

Cross-cultural and cross-ecotype production of a killer whale ‘excitement’ call suggests universality

Nicola Rehn · Olga A. Filatova · John W. Durban ·
Andrew D. Foote

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Abstract Facial and vocal expressions of emotion have been found in a number of social mammal species and are thought to have evolved to aid social communication. There has been much debate about whether such signals are culturally inherited or are truly biologically innate. Evidence for the innateness of such signals can come from cross-cultural studies. Previous studies have identified a vocalisation (the V4 or ‘excitement’ call) associated with high arousal behaviours in a population of killer whales in British Columbia, Canada. In this study, we compared recordings from three different socially and reproductively isolated ecotypes of killer whales, including five vocal

clans of one ecotype, each clan having discrete culturally transmitted vocal traditions. The V4 call was found in recordings of each ecotype and each vocal clan. Nine independent observers reproduced our classification of the V4 call from each population with high inter-observer agreement. Our results suggest the V4 call may be universal in Pacific killer whale populations and that transmission of this call is independent of cultural tradition or ecotype. We argue that such universality is more consistent with an innate vocalisation than one acquired through social learning and may be linked to its apparent function of motivational expression.

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N. Rehn (✉)
Biocenter Grindel, University of Hamburg,
Martin-Luther-King-Platz 3,
20146 Hamburg, Germany
e-mail: nicola.rehn@arcor.de

O. A. Filatova
Department of Vertebrate Zoology, Faculty of Biology,
Moscow State University,
Vorobiovy gory, 1/12,
Moscow 119992, Russia

J. W. Durban
National Marine Mammal Laboratory, Alaska Fisheries Science
Center, National Marine Fisheries Service, NOAA,
7600 Sand Point Way NE,
Seattle, WA 98115, USA

A. D. Foote
Centre for GeoGenetics, Natural History Museum,
University of Copenhagen,
Øster Volgade 5–7,
1350 Copenhagen, Denmark

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Introduction

Darwin noted cross-species and cross-cultural similarities in expressions of emotion and affective communication and suggested a role for natural selection in shaping these predictable stereotyped signals (Darwin 1872). It has been argued that innate expressions of emotion evolve through ritualisation and become exaggerated and highly stereotyped to facilitate social communication (Andrew 1963; Eibl-Eibesfeldt 1989). Evidence for the biological innateness of such expressions of emotion can come from studies of sensory impaired subjects, who could not have learned these expressions from others, or from the universality of an expression in cross-cultural comparisons (Eibl-Eibesfeldt 1989; Izard 1994; Tracy and Matsumoto 2008). Although universal and apparently innate stereotyped postures, facial and vocal expressions of emotion are well documented in humans and non-human primates

(Andrew 1963; Russell et al. 2003; Tracy and Matsumoto 2008; Davila Ross et al. 2009), there is little evidence that this Darwinian framework applies to other taxonomic groups with complex social structure and interactions, including the odontocetes or toothed whales (Connor et al. 1998).

The killer whale (*Orcinus orca*) is a highly social odontocete species (Parsons et al. 2009). The best-studied populations of killer whales are in the Northeast Pacific (Ford et al. 2000). Three culturally, ecologically and genetically distinct ecotypes of killer whale, ‘offshore’, ‘resident’ and ‘transient’, have been identified in this region (Ford et al. 2000; Yurk 2003; Hoelzel et al. 2007; Morin et al. 2010). Genetic and behavioural differences among these ecotypes are so great that it has been proposed that each ecotype be considered a distinct species or sub-species (Morin et al. 2010), and during three decades of study, there has been no social contact observed between ecotypes (Ford et al. 2000; Yurk 2003). Resident populations can be further split into vocal ‘clans’, based on their distinct, culturally transmitted vocal traditions (Ford 1991; Yurk 2003). Within each clan, all groups share at least a part of their vocal repertoire; no calls are shared between clans (Ford 1991; Yurk et al. 2002).

Studies of the vocal behaviour of killer whales found they produce a repertoire of loud stereotyped calls (Ford 1989; Ford 1991), which generally have higher source levels than variable calls (Miller 2006) and are often produced in contexts that involve long-range communication (Ford 1989; Foote et al. 2008; Filatova et al. 2009). There is strong evidence that both the production and usage of these stereotyped calls are learned (Yurk et al. 2002; Foote et al. 2006). In contrast, ‘variable’ calls have previously been reported as being less stereotyped and are used almost exclusively in close-range interactions (Ford 1989; Thomsen et al. 2002; Rehn et al. 2007). Killer whales are believed to express motivation acoustically using variable calls (Ford 1989; Rehn et al. 2007). The low

visibility marine environment is likely to favour the evolution of vocal communication over postures or facial expressions in marine species. In this study, we report a cross-cultural and cross-ecotype production of a variable call that has previously been correlated with high arousal, close-range social interactions; the ‘excitement’ or V4 call (Ford 1989; Rehn et al. 2007). Although this call has historically been categorised as a variable call (Ford 1989), the pattern of frequency modulations are sufficiently stereotyped for examples of the V4 call to be identified as a call class (Rehn et al. 2007). This structure is similar to whistle types produced in social contexts by other delphinids (Blomqvist et al. 2005). The V4 call has previously only been documented in the resident type (Ford 1989; Rehn et al. 2007).

Material and methods

Data collection

We analysed a set of 69 killer whale recordings collected from each of the three Pacific killer whale ecotypes including five vocal clans of the resident ecotype (see Table 1; see Foote et al. 2004; Rehn et al. 2007; Filatova et al. 2009 for additional details). Photo-identification data and in some cases biopsy sampling were carried out during each recording to identify which groups were present. The analysed recordings of Northern residents, Southern residents, offshores and Kamchatka residents were made during close-range interactions, e.g. social-travelling and socialising defined by Ford (1989) and Thomsen et al. (2002) at a distance of <500 m. Both behavioural states include body contacts, percussive behaviours and occasional sexual interactions (Ford 1989; Thomsen et al. 2002). The recording of the Bering Sea transients were made after a successful kill of a Northern fur seal (*Callorhinus ursinus*) when the group were feeding together. Usually,

Table 1 Details of killer whale recordings used in this study

Population	Recording area	Number of recordings	Length of recordings (min)	Number of V4 calls
Northern residents	Johnstone Strait, BC, Canada			
A clan		16	517	44
G clan		8	487	33
R clan		1	45	30
Southern residents	Haro Strait, Washington State, USA			
J clan		32	900	43
Offshores	Johnstone Strait, BC, Canada	2	60	54
Bering Sea transients	St Paul Island, Bering Sea, Alaska, USA	1	37	7
Kamchatka residents	Avacha Gulf, Kamchatka, Russia	9	89	49

the calling behaviour of transient killer whales increases after a successful kill of a marine mammal. The increase of vocal behaviour probably reflects an increase of social interactions during feeding (Deecke et al. 2005).

Acoustic analysis

Spectrograms were produced and inspected with Raven Pro software with a filter bandwidth of 88.24 Hz, FFT size of

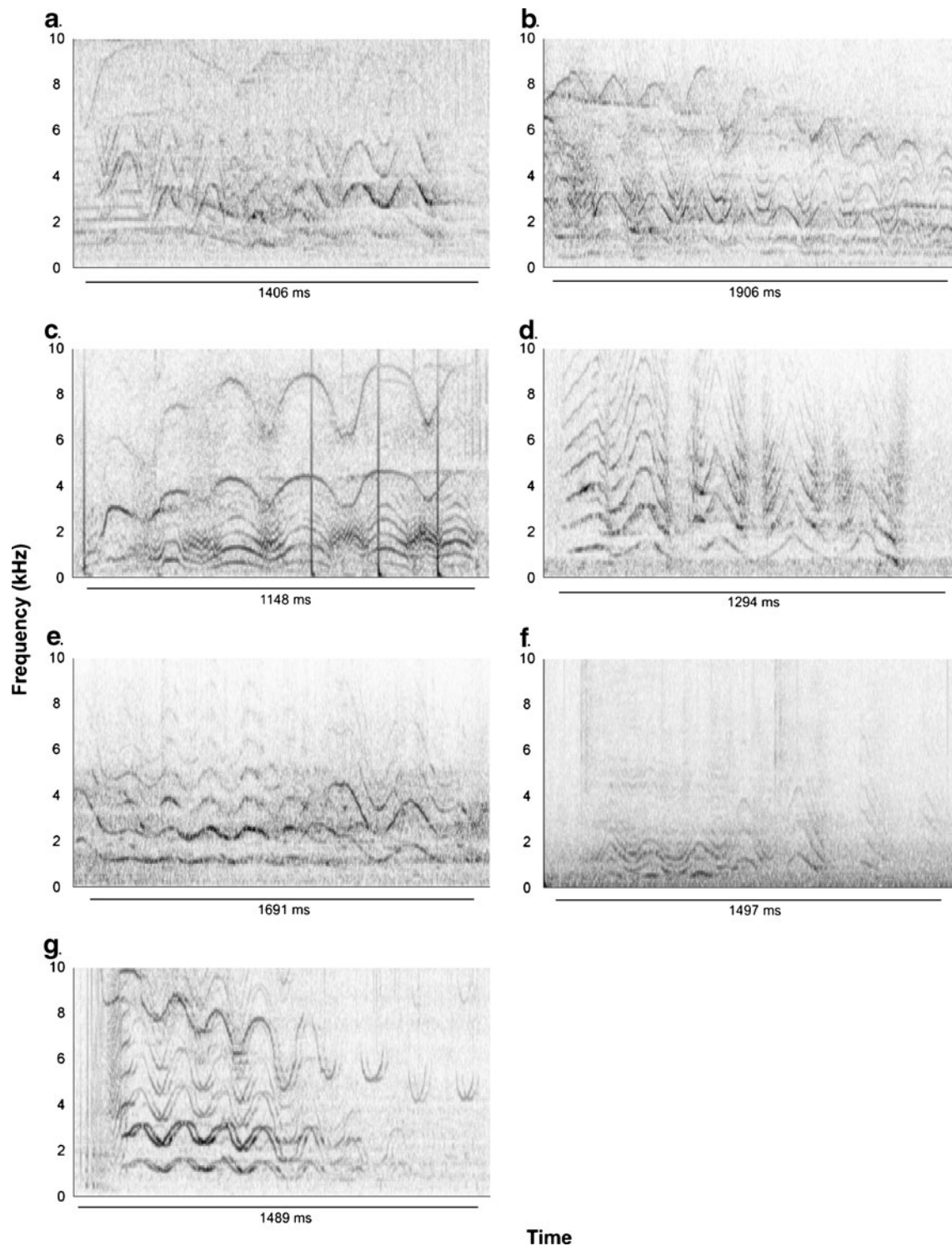


Fig. 1 Representative spectrograms of the V4 call produced by **a** A clan ESM 1; **b** G clan ESM 2; **c** R clan ESM 3; Northern residents; **d** J clan ESM 4; Southern residents; **e** offshores ESM 5; **f** Bering Sea

transients ESM 6; **g** Kamchatka residents ESM 7. Spectrograms were created with SoundRuler software using a fast Fourier transformation size of 512 samples

1,024 and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz. Recording sessions were only used when all calls were of high enough amplitude to be distinguished easily, this precluded approximately 0–30% (population dependent) of recordings. Vocalisations were then classified into categories of discrete call types by aural recognition and visual inspection of the spectrograms. Call type classifications were carried out by N.R. for the Northern residents and offshores, by O.F. for Kamchatka residents and by A.F. for the Bering Sea transients and Southern residents. The V4 call class of Northern residents varies in the mean values of duration (0.45–3.50 s), number of frequency modulations (3.45–28.15), maximum (3.71–13.73 kHz) and minimum (0.61–0.90 kHz) frequency (see Rehn et al. 2007). Despite the variation in the spectrograms, aurally, the V4 call is consistently recognisable (Rehn et al. 2007). This is consistent with a previous experimental demonstration that human observers using pattern recognition give biologically meaningful categorisation of natural signals despite variability in spectral characteristics (Janik 1999). Calls were therefore classified as a V4 call if they consisted of a sequence of rapid highly stereotyped frequency modulations and by using the spectrogram in Ford (1989) as a template.

Human observer classification

To test whether our call categorisation could be reproduced, we gave samples of randomly selected and randomly ordered categorised calls, including 47 stereotyped call types and 16 V4 calls from each population and clan, to nine human observers for reclassification (Electronic supplementary material). These nine volunteers did not include the experienced observers who conducted the original classification. The spectrograms and sound file were numbered and presented in a random order in a PowerPoint presentation. Each observer was allowed to categorise calls into as many classes as they thought appropriate. Two of the observers had previous experience with classifying killer whale calls, four had an understanding of bioacoustics but were inexperienced at call classification and three observers had no bioacoustics experience. Inter-observer agreement was assessed using a Kappa statistic (Siegel and Castellan 1988), a suitable and conservative statistic for testing inter-rater agreement of qualitative categorical items that takes into account of agreement by chance.

Results and discussion

We found calls that were independently classified as V4 calls (Table 1) by two experienced observers (N.R., A.F.) in recordings of each of the three disparate ecotypes and in

recordings of the five discrete vocal clans of the resident ecotype (Fig. 1; Electronic supplementary material). We found no long-range call types shared among vocal clans and ecotypes, consistent with previous studies (Ford 1987, 1991; Yurk 2003). Our classification was supported by the results of the human observer test, as seven out of the nine observers classified the V4 calls, as produced by all populations and clans, as one call class. Two of the observers binned two stereotyped call types in the same class as the V4 call. Two observers split the V4 calls into two and five call classes, respectively; however, both indicated that these were sub-classes of the same call class based on structure. If only the V4 calls were considered and all other stereotyped calls were considered as a single residual class, observer agreement was high (Kappa statistic, $\kappa=0.77$, $Z=13.3$, $P<0.0001$; Table 2). Considering all call type classifications, agreement was reduced but still significant (Kappa statistic, $\kappa=0.60$, $Z=62.9$, $P<0.0001$). This is consistent with a previous experiment that demonstrated both experienced and inexperienced human observers using pattern recognition can perform repeatable, consistent, biologically meaningful categorisation of killer whales call types (Yurk et al. 2002). However, agreement between the two experienced observers when classifying the V4 call was higher (100% agreement; $\kappa=1.0$, $Z=6.2$, $P<0.0001$) than among the seven observers with less or no bioacoustics experience ($\kappa=0.71$, $Z=10.3$, $P<0.0001$).

This call has previously been classified as a variable call, i.e. non-stereotyped (Ford 1989) due to the higher variation in structure than found in long-range call types. Such variation could be dependent upon individual arousal or contextual differences (Ford 1989; Rehn et al. 2007). Variation in a signal does not necessarily mean that it is not stereotyped and cannot be classified as a discrete signal type (van Hooff and Preuschoft 2003). For example, human

Table 2 Classification of the V4 call by human observers

Inter-observer comparison of binning of V4 call examples	
3 (9) OFF	38 (6) BST
12 (7) SR	41 (7) NR-AC
17 (9) NR-GC	48 (6) NR-AC
19 (7) NR-RC	51 (9) OFF
22 (7) NR-GC	54 (7) BST
26 (8) SR	56 (8) KR
30 (8) KR	58 (9) NR-AC
33 (8) NR-RC	61 (9) NR-GC

Bold numbers correspond to the position in the inter-observer agreement test that the call occurred. Numbers in parentheses show how many of the nine observers binned the corresponding V4 call into one call class. Abbreviations indicate ecotype/population/clan: *OFF* offshores, *SR* Southern residents, *NR* Northern residents (*AC*, *GC*, *RC* A, G and R clans), *KR* Kamchatka residents, *BST* Bering Sea transients

laughter and crying are highly variable (Bachorowski et al. 2001; van Hooff and Preuschoft 2003; Russell et al. 2003), but variants are still perceived as laughter or crying by conspecifics (Bachorowski et al. 2001; van Hooff and Preuschoft 2003; Russell et al. 2003). Similarly in this study, it was possible for the observers to independently and reliably replicate the classification of V4 calls despite this variation. Rehn et al. (2007) further subdivided a large dataset of V4 calls produced by the Northern residents into six sub-classes. These sub-classes may be linked to a specific, discrete state or may index the degree of the motivation being expressed; both have been suggested as the cause for such variation in human signals (Russell et al. 2003). Variation can also reduce habituation to the signal by the receiver (Bachorowski and Owren 2002). It is currently not known how killer whales perceive this variation.

Our data therefore suggest that the production of the V4 call is not correlated with ecology or the culturally transmitted stereotyped call repertoire. The production and usage of killer whale stereotyped call repertoires are transmitted through social learning (Deecke et al. 2000; Foote et al. 2006). Such a social production learning process could potentially explain the sharing of the V4 call among the clans and ecotypes included in this study. However, social contact has not been observed between ecotypes in over three decades of observation (Ford et al. 2000), and two of our study populations (Kamchatka residents and Bering Sea transients) are allopatric and out of acoustic range of the other populations included in this study. Additionally, the estimated active space of variable calls such as the V4 call is significantly less (7.8 ± 3.7 km) than the estimated active space of stereotyped calls (11.0 ± 4.7 km), which are not shared among ecotypes or vocal clans (Miller 2006). The vocal repertoires of humans include both learned vocalisations, which are culturally distinct and can be referential, and also innate, universally shared vocalisations, which are typically used in affective communication (Sauter et al. 2010). Such a combination of innate and learned vocalisations could also exist in killer whale vocal repertoires, and the universality of the V4 call may be rooted in its innateness (see Izard 1994). Although our data strongly suggest innateness of the V4 call, this could be further tested. If acquired by social learning, then we would expect the V4 call to change over time due to cultural drift and for there to be a relationship between association and acoustic similarity of the V4 call as found for stereotyped call types (see Deecke et al. 2000, 2010). However, the variability of the V4 call may mask any subtle changes due to cultural drift. The analysis of recordings from different ocean basins could also be used to investigate acquisition through social learning versus innateness. However, even if production of the V4 call is innate, its contextual usage may still have a learned component.

Ford (1989) noted an increase in the production of the V4 call during high arousal, social interactions and suggested it was an 'excitement call'. Although the V4 call is produced almost exclusively during high arousal, close-range social interactions it is still not clear what cues elicit this vocalisation or if there is cross-cultural universality between killer whale populations in the perception or attribution of this signal (see Russell et al. 2003). Cross-cultural testing has proven a useful method to investigate whether expressions of basic emotions are universally recognised across cultures (e.g. Sauter et al. 2010). Conducting such an approach through playback experiments (see Deecke 2006) may provide insights into whether the V4 call communicates the same affective cues to different killer whale vocal clans and ecotypes.

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