Franck, D. & Ford, J.K.B. (2001b). Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. — J. Acoust. Soc. Am. 109: 1240-1246.

Thomsen, F., Franck, D. & Ford, J.K.B. (2002). On the communicative significance of whistles in wild killer whales (*Orcinus orca*). — Naturwissenschaften 89: 404-407.

Tyack, P. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimcry of signature whistles? — Behav. Ecol. Sociobiol. 18: 251-257.

Tyack, P. & Sayigh, L.S. (1997). Vocal learning in cetaceans. — In: Social Influences on Vocal Development (Snowdown, C.T. & Hausberger, M., eds). Cambridge University Press, Cambridge, p. 208-233.

Waser, P.M. (1975). Individual recognition, intragroup cohesion and intergroup spacing: evidence from sound playback to forest monkeys. — Behaviour 60: 28-74.

Weilgart, L.S. & Whitehead, H. (1990). Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioural context. — Behav. Ecol. Sociobiol. 26: 399-402.

Yin, S. & McCowan, B. (2004). Barking in domestic dogs: context specificity and individual identity. — Anim. Behav. 68: 343-355.

Yurk, H. (2003). Do killer whales have culture? — In: Animal social complexity. Intelligence, culture and individualized societies (de Waal, F.B.M. & Tyack P.L., eds). Harvard University Press, Cambridge, MA, p. 465-589.

Zar, J.H. (1996). Biostatistical Analysis, 3rd edition. — Prentice Hall, Englewood Cliffs, NJ.

Appendix

Figures A-1 and A-2 are part of the key results of an unpublished diploma thesis by Teichert on which the distinction of the variable call-classes in this manuscript are based (Teichert, S. (2000). Variabele Rufe als Nahkontaktsignale bei Schwertwalen (*Orcinus orca*) vor Vancouver Island, Britisch Kolumbien. Unpublished Diploma-Thesis, University of Hamburg, Germany).

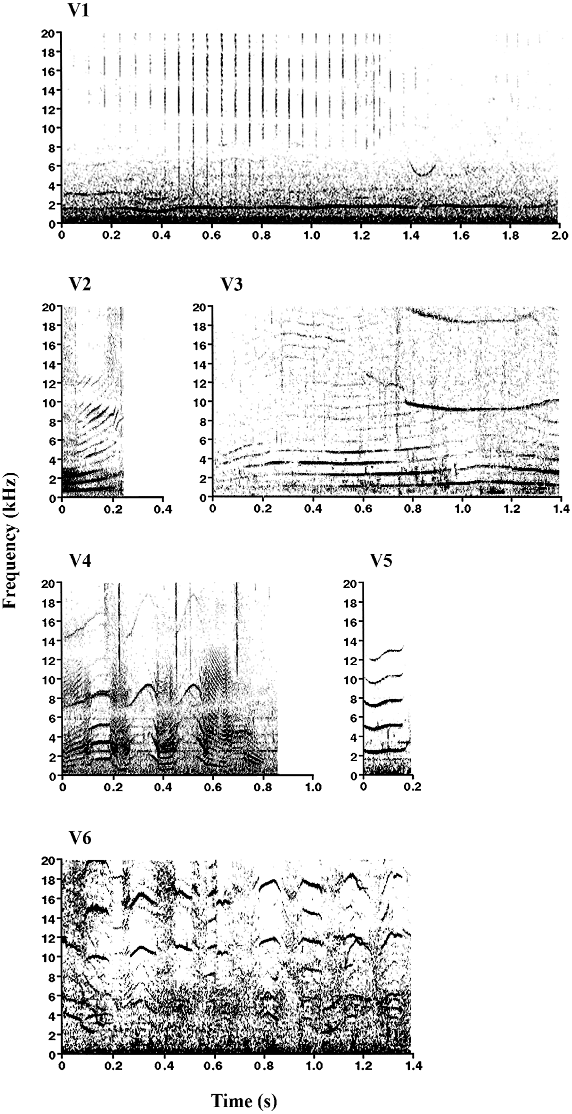


Figure A-1. Exemplary spectrograms of the variable call-classes V1-V6, based on an analysis of 2300 variable calls. The two distinct lines in V3 represent a whistle (DF = 117 Hz, DT = 8.6 ms, FFT = 512 points).

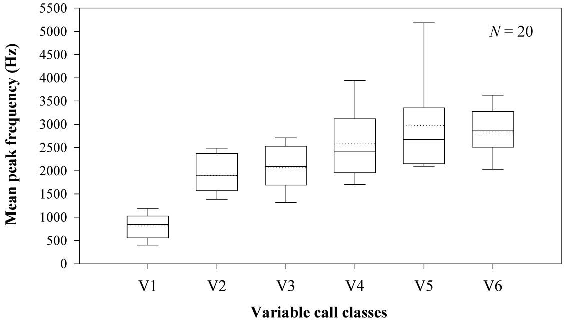


Figure A-2. Mean peak frequencies of the variable call-classes V1-V6. Differences between classes were significant with higher-order calls comprising a significantly higher carrier-sfrequency than lower numbered ones (Dotted lines = mean, N = number of measured calls in each category; H-test, Kruskal-Wallis, df = 5, $H = 69.62$, $p < 0.001$).