

Whistle communication in mammal-eating killer whales (*Orcinus orca*): further evidence for acoustic divergence between ecotypes

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Abstract Public signaling plays an important role in territorial and sexual displays in animals; however, in certain situations, it is advantageous to keep signaling private to prevent eavesdropping by unintended receivers. In the northeastern Pacific, two populations of killer whales (*Orcinus orca*), fish-eating “resident” killer whales and mammal-eating “transient” killer whales, share the same habitat. Previous studies have shown that residents use whistles as private signals during close-range communication, where they probably serve to coordinate behavioral interactions. Here, we investigated the whistling behavior of mammal-eating killer whales, and, based on divergent

social structures and social behaviors between residents and transients, we predicted to find differences in both whistle usage and whistle parameters. Our results show that, like resident killer whales, transients produce both variable and stereotyped whistles. However, clear differences in whistle parameters between ecotypes show that the whistle repertoire of mammal-eating killer whales is clearly distinct from and less complex than that of fish-eating killer whales. Furthermore, mammal-eating killer whales only produce whistles during “milling after kill” and “surface-active” behaviors, but are almost completely silent during all other activities. Nonetheless, whistles of transient killer whales may still serve a role similar to that of resident killer whales. Mammal-eating killer whales seem to be under strong selection to keep their communication private from potential prey (whose hearing ranges overlap with that of killer whales), and they appear to accomplish this mainly by restricting vocal activity rather than by changes in whistle parameters.

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Introduction

Acoustic communication often involves several signalers and receivers in a network (McGregor et al. 1999). This is especially pertinent in long-range communication, where a signal might reach a large number of individuals, but it is also relevant at close ranges, where under certain circumstances signals can reach multiple receivers (Peake 2005). Thus, information is sometimes passed on to unintended receivers, so-called eavesdroppers (McGregor et al. 1999; Dabelsteen 2005; Peake 2005), which can be competitors

(McGregor et al. 1999; Dabelsteen 2005; Peake 2005), predators searching for prey (e.g., Zuk and Kolluru 1998; Mougeot and Bretagnolle 2000), parasitoids searching for a host (e.g., Zuk and Kolluru 1998; Wagner and Basolo 2007), or potential prey (e.g., Barrett-Lennard et al. 1996; Fenton 2003).

For this reason, it can be advantageous for senders to either facilitate or counter eavesdropping by altering signal design depending on circumstances. Signals facilitating eavesdropping are called public signals (Dabelsteen 2005). Those used as territorial or sexual displays, especially, are often designed to reach as many receivers as possible, and examples are sounds of chorusing insects and anurans, bird songs, or acoustic displays in mammals (e.g., Marler and Tenaza 1977; Ryan et al. 1981; Tyack 1998; Slater 2003). In certain social interactions, however, it might be advantageous to use signals that counter eavesdropping. This is true for situations where public signaling would incur risks, for example, alerting predators, parasitoids, prey, or competitors. Such acoustic signals have been defined as private, and they are usually rather quiet, comparatively high in frequency, and highly modulated in order to be more prone to attenuation and degradation over distance (reviewed in Dabelsteen 2005). Furthermore, these kinds of signals are characterized by a high degree of directionality aimed only at the intended receiver (Dabelsteen 2005).

Acoustic communication in killer whales

In the inshore waters of the northeastern Pacific, two distinct ecotypes of killer whales, *Orcinus orca*, coexist in sympatry (Ford et al. 1998; Saulitis et al. 2000). Divergence between these ecotypes seems to be primarily driven by differences in feeding ecology, with “resident” killer whales feeding exclusively on fish and “transient” killer whales foraging for mammals and the occasional seabird (Ford et al. 1998; Saulitis et al. 2000). The precise taxonomic status of different killer whale ecotypes is under debate with some researchers postulating separate species status (Morin et al. 2010). Like most other delphinids, killer whales produce three different types of acoustic signals: echolocation clicks, pulsed calls, and whistles (Popper 1980; Ford 1989; Janik 2009). While echolocation clicks are used primarily for navigation and prey detection, both pulsed calls and whistles serve as social signals. Most social sounds in killer whales are pulsed calls, which are thought to help maintain group cohesion, coordinate behaviors, and mediate group recognition (Ford 1989, 1991; Miller 2002; Thomsen et al. 2002). Based on spectrographic contour and signal stereotypy, they can be classified as discrete, aberrant, or variable (Ford 1989; Rehn et al. 2007). Each resident killer whale kin-group (matriline) has a matriline-specific dialect, a unique set of discrete pulsed call types

(Ford 1989, 1991) with closely related matriline having similar dialects (Ford 1991; Barrett-Lennard 2000; Deecke et al. 2010). Furthermore, in resident killer whales, discrete pulsed calls seem to function as public signals, as they are high-intensity signals that are audible over several kilometers underwater and are predominantly used for long-range communication (Ford 1989, 1991; Miller 2002, 2006; Thomsen et al. 2002). Transient killer whales have a more flexible social structure with some juvenile dispersal from matriline (Baird and Whitehead 2000; Baird and Dill 1996; Ford et al. 1998; Ford and Ellis 1999), and all members of a population appear to share at least some call types (Deecke 2003). Transient killer whales also run the risk of alerting potential prey to their presence because all of their prey have excellent underwater hearing ability (reviews in Au et al. 2000; Berta et al. 2006) and respond to transient pulsed calls with anti-predator behavior (Deecke et al. 2002). Accordingly, mammal-hunting killer whales show greatly reduced rates of echolocation (Guinet 1992; Barrett-Lennard et al. 1996) and usually restrict calling to the time after a successful kill or periods of social interaction (Guinet 1992; Deecke et al. 2005; Saulitis et al. 2005).

Whistle communication in killer whales

Killer whale whistles are highly modulated signals that show some degree of directionality and have lower sound pressure levels and higher fundamental frequencies compared to pulsed calls (Ford 1989; Thomsen et al. 2001; Miller 2002, 2006; Riesch et al. 2006, 2008). Fundamental frequencies of resident whistles range between 2–17 kHz (Ford 1989; Thomsen et al. 2001). Samarra et al. (2010) recently described whistles with frequencies of 17–75 kHz from some North Atlantic populations, but found that such ultrasonic whistles did not occur in recordings of North Pacific residents or transients. Although the vast majority of resident whistles seem to be variable in nature, several stereotyped whistle types have been described that are often emitted in complex sequences (Riesch et al. 2006, 2008). Compared with pulsed calls, killer whale whistles show all the characteristics of private signals designed to limit the number of eavesdroppers (Holland et al. 1998; Dabelsteen 2005; Riesch et al. 2008). However, the whistling behavior of transients has not been investigated so far.

In the present study, we conducted an in-depth analysis of whistle structure of mammal-eating killer whales and analyzed the behavior context in which transient killer whales engage in whistle communication. We then compared both the behavior context and the whistle structure to findings in fish-eating resident killer whales. Since fish-eating and mammal-eating killer whales clearly differ in

their social structure and social behavior, we predicted to find differences in whistle usage between the two ecotypes. Because of greater costs from eavesdropping prey, we expected to find (1) that whistle characteristics of mammal-eating killer whales should show even stronger shifts toward those of private signals than observed in fish-eating killer whales, (2) that like pulsed calls, overall whistle rates of transients should be lower than those of residents, and (3) that transient killer whales should use whistles preferentially to pulsed calls in contexts associated with active search for prey.

Materials and methods

Analysis of whistle structure

We screened approximately 60 h of recordings of West Coast transient killer whales for whistles using real-time spectrographic analysis (Raven version 1.2.1, Cornell Lab of Ornithology, 2005). Whistles were classified into variable and stereotyped. Stereotyped whistles had a discrete spectrographic contour and were found repeatedly in 12 or more recordings (see also supplementary Table S1). Variable whistles, on the other hand, did not have stereotyped contours and were thus only found once and in a single recording. We named stereotyped whistles alphanumerically as TW1 (transient whistle type 1), TW2, and so on (see also Riesch et al. 2006, 2008). Original whistle categorization was conducted by only one of the authors (R.R.), but was subsequently confirmed by a test for interobserver reliability (see below).

For the analysis of whistle structure, we measured bioacoustic parameters of all whistles that had adequate signal-to-noise ratios. Using the “selection and measurements” functions in Raven, version 1.2.1, we measured start frequency, end frequency, minimum frequency, maximum frequency, frequency bandwidth, dominant frequency, and whistle duration. Furthermore, following the definition of Steiner (1981), we counted the number of frequency modulations (i.e., changes of direction in the fundamental frequency from rising to falling and vice versa).

Recordings came from the entire known range of West Coast transients between Monterey Bay, California and Glacier Bay, Alaska. Approximately 41 h of these were made during dedicated focal follows conducted in 1999–2008 by one of the authors (V. Deecke). During focal follows, the animals were followed in small (6–7 m) boats and recordings were made using dippable (Offshore Acoustics) hydrophones or towable hydrophone arrays (Benthos AQ-4 elements with Texas Instruments INA106 or Magrec HP-02 pre-amplifiers) onto DAT (Sony TCD-D8 and Sony PCM-M1) or solid-state recorders (Alesis ADAT

HD-24 or Marantz PMD671). All systems used for this analysis had a flat (± 3 dB) frequency response from 0.1 to 20 kHz. To increase sample size, additional 18 h of transient recordings (obtained 1970–2002) were provided by fellow researchers (see acknowledgements for a complete list of names). These were made using a variety of recording systems, all of which had a flat frequency response from 0.1 to 12 kHz, although, for some systems, the range of the flat response extended up to 20 kHz.

Test of interobserver reliability

We used a subset of 45 randomly chosen whistles to confirm our initial classification of whistle categories, following a well-established protocol (for details, see Janik 1999; Riesch et al. 2006; Rehn et al. 2007). In short, we presented spectrograms (fast Fourier transformation size, 4,096 samples; frame length, 512 samples; overlap between frames, 75%; normalization, Hamming) of mammal-eating killer whale whistles to three observers. All whistles were printed on separate 8×10-cm sheets, and spectrograms were presented in a random order. All observers were naïve to spectrographic analysis and were asked to divide the whistles independently by their spectrographic contour and length into as many categories as appropriate to them. We then used Kappa statistic to test for interobserver reliability (Siegel and Castellan 1988).

Behavior context of transient killer whale whistles

Since information on distance and behavior of recorded animals was not always available for recordings contributed by other researchers, this analysis was restricted to recordings made during dedicated focal follows. These were made between 1999 and 2008 in Southeast Alaska and British Columbia by V. Deecke. When killer whales were encountered, the identity and size of the group was confirmed by taking identification photographs of all individuals for comparison with existing catalogs (Ford and Ellis 1999; Ellis et al. 2008). While following a group, its behavior was noted on each approach, and distance to the nearest animal was estimated on each surfacing or measured using laser rangefinders (Bushnell Yardage Pro 1000 or Leica Geovid 7×42 BDA) whenever possible. Behavior was classified as “travel”, “slow travel”, “milling”, and “surface-active” according to the group’s swim speed, synchronicity of surfacing, and directionality and occurrence of surface-active behaviors (slapping the surface with tail or pectoral fin, breaching, etc.). Milling behavior following a confirmed predation event was listed as a separate behavior category “milling after kill”. See Deecke et al. (2005) for additional detail on distance estimation and the classification of behaviors.

While pulsed calls of resident killer whales carry far underwater (detectable over several kilometers: Miller 2006), whistles and transient pulsed calls are often relatively faint (Thomsen et al. 2001; Deecke et al. 2005; Miller 2006). Hence, to minimize the number of missed sounds, we restricted this analysis to sections of recordings where at least one individual was within 500 m of the hydrophone. These sections were then further separated according to behavioral category.

To compare levels of whistle activity between different behavior contexts, and to be able to compare our findings to whistle activity in resident killer whales, we followed the protocol of Thomsen et al. (2002). In a first step, we divided all selected sections into discrete subsamples that were characterized by the same behavior context. We then divided all samples of the same encounter from the same behavioral category into 3-min sample intervals. Finally, from each pool of 3-min samples that we thus derived for each encounter and each behavioral category, we now selected every other 3-min sample interval for further analysis. If total recording time for a behavioral category from one encounter was shorter than 6 min total, we analyzed only the central 3 min, while sections shorter than 3 min were discarded. This resulted in 244 samples from 29 encounters. For each sample, we counted the number of whistles, and whistle sequences (a sequence consisted of at least two whistles that occurred within 5 s of each other; sensu Riesch et al. 2008), and then calculated the number of whistles and whistle sequences per animal per minute. To avoid pseudoreplication, we pooled all samples from the same encounter and same behavior context, which means that all data points within a behavioral category are independent, but some data points in different behavioral categories stem from the same encounter. Since whistle behavior was not normally distributed, we tested for differences in whistle activity with a Kruskal–Wallis H test, and then used Dunn’s multiple comparisons to identify homogeneous subsets.

Comparison of variable vs. stereotyped and resident vs. transient killer whale whistles

Prior to all multivariate analyses, whistle parameters (start frequency, end frequency, minimum frequency, maximum frequency, frequency range, dominant frequency, whistle duration, and frequency modulations) were z-transformed to normalize the variables with regards to differences in the unit of measure and in variance (Gotelli and Ellison 2004). We tested for differences in bioacoustic parameters between variable and stereotyped whistles of mammal-eating killer whales by means of a multivariate GLM (MANOVA) with z-transformed whistle parameters as dependent variables and whistle type (‘variable’ vs. ‘stereotyped’) as fixed

factor. In a similar MANOVA model, we subsequently tested for differences between stereotyped transient whistle categories with z-transformed whistle parameters as dependent variables, and stereotyped whistle categories (“TW1”, “TW2” or “TW3”) as fixed factor.

To provide an intuitive metric for differences between stereotyped whistles of transient killer whales, we conducted discriminant function analysis (DFA) on z-transformed whistle parameters. We used a jack-knife (“leave-one-out”) sampling scheme as a cross-validation technique (i.e., each case is classified by the functions derived from all cases other than that case). *A priori* probabilities were calculated based on group-sizes, and these were then used to calculate the proportional-by-chance accuracy by summing the squares of all prior probabilities. An overall classification success for the model was provided, and the grouping variable was stereotyped whistle category (“TW1”, “TW2”, or “TW3”).

We extracted and reanalyzed bioacoustic parameters of northern and southern resident killer whales from a previous study (Riesch et al. 2006) and tested for differences between stereotyped whistles of different killer whale populations by means of a full-factorial multivariate GLM (MANOVA). The dependent variables were again z-transformed whistle parameters, and population (“transient”, “northern resident” or “southern resident”) was the fixed factor.

Finally, we tested for differences between stereotyped whistles from different killer whale ecotypes by conducting another jack-knife DFA. *A priori* probabilities were again calculated based on group-sizes, the grouping variable was population (“transient”, “northern resident”, or “southern resident”), and the dependent variables were the same as for the previous DFA.

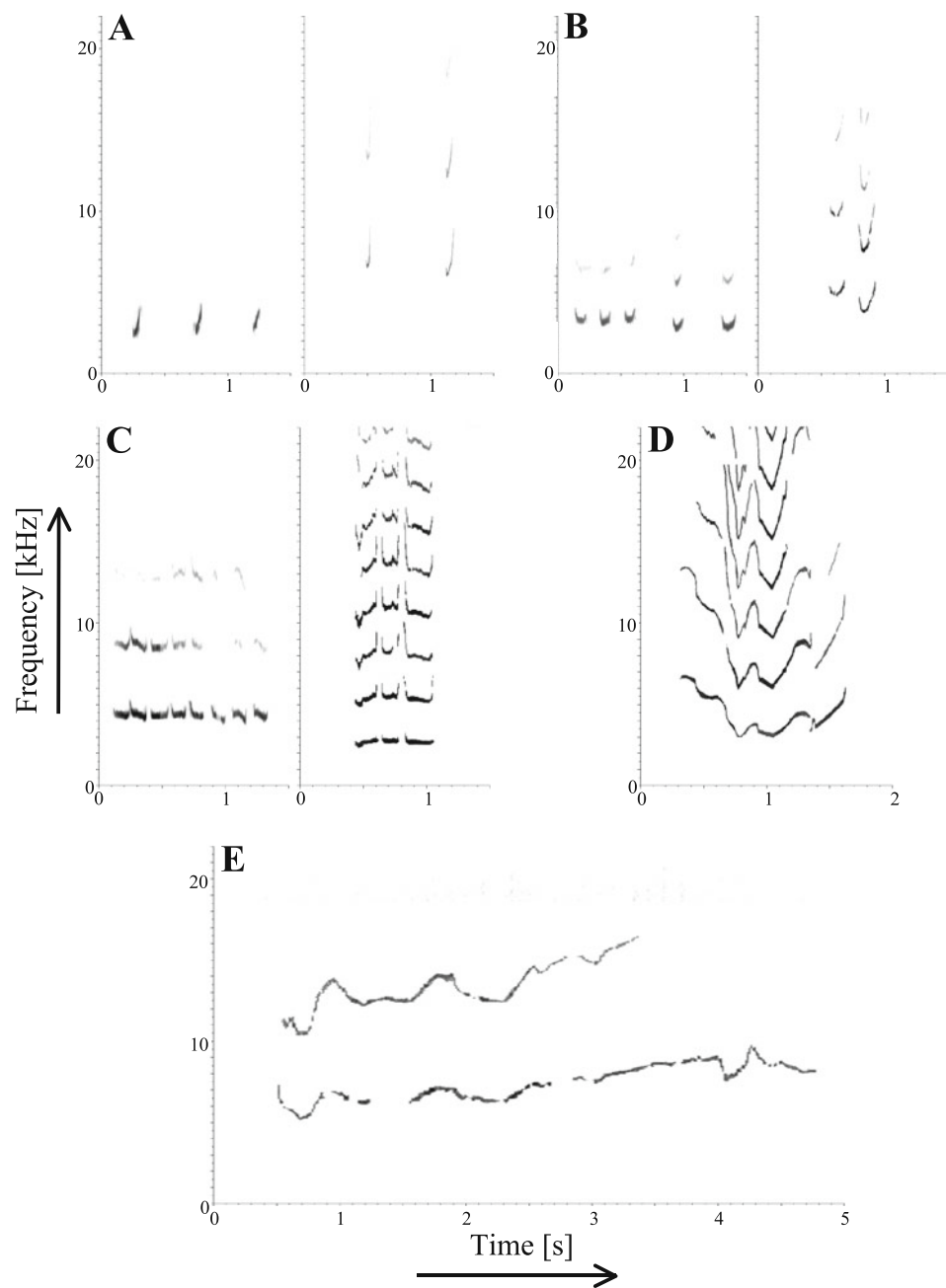
All statistical analyses were conducted using PASW Statistics 18.0.2 for Mac (SPSS Inc. 2010), with the exception of the Kruskal–Wallis H test and Dunn’s multiple comparisons, which were calculated using InStat 3.0b for Mac (GraphPad Software, Inc. 2003).

Results

Transient killer whale whistles

We measured bioacoustic parameters of 1,218 whistles. Most of these (897) appeared to be variable in structure with no apparent similarities in spectrographic contour, while 321 could be grouped into one of three discrete whistle categories: TW1, TW2, and TW3 (Fig. 1). These whistles were comprised of “chirps” with a U- to W-shaped frequency contour and were often multilooped (i.e., repetitive sequences of the same whistle type; Fig. 1).

Fig. 1 Representative spectrograms of multilooped transient whistle types **A** TW1, **B** TW2, and **C** TW3, as well as **D** and **E** two variable whistles (fast Fourier transformation size: 4,096 samples; frame length: 512 samples; overlap between frames: 75%; normalization: Hamming)



However, all stereotyped whistles were also found as isolated whistles. Overall, 42% (507 whistles) of all analyzed transient whistles were produced as isolated signals, while 58% (711 whistles) were produced as part of whistle sequences. These sequences consisted of 3.48 ± 2.13 (mean \pm SD) individual whistles, the interval between consecutive whistles within the sequence was 0.42 ± 0.77 s, and on average 6.00 ± 3.55 animals (encounters with reliable animal count, $N=21$) were present during recordings that contained whistle sequences. Average intervals between isolated whistles lasted $102.33 \pm$

153.16 s, and on average, 4.90 ± 2.28 animals were present during recordings containing isolated whistles (encounters with reliable animal count, $N=30$). Variable and stereotyped whistles differed significantly in their whistle parameters (MANOVA: $F_{8,1209}=27.393$, $P<0.001$): In general, variable whistles tended to be longer in duration than stereotyped whistles, had slightly higher maximum frequencies, and exhibited more frequency modulations (Table 1). We could not find any indication for differences in whistle repertoires between different transient groups (Online Supplementary Table S1). Instead, all three stereo-

Table 1 Descriptive statistics (mean±SD) of transient killer whale whistles and of stereotyped whistles between communities of T (transients), NR (northern residents), and SR (southern residents)

Whistle	N	Start frequency [kHz]	End frequency [kHz]	Minimum frequency [kHz]	Maximum frequency [kHz]	Frequency range [kHz]	Dominant frequency [kHz]	Whistle duration [s]	Frequency modulations
Among transients									
Variable	897	4.56±1.69	4.85±1.92	3.81±1.41	5.49±1.99	1.69±1.22	4.90±1.98	0.65±0.84	2.8±4.4
TW1	70	3.79±1.34	4.86±1.96	3.24±1.12	4.89±1.95	1.65±1.13	3.68±1.36	0.10±0.05	1.0±0.0
TW2	154	4.58±1.30	4.61±1.33	3.64±1.13	4.86±1.32	1.22±0.53	4.93±2.17	0.13±0.04	1.1±0.5
TW3	97	4.07±0.92	4.13±0.97	3.33±0.72	4.34±0.97	1.01±0.49	4.11±1.38	0.13±0.04	1.7±1.1
Between communities									
T	321	4.25±1.25	4.52±1.42	3.46±1.03	4.71±1.41	1.25±0.73	4.41±1.87	0.12±0.04	1.3±0.8
NR	395	8.42±2.81	4.63±1.11	4.23±0.84	9.56±2.75	5.31±2.68	8.60±3.23	1.19±0.46	21.2±26.5
SR	45	5.78±1.18	5.35±0.83	4.50±0.54	6.80±1.19	2.30±0.99	5.98±1.63	4.47±2.91	26.8±22.6

NR and SR values were reanalyzed from Riesch et al. 2006

typed whistles appear to be part of the same, shared repertoire.

The MANOVA confirmed that stereotyped whistle categories differed significantly in their whistle parameters ($F_{16,622}=19.995$, $P<0.001$), and post hoc analysis revealed that this was due to significant differences in acoustic parameters between at least two whistle types (Fisher's Least Significant Differences, all comparisons $P\leq 0.021$; except for TW1 vs. TW2 (end frequency, maximum frequency, and frequency modulations), TW1 vs. TW3 (start frequency, minimum frequency, and dominant frequency), and TW2 vs. TW3 (whistle duration), all $P>0.120$).

The DFA classified 70.4% of all stereotyped whistles into the correct whistle category (compared with the proportional-by-chance probability of 36.9%; Fig. 2a), the variable with the most discriminatory power was start frequency (Wilks' lambda=0.931, $F_{2,318}=11.829$, $P<0.001$; see Online Supplementary Table S2), and individual classification success was 94.2% for TW1, 67.1% for TW2, and 35.1% for TW3 (Fig. 2a).

In two different recordings, we found one whistle each that closely resembled stereotyped whistles of resident killer whales in spectrographic contour and bioacoustic parameters. One resembled whistle W6 of the northern resident killer whales, the other SW1 of the southern resident killer whales (Riesch et al. 2006; see Online Supplementary Fig. S1). For both recordings, no resident killer whales were observed during the recorded encounter with transients (V. Deecke, pers. observation, and J.K.B. Ford, pers. communication).

Test for interobserver reliability

The visual inspection method showed that observers overall agreed on the classification of stereotyped whistles versus

variable whistles. If only stereotyped whistle types were considered independently and all variable whistles were considered as a single residual class, the degree of

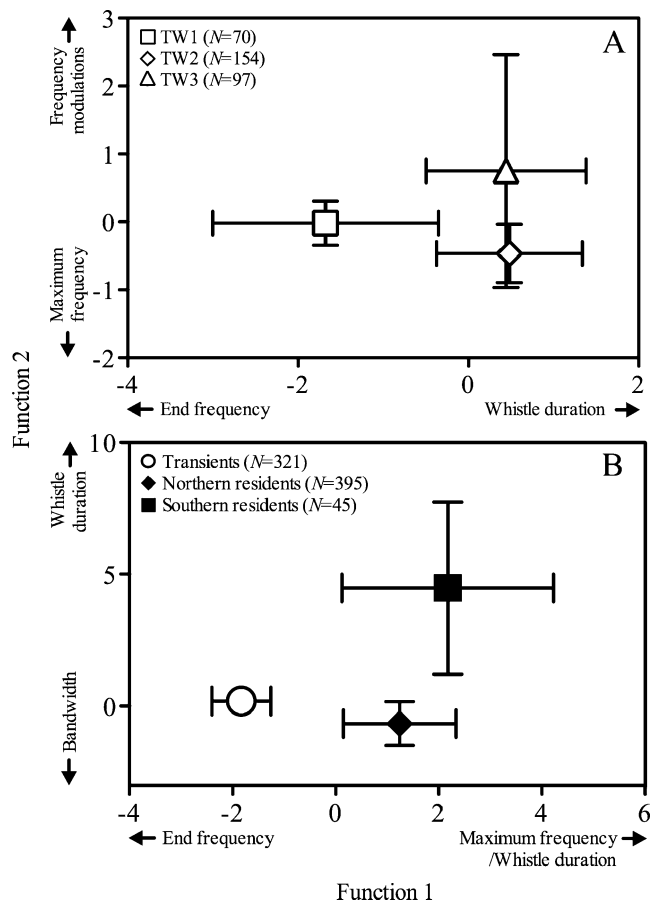


Fig. 2 Discriminant function analyses (group centroids±SDs) for separation of stereotyped whistles of **A** transient killer whales and **B** three different populations of killer whales from the northeastern Pacific

interobserver reliability was very high (Kappa statistic, $\kappa=0.88$; $Z=8.47$; $P<0.0001$; Table 2). However, two observers placed two stereotyped whistles from category TW3 into a separate whistle category, and one observer placed two variable whistles into their own stereotyped whistle category (Table 2; Online Supplementary Fig. S2).

Behavior context of transient killer whale whistles

Most whistling occurred during “milling after kill” (median whistle rate, 0.14 whistles per animal per min; interquartile range (IQR), 0.05–0.48) and “surface-active” (median, 0.00 whistles per animal per min; IQR, 0.00–1.01), while transients were usually silent during “milling” (median, 0.00 whistles per animal per min; IQR, 0.00–0.05), “slow travel” (median, 0.00 whistles per animal per min; IQR, 0.00–0.00), and “travel” (median, 0.00 whistles per animal per min; IQR, 0.00–0.01). Accordingly, we found significant differences between whistling rates across behavioral categories (Kruskal–Wallis H test: $H_4=19.622$, $P=0.0006$), and “milling after kill” had significantly higher whistling rates than “slow travel” (Dunn’s test, $Q_{11,10}=3.486$, $P<0.001$) and “travel” ($Q_{11,17}=3.277$, $P<0.01$). All other comparisons were not significant (Fig. 3).

Comparison of resident and transient killer whale whistles

In the GLM, “population” had a significant influence on stereotyped whistle parameters ($F_{16,1502}=180.096$, $P<0.001$), and post hoc analysis revealed that this was due to significant differences in most acoustic parameters between all three populations (Fisher’s Least Significant Differences: all comparisons $P\leq 0.001$ except for end

frequency, northern residents vs. transients, $P=0.253$; minimum frequency, northern residents vs. southern residents, $P=0.062$; and frequency modulations, northern vs. southern residents, $P=0.072$).

The DFA classified 91.7% of all stereotyped whistles into the correct group (compared to the proportional-by-chance probability of 45.1%; Fig. 2b) and the variables with the most discriminatory power were maximum frequency (Wilks’ lambda=0.468, $F=430.555$, $P<0.001$) for discriminant function 1, and whistle duration (Wilks’ lambda=0.363, $F=665.804$, $P<0.001$; see Online Supplementary Table S3) for discriminant function 2. Classification success was highest for transient whistles (98.8%), second best for northern resident whistles (88.9%), and lowest for southern resident whistles (66.7%). Furthermore, differences between ecotypes and within ecotypes clearly follow a different trajectory: transient whistles differed from those of residents mainly in whistle duration, end frequency, and maximum frequency, while northern residents differed from southern residents mainly in whistle duration and bandwidth (Fig. 2b).

Discussion

We investigated whistle communication in mammal-eating killer whales from the northeastern Pacific and found that similar to fish-eating resident killer whales, transients also use a combination of variable and stereotyped whistles, and have a tendency to emit whistles as whistle sequences (Riesch et al. 2006, 2008). Using three different statistical methods (MANOVA, DFA, and the test for interobserver reliability), we found evidence for pronounced differences

Table 2 Categorization of whistles by mammal-eating killer whales according to three naïve human observers

Whistle type	Whistle type					
	Variable	TW1	TW2	TW3	Stereotyped X	Stereotyped Y
2 (3)	25 (3)	4 (3)	1 (3)	13 (3)	23 (2)	8 (1)
3 (3)	27 (3)	10 (3)	9 (3)	16 (3)	26 (2)	20 (1)
5 (3)	28 (3)	30 (3)	19 (3)	23 (1)		
6 (3)	29 (3)	39 (3)	24 (3)	26 (1)		
7 (3)	31 (3)	40 (3)	35 (3)	34 (3)		
8 (2)	32 (3)					
11 (3)	33 (3)					
12 (3)	36 (3)					
14 (3)	37 (3)					
15 (3)	38 (3)					
17 (3)	41 (3)					
18 (3)	42 (3)					
20 (2)	43 (3)					
21 (3)	44 (3)					
22 (3)	45 (3)					

Numbers correspond to the internal identification number of the whistle, while numbers in parentheses indicate how many of the three observers put the corresponding whistle into one type. Identification numbers of stereotyped whistles are in bold

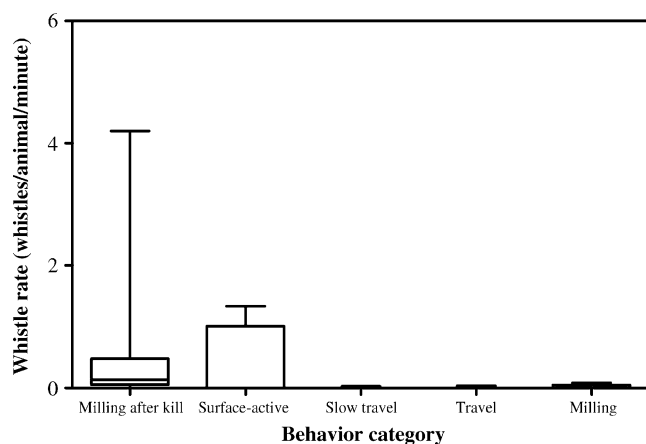


Fig. 3 Rates of whistle production across behavior categories in transient killer whales. Milling after kill, $N=12$; surface-active, $N=5$; slow travel, $N=11$; travel, $N=18$; and milling, $N=5$

between variable and three distinct stereotyped whistle categories. However, all West Coast transients seem to share the same whistle repertoire. Furthermore, the behavior context and the bioacoustic parameters of transient whistles are clearly distinct from those in resident killer whales.

Whistles of the type TW3 clearly exhibit the most intra-category variability (Fig. 1c), which led to low classification success in the DFA and to two observers dividing TW3s into two distinct subcategories (Online Supplementary Figure S2). Based on those results, one could make the argument that TW3 potentially should have been split into two different subcategories, or that some whistles that we incorporated into the category TW3 (the right-hand spectrogram in Fig. 1; Online Supplementary Figure S2) should rather be classified as aberrant TW3 (i.e., are signals that are based clearly on discrete whistles, but were highly modified or distorted in structure; Ford 1989). Nonetheless, it is also important to keep in mind that we did not include any bioacoustic measurements in our statistical analysis that incorporate whistle contour. Therefore, we decided to stay with our original classification that lumps all of these whistles into the same category (TW3), but suggest that future work that incorporates more in-depth contour analysis (e.g., neural network analyses; Deecke and Janik 2006) could attempt to better resolve this issue. However, whether or not TW3 were actually split into two different categories, would not change any of our general interpretations that we will discuss in the following paragraphs.

Transient whistles versus resident whistles

Stereotyped whistles of mammal-eating killer whales are clearly different from those of resident fish-eating killer whales: whistles of transient killer whales generally have lower dominant frequencies, narrower frequency ranges, are

shorter in duration, and have fewer frequency modulations (Thomsen et al. 2001; Riesch et al. 2006, 2008). Contrary to our first prediction, this means that transient whistles are actually moving away from the characteristics that are usually ascribed to private signals (higher frequencies, wider frequency range, and greater degree of frequency modulations; Holland et al. 1998; Dabelsteen 2005). We did find support for our second prediction, however, as whistle rates across behavior categories were lower in transients compared with whistle rates published for resident killer whales (Thomsen et al. 2002). While stereotyped whistles of resident killer whales (in particular, northern resident whistles) show relatively high variability in several bioacoustic parameters as well as in general spectrographic contour between whistle types, transient whistle types all seem to be variations of a common U- to W-shaped contour (see Riesch et al. 2006, 2008). Hence, in addition to having repertoires of pulsed calls that are distinct from residents (Ford 1984; Deecke 2003), transient killer whales also have a distinct, population-specific repertoire of whistles.

Vocal imitation/mimicry of resident whistles

We found two whistles that could have been imitations of stereotyped whistles of resident killer whales. Both mimicked whistles were recorded within the range of the resident killer whale population producing the template whistle types (i.e., the W6-like whistle within the northern resident home range and the SW1-like whistle within the southern resident home range), but killer whale whistles are relatively faint signals that have a detection range of approximately 500 m (Thomsen et al. 2001). For this reason, we feel that it is unlikely that these were produced by close-by matriline of resident killer whales. Given the complexity of killer whale whistles, it is also relatively unlikely that these match resident killer whale whistle types by chance. Combined with the fact that these were the only such examples in over 40 h of recordings, this suggests that they probably are not part of the normal repertoire of transient killer whales, but most likely represent vocal imitation/mimicry, which has previously been described for killer whales and other delphinids (Ford 1991; Janik 2009; Weiß et al. 2010). However, future research will have to investigate this further.

Possible function of transient whistles

In other delphinids, stereotyped whistles often serve as individual-specific signature whistles thought to facilitate group cohesion (e.g., Caldwell and Caldwell 1971; Janik and Slater 1998; Tyack 1998; Janik 2009). In the case of male alliances in bottlenose dolphins (*Tursiops truncatus*), signature whistles are thought to additionally encode social

affiliation, as signature whistles within an alliance become more alike over time (Watwood et al. 2004). However, Riesch et al. (2006) demonstrated that stereotyped whistles in resident killer whales clearly do not serve as individual signatures. The stereotyped whistles of transients are distinct from those of residents, but there is also no indication that contour shape of whistles encodes individual identity: the transient killer whale community comprises more than 250 individuals (Ellis et al. 2008), yet there are only three stereotyped whistle types. Hence, our results are further evidence against signature whistle variation of the type described for bottlenose dolphins and other delphinids in killer whales. Nonetheless, there are two alternative hypotheses. First, the observed variability between whistles within the same type (Fig. 1) could be a sign of individual variability. In this case, all mammal-eating killer whales would use the same three whistle types, but each individual would have its own unique version of it, as has been suggested for resident killer whale pulsed calls (Nousek et al. 2006). Second, some of the whistles we classified as variable could be signature whistles. However, based on what is known about signature whistles from other delphinids, we think the second scenario is highly unlikely. According to Janik (2009), more than 50% of all whistles recorded in other delphinids are signature whistles. Yet, even though we recorded certain individuals on several different occasions (supplementary Table S1), we did not find any evidence for signature whistles in transient killer whales. While one could make the argument that individual killer whales simply have more than one signature whistle, and we thus, by chance, failed to record the same signature whistle twice, this is again unlikely. In other delphinids, individuals are able to establish their identity within a community/population with only a single signature whistle (Janik 2009). Why then would killer whales need more than a single signature whistle per individual in addition to individual variability in call characteristics (Nousek et al. 2006) and potentially signature whistle characteristics (see above) to achieve essentially the same goal?

If they are not signature whistles, what then is the function of stereotyped whistles? In resident killer whales, whistles are thought to be important close-range signals that facilitate and coordinate social interactions (Thomsen et al. 2001, 2002; Riesch et al. 2006, 2008), and consequently they are the predominant acoustic signal during close-range interactions, while pulsed calls dominate all other behavior states (Thomsen et al. 2002; Riesch et al. 2008). Furthermore, their physical characteristics (Table 1, reanalyzed from Riesch et al. 2006, 2008) suggest that they are signals designed to prevent eavesdropping by unintended receivers, which in the case of residents are most likely competitors/rivals (i.e., other resident killer whales; Riesch et al. 2008).

The function of transient whistles, on the other hand, is more difficult to identify, because rather than being the predominant acoustic signal during social interactions, transients generally do not vocalize at all except during “milling after kill” and “surface-active” behaviors (Deecke et al. 2005; this study). However, once the animals start to get vocally active both pulsed call and whistle rates increase simultaneously (Deecke et al. 2005; this study). This is strong evidence against our third prediction that transients should preferentially use their less conspicuous signals (whistles) during behaviors correlated with active search for prey because they are less likely to be detected than calls. Since transients do not appear to use whistles as a safe means of communication to avoid alerting eavesdropping prey, why do they not attempt to at least restrict conspecific eavesdropping (i.e., rival transient groups)? Compared with the resident killer whale communities, the transient killer whale community is spread out over a much larger geographic area (ranging from southern California to southeastern Alaska; Ford and Ellis 1999; Ford et al. 2000) so that chance-encounters with “rival” transient groups are much less likely. Furthermore, as Deecke et al. (2005) already argued, the noise created by an attack on marine mammals (e.g., sounds generated during prey handling and prey vocalizations) would have already alerted potential competitors to the scene, thus further decreasing the need to make whistle communication private in this particular behavior context.

Does this mean that transient whistles serve a different function than resident killer whale whistles? We can currently only speculate, as direct data are lacking. However, several indirect lines of evidence suggest that resident and transient killer whale whistles could share a similar function. First, food sharing is often observed in mammal-eating killer whales (Jefferson et al. 1991), and Deecke et al. (2005) proposed that transient pulsed calls may be important in delineating social relationships during these and similar events. If whistles served a similar function in transients and residents, we would expect the whistle rate to also increase under these circumstances, which is exactly what we found in the present study. Additionally, prey carcasses often show evidence of intricate manipulation (e.g., porpoise carcasses are completely stripped of skin and blubber; V. Deecke, pers. observation), which is bound to require a high degree of coordination between individuals. Since whistles in fish-eating killer whales are thought to coordinate behavior or social interactions (Riesch et al. 2006, 2008), whistles in mammal-eating killer whales could also play an important role here. Hence, we hypothesize that whistles in transient killer whales may also serve as signals that facilitate and coordinate close-range interactions during surface-active behavior (similar to socializing in resident killer whales)

and prey handling during feeding. Future studies will have to focus more on the specific function of whistles in transient killer whales to unequivocally answer this question.

Why do transient killer whales have such a small whistle repertoire (three stereotyped whistle types with rather similar contours), when that of resident killer whales is so elaborate (up to 11 stereotyped whistles of varying contour; Riesch et al. 2006, 2008)? We propose two mutually not exclusive hypotheses. First, as we argued above, whistles in transient killer whales may have the same function as pulsed calls during food sharing (Deecke et al. 2005), so the actual acoustic repertoire for this behavior probably encompasses the combined repertoires of pulsed calls and whistles. This decreases the need for an extensive whistle repertoire. Second, transient social structure is much more fluid than that of residents (Baird and Whitehead 2000; Baird and Dill 1996; Ford et al. 1998; Ford and Ellis 1999), and transient individuals may form temporary hunting groups with others they only encounter infrequently. In this scenario, a less complex whistle repertoire would be of great advantage in ensuring successful cooperation and temporary bonding between infrequent social companions.

Costly communication and predator–prey coevolution

The stereotyped whistles of resident and transient killer whales are clearly distinct, and it therefore seems reasonable to believe that potential prey species would be able to tell them apart as has been shown for stereotyped pulsed calls (Deecke et al. 2002). However, if this is the case, how can we explain that, compared with residents, transient whistle parameters are shifted back towards those characteristic for public signals (Holland et al. 1998; Dabelsteen 2005)?

A shift of communication to frequencies outside of the hearing range of their prey has been proposed for echolocation in bats (e.g., Fullard and Dawson 1997; but see Windmill et al. 2005). However, potential killer whale prey (pinnipeds and other cetaceans) all have hearing ranges overlapping and sometimes even exceeding that of killer whales making a shift of communication frequency not a feasible option for mammal-eating killer whales (see discussion in Deecke et al. 2005). Hence, the main strategy of transients to minimize detection by potential prey is to limit vocal communication to certain behavioral contexts, making detection based on whistle recognition by prey impossible during foraging, regardless of a potential receiver's hearing capabilities (Barrett-Lennard et al. 1996; Deecke et al. 2005). This in turn seems to have relaxed the selection on making whistles acoustically private (i.e., higher frequencies and more frequency modulations). Together with the differences in social

structure, this could explain the observed differences in acoustic parameters between resident and transient whistles.

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