

Whistle sequences in wild killer whales (*Orcinus orca*)

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Combining different stereotyped vocal signals into specific sequences increases the range of information that can be transferred between individuals. The temporal emission pattern and the behavioral context of vocal sequences have been described in detail for a variety of birds and mammals. Yet, in cetaceans, the study of vocal sequences is just in its infancy. Here, we provide a detailed analysis of sequences of stereotyped whistles in killer whales off Vancouver Island, British Columbia. A total of 1140 whistle transitions in 192 whistle sequences recorded from resident killer whales were analyzed using common spectrographic analysis techniques. In addition to the stereotyped whistles described by Riesch *et al.*, [(2006). "Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia," *Anim. Behav.* **71**, 79–91.] We found a new and rare stereotyped whistle (W7) as well as two whistle elements, which are closely linked to whistle sequences: (1) *stammers* and (2) *bridge* elements. Furthermore, the frequency of occurrence of 12 different stereotyped whistle types within the sequences was not randomly distributed and the transition patterns between whistles were also nonrandom. Finally, whistle sequences were closely tied to close-range behavioral interactions (in particular among males). Hence, we conclude that whistle sequences in wild killer whales are complex signal series and propose that they are most likely emitted by single individuals.

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I. INTRODUCTION

Combining different stereotyped vocal signals into specific sequences increases the range of information that can be transferred between individuals. With regard to message possibilities, using established signals is even more efficient than producing new ones (Hauser, 1997; Bradbury and Vehrencamp, 1998). However, in order to ascribe a specific function to vocal sequences, at least two prerequisites have to be fulfilled: (1) the signals within the sequence have to follow a specific and nonrandom pattern, and (2) the behavioral context in which the sequence takes place has to be identified.

Both the temporal emission pattern and the behavioral context of vocal-signal sequences have been described in detail for a variety of birds and mammals, where they are often called "songs" and serve a variety of functions (general reviews by Hauser, 1997; Bradbury and Vehrencamp, 1998; songbirds: Catchpole and Slater, 1995; Slater, 2003; terrestrial mammals: Marler and Tenaza, 1977; Byrne, 1982; Geissmann and Orgeldinger, 2000; Gourbal *et al.*, 2004; Holy and Guo, 2005; marine mammals: Tyack, 1998).

For cetaceans, the study of vocal sequences is still in its infancy: they have been described for some species such as bowhead whales (*Balaena mysticetus*), fin whales (*Balaenoptera physalus*), bottlenose dolphins (*Tursiops truncatus*), killer whales (*Orcinus orca*), and humpback whales (*Megaptera novaeangliae*) (Lilly and Miller, 1961; Payne and McVay, 1971; Bain, 1986; Ford, 1989; Tyack, 1998; Miller *et al.*, 2004); yet, only for the latter two were more detailed insights into their function provided. In killer whales, vocal sequences are often comprised of repetitions of similar stereotyped calls by different members within a social group and are probably used to coordinate group movements (Ford, 1989; Miller *et al.*, 2004). Best studied are the songs of male humpback whales by which females gain information about the location of the singer, as well as his willingness to breed and compete with other males for females (Tyack, 1998).

Resident killer whales off British Columbia produce burst-pulsed calls and tonal sounds called whistles in underwater communications (Ford, 1989). Pulsed calls can be either variable or stereotyped (discrete) in structure. Discrete calls can be quite intense (>160 dB re: $1 \mu\text{Pa}$ at 1 m; Miller, 2006) and are proportionally most often used during behaviors where animals are widely spaced out such as traveling and foraging. Repertoires of stereotyped pulsed calls are

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group specific and probably function as long-range contact signals and in group affiliation (Ford, 1989, 1991; Miller *et al.*, 2004). Whistles on the other hand are high pitched, complex, and comparably low-intensity sounds that are almost entirely associated with close-range interactions among individuals (Ford, 1989; Thomsen *et al.*, 2001, 2002; Miller, 2006). Recently, we demonstrated the presence of 15 stereotyped whistle types in resident killer whales off Vancouver Island, with some types unchanged in spectrographic contour over a period of at least 15 years (Riesch *et al.*, 2006). We also showed that killer whales that have no overlap in their call repertoire use essentially the same set of stereotyped whistles. Based on these results, we suggested that stereotyped whistles provide a community-level means of recognition that facilitates association and affiliation of members of different clans, which otherwise use different communicative signals (Riesch *et al.*, 2006). In the process of data analysis, we constantly noted repetitive and rather elaborate series of stereotyped whistles that occurred during socializing (Ford, 1991; Riesch *et al.*, 2006). However, a detailed analysis of whistle sequences was lacking to date. Therefore, the function of whistle sequences for underwater communication in wild killer whales was completely unknown.

In the present study, we provide a detailed analysis of whistle sequences in resident killer whales off Vancouver Island, British Columbia. We examine the frequency of occurrence of different whistle types and the transition patterns of stereotyped whistles within the sequences. We also consider the behavioral context in which whistle sequences were produced. Based on our results, we discuss the likely function of whistle sequences in underwater communication of resident killer whales.

II. METHODS

A. Acoustic data collection

Our study animals belong to the northern community of resident killer whales, which ranges from mid-Vancouver Island north to southeastern Alaska and consisted at the time of the study of 216 individuals in 33 matriline (1999 census; Ford *et al.*, 2000). The majority (70%–95%) of burst-pulsed calls is highly stereotyped and can be assigned to different call types, called “discrete calls” (Ford and Fisher, 1983; Ford, 1989). Based on discrete pulsed call similarities, the northern resident killer whales are grouped into three distinct vocal clans: A-clan is by far the largest, followed by G-clan, and the smallest is the R-clan (Ford, 1991).

Fieldwork was undertaken in western Johnstone Strait and adjacent waters, British Columbia (50° 30' N, 126° 35' W) in 1996–1997 and in 2001 and 2003. A total of 281 field trips were conducted with more than 1300 h spent at sea. Killer whales were observed on 254 field excursions with a total of >250 h observation time. Killer whale individuals were identified by visual inspection of natural markings on the dorsal fin and back (Ford *et al.*, 2000). Underwater sounds were recorded using digital and analog recorders (1996: Sony TCD-D8, 1997: Sony TCD-D7, 2001/2003: Sony WMD-6C) and three different hydrophones (1996: Bruel & Kjaer 8101, 1997/2003: Offshore Acoustics, 2001:

DEEPSEA Powerlight hydrophone (SM 1000 S/N 153); sensitivities: (–180 dB re: 1 V/ μ Pa or greater; frequency responses: 20 Hz–18/20 kHz \pm 1 dB). Simultaneous voice recordings of behavioral observations were made on a separate track of the same tape (for more details see Thomsen *et al.*, 2002; Riesch *et al.*, 2006). In addition, we used recordings obtained between 1978–1983 and 1993–1999 by one of us (J.K.B.F.). V. Deecke generously provided additional tapes of northern residents obtained between 1999 and 2001. Details of recording equipment and methodology are given by Ford (1989, 1991) and Deecke *et al.* (2000, 2005)

B. Acoustic analyses

More than 90 h of killer whale recordings were initially scanned for whistle sequences using real-time spectrographic analysis (Raven 1.2, Cornell Laboratory of Ornithology; sample rate=50 kHz, frequency range=0–22 kHz, dynamic range=42 dB, FFT size=512 points; window type =Hanning). Based on previous analysis (e.g., Thomsen *et al.*, 2001, 2002; Riesch *et al.*, 2006), we defined *a priori* that a sequence had to consist of at least two whistles occurring within 5.0 s of each other. Structural parameters of 192 whistle sequences in 41 recordings from 1978 to 2003 that had a good signal-to-noise ratio were further analyzed. Whistles were classified according to their spectrographic contour, and defined as being either stereotyped, variable, *stammers*, or *bridge* elements (please refer to Sec. III for definitions of stammers and bridge elements). Stereotyped whistles were repetitive with a distinct spectrographic contour. These were classified alphanumerically as W1 (whistle-type 1), W2, and so on (Riesch *et al.*, 2006). Furthermore, some whistle types occur in two versions, either with or without a trill-like ending. Hence, some stereotyped whistles are denoted with a *T* to indicate the version with a trill at the end (e.g., W1 exists as W1 or W1_T; Riesch *et al.*, 2006).

For each sequence, the duration of each whistle and each interval between whistles was measured. Also, the numbers of stereotyped whistles, variable whistles, stammers, and bridge elements were counted for each sequence. Furthermore, the numbers of pure whistle transitions (defined as the transition between two stereotyped whistles), mixed whistle transitions (defined as the transition between a stereotyped whistle and a nonstereotyped whistle), and impure whistle transitions (defined as the transition between two nonstereotyped whistles) were counted.

C. Temporal emission patterns within the sequence

For a total of 1140 whistle transitions, the observed numbers of transitions of each whistle type to itself and all other whistle types were compared to a random distribution using an χ^2 -test. However, only W1, W3, W3_T, bridge elements, stammers, and variable whistles could be compared in this way, because all other whistle types had expected values below 5 (Quinn and Keough, 2002). Furthermore, the degree of uncertainty in predicting what whistle type follows after a given whistle type was estimated by information theory procedures (H_2 -statistic; see Frick and Miller, 1951; Attneave, 1959; Devenport and Merriman, 1983). The H_2 -statistic

scores range between 0 and 1, with low scores implying rigid sequences and 1 implying complete randomness/uncertainty (Frick and Miller, 1951; Attneave, 1959; Devenport and Merriman, 1983). This statistic is sensitive to the degree to which one vocal signal is predictive of the following vocal signal. In a first step, a first-order uncertainty value (H_1) is calculated that describes whether the first vocal signal in a sequence is chosen randomly or based on some underlying pattern (as described above, values range from 0 to 1). In a second step, the second-order uncertainty value (H_2) is calculated that describes if the first signal in a two-signal sequence has an impact on the identity of the second signal. Finally, a χ^2 -analysis is applied that tests whether the total sequence differs significantly from chance, or in other words if the predictability of the second signal increases with knowledge of the first (Frick and Miller, 1951; Attneave, 1959; Devenport and Merriman, 1983). However, other studies used the H_2 -statistic on binary choices, whereas in the present study there were 15 different possibilities; therefore, the analyses were carried out using \log_{15} instead of \log_2 .

Furthermore, we ran an additional χ^2 -analysis that tested whether the transitions from an individual given whistle type to the subsequent whistle type deviated significantly from chance. Since the H_2 -statistic only provides information whether there is a general pattern in the transitions, this test was designed to identify if certain whistle types follow a more rigid pattern of transition than others. However, to meet the χ^2 -assumptions that not more than 20% of the expected values were below 5 (Quinn and Keough, 2002), the six least common whistle types ($W1_T$, $W2_T$, $W4$, $W5$, $W6_T$, and $W7$) were grouped into one category for this analysis.

D. Whistle sequences and activity state

The behavioral activities of the northern resident killer whales were grouped into six categories: beach rubbing, foraging, resting, socializing, social traveling, and traveling (defined after Ford, 1989; Barrett-Lennard *et al.*, 1996; Thomson *et al.*, 2002). Activity states were recorded *ad libitum* (Martin and Bateson, 1993) whenever a general change in group activity was observed. In all cases, the activity state of the recorded group of whales was considered to be the activity of most group members. Thus, for a subset of 489 recordings, a distinct behavioral state could be ascribed, while 46 recordings had to be removed from the analysis due to lack of information on the whales' activity state.

The observed frequency of behavioral activities was compared to a random distribution across behavioral states for a total of 489 recordings, which were extracted from more than 90 h of *ad libitum* recording of killer whale vocal behaviors. The observed and expected frequencies of behavioral states were then compared using a χ^2 -test.

III. RESULTS

A. Identification of new whistle types

In addition to the stereotyped whistle types described in (Riesch *et al.*, 2006), we found a rare new stereotyped whistle, which was called $W7$ (Fig. 1). $W7$ was found only ten times in six different recordings in the whole data

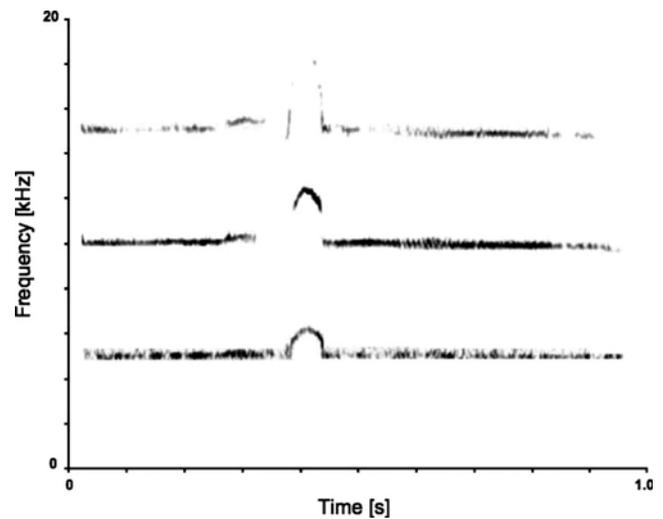


FIG. 1. Representative spectrogram of the new stereotyped whistle-type $W7$ (frequency resolution=98 Hz, time resolution=10.2 ms, FFT size=512 points, window type=Hanning).

set; however, only five $W7$ s were strong enough in their signal-to-noise ratio for acquiring measurements ($N=5$, “start frequency”= 5270.6 ± 324.6 Hz (mean \pm S.D.), “end frequency”= 5098.4 ± 288.2 Hz, “minimum frequency”= 4900.4 ± 123.1 Hz, “maximum frequency”= 6700.6 ± 436.8 Hz, “bandwidth”= 1800.2 ± 376.1 Hz, “carrier frequency”= 7106.0 ± 4587.0 Hz, “duration”= 757.4 ± 164.2 ms, “frequency modulations”= 4.6 ± 0.9 ; Fig. 1). However, there was no particular affiliation of this whistle type with specific killer whale groups (at least five different matriline emitted this whistle) or behaviors (it occurred during traveling, social traveling, and socializing).

Furthermore, we found whistles that only occurred as part of whistle sequences: (1) stammers and (2) bridge elements (Fig. 2). Both are not stereotyped whistles in the common sense, but are categories that we defined for this analysis. Stammers look like the beginning of a $W1$, $W1_T$, $W3$, or $W3_T$ whistle; however, the characteristic downsweep and/or trill-like ending is never produced (stammers: $N=140$, “whistle duration”= 0.97 ± 0.25 s; Fig. 2; Riesch *et al.*, 2006). Often, stammers can be found at the start or end of a sequence. Bridge elements, on the other hand, seem to be used as connecting pieces that link individual stereotyped whistles within a sequence (bridge elements: $N=173$, whistle duration= 0.82 ± 0.30 s; Fig. 2). Even though bridge elements seem highly variable in contour they were grouped together for this analysis.

B. Parameters of whistle sequences

The vast majority (84%) of all stereotyped whistles found in the recordings were associated with whistle sequences, while only 16% of stereotyped whistles appeared as isolated whistles. Figure 2 shows representative spectrograms of whistle sequences. The 192 whistle sequences had an average duration of 9.84 ± 7.43 s (mean \pm S.D.) and consisted of 6.16 ± 3.44 whistle elements (3.91 ± 1.99 stereotyped whistles, 1.37 ± 1.15 variable whistles, 1.35 ± 1.20 stammers, and 1.10 ± 0.85 bridge elements), with an average

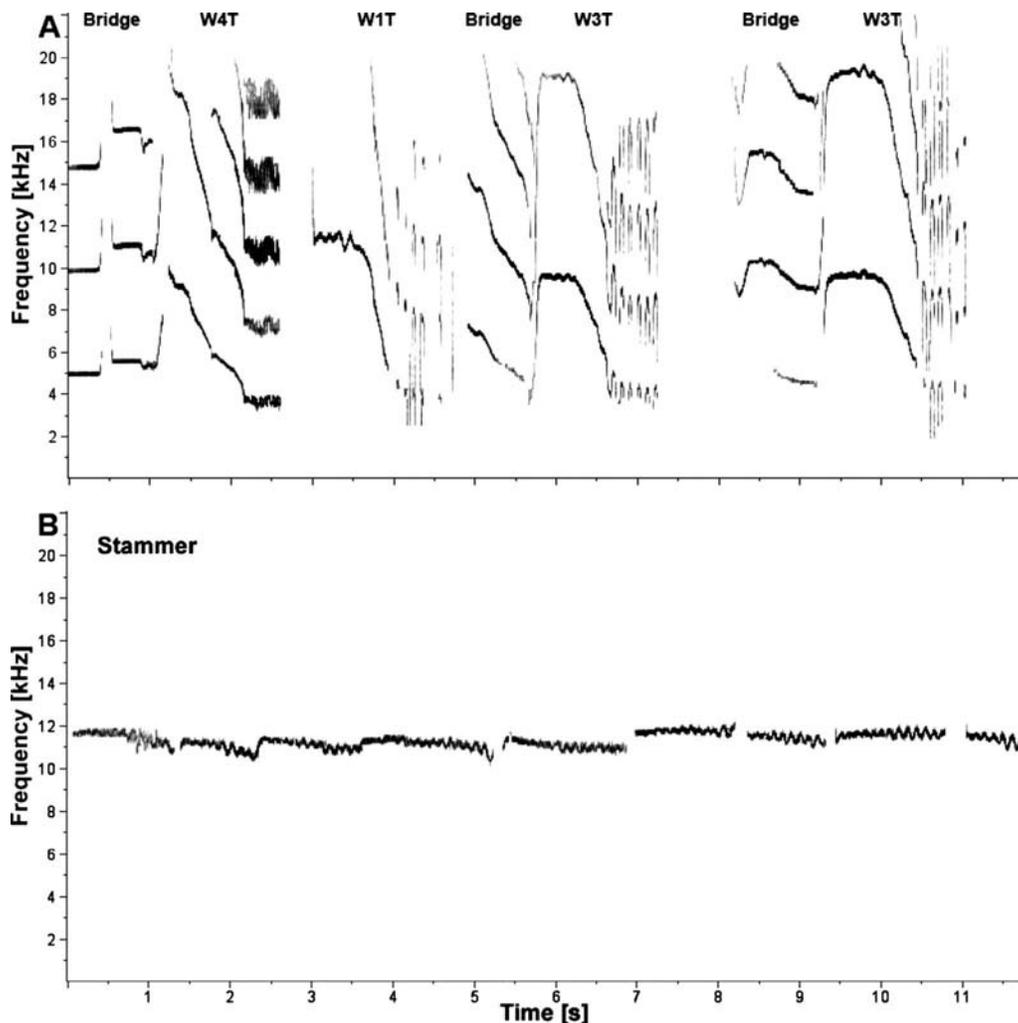


FIG. 2. Representative spectrograms of whistle sequences (frequency resolution=98 Hz, time resolution=10.2 ms, FFT size=512 points, window type =Hanning). A: sequence of bridge-W4_T-W1_T-bridge-W3_T-bridge-W3_T; B: sequence of stammers.

of 2.57 ± 0.83 different stereotyped whistle types per sequence. Whistle sequences comprised 2.09 ± 1.42 pure transitions, 2.73 ± 2.04 mixed transitions, and 1.31 ± 1.23 impure transitions. The duration of the intermission between two whistles within a sequence was 0.36 ± 0.21 s and on average 23.63 ± 14.51 animals were present during recordings that contained whistle sequences.

C. Frequency of occurrence of whistle types

The frequency of occurrence of different stereotyped whistle types within the sequences was not randomly distributed ($\chi^2_{11}=657.094$, $N=1321$, $P<0.001$; Fig. 3). Some whistle types were rather scarce (W4, W5, and W7), while others were predominant (W1, W3, W3_T, and W4_T; Fig. 3).

D. Temporal emission patterns within the sequence

For six whistle types (W1, W3, W3_T, bridge elements, stammers, and variable whistles), the transition patterns to following whistles differed significantly from the expected random distribution (Tables IA and IB). The transition patterns of the remaining whistle types (W1_T, W2, W4_T and the

grouped whistle types: W2_T, W4, W5, W6_T, and W7) did not differ significantly from randomness (Table IA). For certain pairs of whistle types, the difference between observed and expected frequency was greater than for other pairs (Table

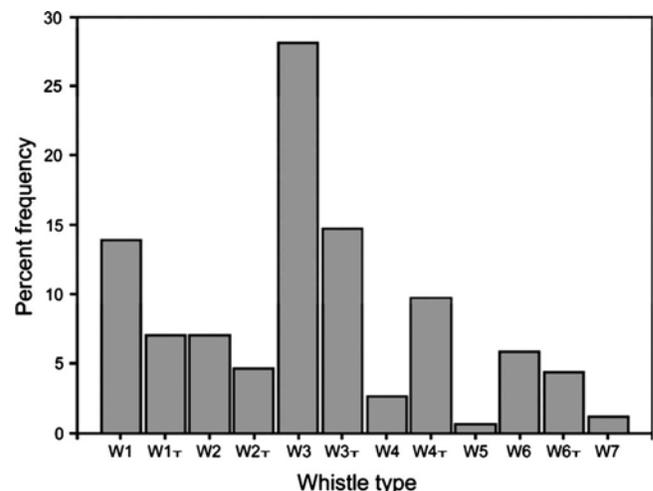


FIG. 3. Frequency of occurrence of stereotyped whistle types during 192 whistle sequences.

TABLE I. Contingency table analysis of transitions among whistle types within 192 whistle sequences. Transition frequency matrix for 1140 whistle transitions. A: total transitions. B: listing of only the significant Chi-square results for the comparison between the expected and observed transition patterns.

A Preceding whistle	Following whistle														
	W1	W1 _T	W2	W2 _T	W3	W3 _T	W4	W4 _T	W5	W6	W6 _T	W7	Bridge	Stammer	Variable
W1	7	7	3	3	17	14	1	3	1	7	0	1	28	8	7
W1 _T	7	5	4	1	1	2	1	0	0	2	1	0	6	5	7
W2	3	1	3	3	11	7	0	2	0	3	0	1	3	5	3
W2 _T	4	4	2	1	5	2	0	0	0	1	0	1	2	3	3
W3	10	3	10	8	45	19	0	11	0	5	2	1	57	15	22
W3 _T	3	5	12	6	8	12	0	1	0	2	2	1	17	8	15
W4	1	0	1	0	1	1	4	3	0	2	2	0	1	1	2
W4 _T	6	4	5	3	9	3	0	9	0	3	3	4	7	1	6
W5	0	0	0	0	0	0	1	2	0	0	1	0	1	0	0
W6	6	1	3	3	0	1	0	3	0	2	16	0	6	0	4
W6 _T	2	2	0	0	3	0	3	4	0	1	1	0	1	0	4
W7	2	0	3	1	0	0	0	0	0	0	0	0	2	0	2
Bridge	16	7	2	2	62	25	2	26	1	5	3	0	13	5	2
Stammer	18	2	1	1	20	4	0	0	0	2	0	0	4	81	5
Variable	8	5	3	5	23	15	3	7	2	5	2	0	6	4	58

B Preceding whistle	Chi-square test			
	N	χ^2	df	P
W1	107	111.60	14	<0.001
W3	208	280.01	14	<0.001
W3 _T	92	72.71	14	<0.001
Bridge	171	328.56	14	<0.001
Stammer	138	661.13	14	<0.001
Variable	146	303.03	14	<0.001

IA). Stammers, for example, were almost exclusively found at the beginning and at the end of sequences while others, such as bridge elements, predominantly connected W3's, W3_T's, and W4_T's with each other within the sequences. Furthermore, the majority of variable whistles were successive, and some pairs of whistles were highly stereotyped in themselves, as is the case with the W6-W6_T-pair.

On the first order of estimation the uncertainty (H_1) was 87%, while on the second order the uncertainty (H_2) was only 72%. However, the second-order probability was significantly different from the first-order probability ($\chi^2_{81} = 756.461$, $N = 1140$, $P < 0.001$).

E. Whistle sequences and activity state

The occurrence of the 192 whistle sequences within the 41 recordings was closely linked to certain activity states (Fig. 4). Contrary to the expected random distribution, whistle sequences occurred predominantly during socializing and social traveling, but only rarely during foraging and traveling ($\chi^2_5 = 35.554$, $N = 41$, $p < 0.001$; see also Thomsen *et al.*, 2002). We were not able to identify the whistle-emitting individuals for the recordings analyzed for this study. However, in some cases we were able to appoint a certain group of whales as the most likely source of the recorded whistle sequences (based on changes in the sound intensity of whistle sequences in combination with movement patterns of certain subgroups of whales). Interestingly, in all six (15% overall) of these cases, the emitting group of whales was an

all-male group. Furthermore, in all cases males were present and in at least four other cases, an all-male group was present during the recording [6 (all-male groups only) + 4 (all-male groups present) + 31 (at least one male present) = 41 recordings].

IV. DISCUSSION AND CONCLUSIONS

This study describes a new stereotyped whistle (W7) in northern resident killer whales, and two relative broad categories of stereotyped whistles produced as part of whistle sequences (stammers and bridge elements). However, since

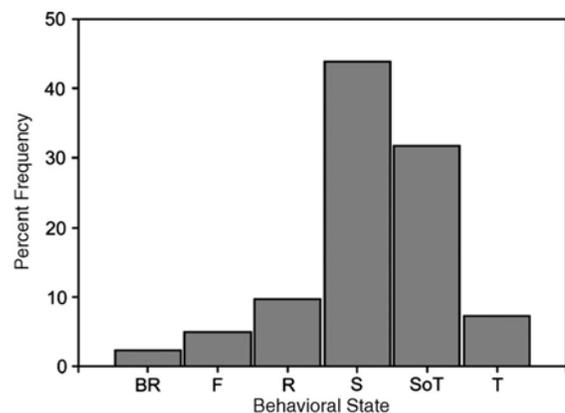


FIG. 4. Relative occurrence of whistle sequences during different activity states ($N = 41$ recordings). BR: beach rubbing; F: foraging; R: resting; S: socializing; SoT: social traveling; T: traveling.

we could not find an association of them with particular behaviors or usage by particular groups, no further conclusions on possible functions of these signals can be drawn yet. We could further show that sequences of stereotyped whistles consist of whistle types that follow a nonrandom pattern of emission. Finally, we found some indications that sequences are particularly associated with male-male social behaviors within socializing and social traveling behavioral states.

Whistle sequences in killer whales are rather complex: Parts of the sequences are made up of multiloops, which are repetitions of the same whistle type (Table IA). Multilooped stammers are predominantly emitted at the start or end of a sequence (personal observation). Hence, they might serve as a “lead-in” and “lead-out” for the killer whales in such a way that they open and close the acoustical channel used for the transmission of whistle sequences. Another form of multiloops is composed of $W4$'s or $W3$ -bridge-, $W3$ -bridge-, and $W4$ -bridge-combinations, respectively. These different multiloops might be used to enhance and stress the respective information encoded in the whistle types within the sequences. However, this does not mean that sequences merely consist of different multilooped whistles put together. On the contrary, whistle sequences are quite complex and consist of a variety of different whistle combinations, some of which are rather common (e.g., $W6$ - $W6_T$; Table IA) while others are either rare or not found at all (e.g., *stammer*- $W4$; Table IA).

There are three possible explanations for how whistle sequences might be formed. First, several members within a group could contribute to them. Thus, whistle sequences would be structurally similar to the choruses found in several terrestrial mammals where they serve to synchronize behaviors (Estes and Goddard, 1967; Mitani and Gros-Louis, 1998). Although several studies already suggest that in resident killer whales discrete calls serve in behavioral synchronization especially during long-range communication (Ford, 1989, 1991; Miller *et al.*, 2004; Miller, 2006), whistle sequences may have this function during close-range interactions. However, if whistle sequences represent choruses, we would expect to find overlapping whistles within them, which was almost never the case. Finally, the energy levels of whistles within a given sequence were more or less the same throughout (Fig. 2). If sequences represent choruses, we would expect to find whistles of different intensities within a sequence, since a variety of animals of different sizes and different positions to the hydrophone (resulting in different sound levels) would “join in.” This was clearly not the case. Thus, even though the whistle sequences could be used to synchronize behaviors, we do not think that they represent choruses.

Second, sequences could be formed by two individuals. If so, then two interacting individuals could be answering each other with the same or with other whistle types. Such whistling behavior has been described for common dolphins (*Delphinus delphis*; Caldwell and Caldwell, 1968) and bottlenose dolphins (*Tursiops truncatus*; Lilly and Miller, 1961; Janik, 2000). In gibbons and songbirds, duets are used for pair bonding ceremonies, agonistic interactions, territorial defense, and mate defense against rivals of the same sex (Estes and Goddard, 1967; Marler and Tenaza, 1977; Arro-

wood, 1988; Malacarne *et al.*, 1991; Geissmann and Orgeldinger, 2000; Slater, 2003). However, the results of this study do not seem to support this interpretation since only a few whistle types had the tendency to follow one another more often than different types. In a different scenario, two individuals could answer each other's whistles with a different whistle type rather than the same. If that were the case, whistle sequences could potentially be formed by two or more individuals. However, even though we do not have any direct evidence for or against this possibility, we think that this scenario is rather unlikely.

We propose therefore that whistle sequences are mainly emitted by single individuals and may at the most be answered by another sequence from a different whale, which is close by. In particular, the nonexistent overlap of different whistles and the continuous energy level within the sequences (see Fig. 2) support this possibility.

Compared to the loud songs of humpback whales (Au *et al.*, 2006), gibbons (e.g., McAngus Todd and Merker, 2004), and songbirds (e.g., Brackenbury, 1979), killer whale whistle sequences are relatively low in sound pressure levels (Thomsen *et al.*, 2001; Miller 2006). Thus they may be used as more intimate signals between a limited number of close individuals, which would vastly limit the number of eavesdroppers listening in on the sequences (for a review on public and private signals refer to Dabelsteen, 2005). If this were the case, then these sequences would almost definitely not be used as advertisement displays such as songs in other species. It is possible that whistles are body-contact enjoyment sounds, such as laughter in chimpanzees (*Pan troglodytes*; Marler and Tenaza, 1977; Goodall, 1986) or purring in cats (Peters, 1984); however, the elaborate nature of whistle sequences and the stereotypy of a variety of different whistle signals do not support this idea.

In this context, it should be noted that all members within one community probably share the same set of stereotyped whistles (Riesch *et al.*, 2006). Thus, information provided by them might be potentially available to all members of the community and it is unclear then why such a rather universal signal should be kept private. It is noteworthy that sequences were often heard when groups of interacting males were in the vicinity, and often were the only group within range of the hydrophone. These male-only social interactions are quite frequent in northern resident killer whales and usually involve at least one adult male and one or more adolescents [age class assigned according to age-related morphological changes: Olesiuk *et al.*, 1990; for details on all-male groups see Rose, N.A. (1992). Ph.D. thesis, University of California, Santa Cruz, CA (unpublished)]. Rose (1992) proposed that male-only social interactions serve an affiliative function, since agonistic behavior was not observed during surface interactions and males from all age groups (primarily unrelated individuals) were involved. However, one cannot rule out that these are competitive but highly ritualized interactions where, for example, some of the males might compete for access to breeding females. Whistle sequences might function as a means to coordinate these interactions. Here, they could encode the affiliative or agonistic/competitive motivation of the signaler with long and complex sequences

representing a higher motivation than shorter and simpler ones. Communication during these events may be kept private to prevent or minimize attraction by rival males. Alternatively, whistle sequences might function to initiate or strengthen male-specific relationships, and to give adolescents the possibility to learn male-specific cognitive and social skills (Rose, 1992). Finally, if these represent alliances of males used to herd females for mating, as described for bottlenose dolphins (e.g., Connor *et al.*, 1992), male talk should also be kept rather quiet so as not to alert potential competitors to a mating site.

A more detailed look at bridge elements may lead them to being grouped into several structurally similar categories, as structural variability was strong. Finally, future studies using underwater cameras together with hydrophone arrays could help us clarify the specific function of whistle sequences in their repertoire of social behavior among individual males.

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Arrowood, P. C. (1988). “Duetting, pair bonding and agonistic display in parakeet pairs.” *Behaviour* **106**, 129–157.

Attneave, F. (1959). *Application of Information Theory to Psychology* (Rinehart and Winston, New York).

Au, W. W. L., Pack, A. A., Lammers, M. O., Herman, L. M., Deakos, M. H., and Andrews, K. (2006). “Acoustic properties of humpback whale song,” *J. Acoust. Soc. Am.* **120**, 1103–1110.

Bain, D. E. (1986). “Acoustic behavior of *Orcinus*: Sequences, periodicity, behavioral correlates and an automated technique for call classification,” in *Behavioral Biology of Killer Whales*, edited by B. C. Kirkeveld and J. S. Lockard (Alan R. Liss, Inc., New York), pp. 335–371.

Barrett-Lennard, L. G., Ford, J. K. B., and Heise, K. A. (1996). “The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales,” *Anim. Behav.* **51**, 553–565.

Brackenbury, J. H. (1979). “Power capabilities of the avian sound-producing system,” *J. Exp. Biol.* **78**, 163–166.

Bradbury, J. W., and Vehrencamp, S. L. (1998). *Principles of Animal Communication* (Sinauer Associates, Sunderland, MA).

Byrne, R. W. (1982). “Primate vocalizations: Structural and functional approaches to understanding,” *Behaviour* **80**, 241–258.

Caldwell, M. C., and Caldwell, D. K. (1968). “Vocalizations of naive captive dolphins in small groups,” *Science* **159**, 1121–1123.

Catchpole, C. K., and Slater, P. J. B. (1995). *Bird Song: Biological Themes and Variations* (Cambridge University Press, Cambridge).

Connor, R. C., Smolker, R. A., and Richards, A. F. (1992). “Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.),” *Proc. Natl. Acad. Sci. U.S.A.* **89**, 987–990.

Dabelsteen, T. (2005). “Public, private or anonymous? Facilitating and

countering eavesdropping,” in *Animal Communication Networks*, edited by P. K. McGregor (Cambridge University Press, Cambridge), pp. 38–62.

Deecke, V. B., Ford, J. K. B., and Spong, P. (2000). “Dialect change in resident killer whales: Implications for vocal learning and cultural transmission,” *Anim. Behav.* **60**, 629–638.

Deecke, V. B., Ford, J. K. B., and Slater, P. J. B. (2005). “The vocal behaviour of mammal-eating killer whales: Communicating with costly calls,” *Anim. Behav.* **69**, 395–405.

Devenport, L. D., and Merriman, V. J. (1983). “Ethanol and behavioral variability in the radial-arm maze,” *Psychopharmacology (Berlin)* **79**, 21–24.

Estes, R. D., and Goddard, J. (1967). “Prey selection and hunting behavior of the african wild dog,” *J. Wildl. Manage.* **31**, 52–70.

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., Ellis, G. M., and Balcomb III, K. C. (2000). *Killer Whales*, 2nd ed. (UBC Press, Vancouver).

Ford, J. K. B., and Fisher, H. D. (1983). “Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia,” in *Communication and Behavior of Whales*, edited by R. Payne (West View Press Inc., Boulder, Colorado), pp. 129–161.

Frick, F. C., and Miller, G. A. (1951). “A statistical description of operant conditioning,” *Am. J. Psychol.* **64**, 20–36.

Geissmann, T., and Orgeldinger, M. (2000). “The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*,” *Anim. Behav.* **60**, 805–809.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior* (The Belknap Press of Harvard University Press, Cambridge).

Gourbal, B. E. F., Barthelemy, M., Petit, G., and Gabrion, C. (2004). “Spectrographic analysis of the ultrasonic vocalisations of adult male and female BALB/c mice,” *Naturwiss.* **91**, 381–385.

Hauser, M. D. (1997). *The Evolution of Communication* (MIT Press, Cambridge, MA).

Holy, T. E., and Guo, Z. (2005). “Ultrasonic songs of male mice,” *PLoS Biol.* **3**, 2177–2186.

Janik, V. M. (2000). “Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*),” *Science* **289**, 1355–1357.

Lilly, J. C., and Miller, A. M. (1961). “Vocal exchanges between dolphins,” *Science* **134**, 1873–1876.

Malacarne, G., Cucco, M., and Camanni, S. (1991). “Coordinated visual displays and vocal duetting in different ecological situations among Western Palearctic non-passerine birds,” *Ethol. Ecol. Evol.* **3**, 207–219.

Marler, P., Tenaza, R. (1977). “Signaling behavior of apes with special reference to vocalization,” in *How Animals Communicate*, edited by T. A. Sebeok (Indiana University Press, Bloomington, IN), pp. 965–1033.

Martin, P., and Bateson, P. (1993). *Measuring Behavior: An Introductory Guide*, 2nd ed. (Cambridge University Press, Cambridge).

McAngus Todd, N. P., and Merker, B. (2004). “Siamang gibbons exceed the secular threshold: Intensity of the song of *Hylobates syndactylus*,” *J. Acoust. Soc. Am.* **115**, 3077–3080.

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., and Solow, A. R. (2004). “Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*,” *Anim. Behav.* **67**, 1099–1107.

Mitani, J. C., and Gros-Louis, J. (1998). “Chorusing and call convergence in chimpanzees: Tests of three hypotheses,” *Behaviour* **135**, 1041–1064.

Olesiuk, P. F., Bigg, M. A., and Ellis, G. M. (1990). “Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State,” *Rep. Int. Whal. Comm.* **12**, 209–243.

Payne, R. S., and McVay, S. (1971). “Songs of the humpback whales,” *Science* **173**, 585–597.

Peters, G. (1984). “On the structure of friendly close range vocalizations in terrestrial carnivores (Mammalia: Carnivora: Fissipedia),” *Z. Säugetierkunde* **49**, 157–182.

Quinn, G. P., and Keough, M. J. (2002). *Experimental Design and Data Analysis for Biologists* (Cambridge University Press, Cambridge).

Riesch, R., Ford, J. K. B., and Thomsen, F. (2006). “Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*,

- off British Columbia,” *Anim. Behav.* **71**, 79–91.
- Slater, P. J. B. (2003). “Fifty years of bird song research: A case study in animal behaviour,” *Anim. Behav.* **65**, 633–639.
- Thomsen, F., Franck, D., and Ford, J. K. B. (2001). “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., and Ford, J. K. B. (2002). “On the communicative significance of whistles in wild killer whales (*Orcinus orca*),” *Naturwiss.* **89**, 404–407.
- Tyack, P. L. (1998). “Acoustic communication under the sea,” in *Animal Acoustic Communication—Sound Analysis and Research Methods*, edited by S. L. Hopp, M. J. Owren, and C. S. Evans (Springer-Verlag, Berlin), pp. 163–220.