

# Temporal and Contextual Patterns of Killer Whale (*Orcinus orca*) Call Type Production

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## Abstract

Fish-eating killer whales *Orcinus orca* in the northeastern Pacific live in highly stable matrifocal social groups called pods. Each pod produces a repertoire of seven or more stereotyped call types. We compared the relative production of call types of free-ranging killer whale pods over time and between social contexts. The relative production of call types by each pod during directional travel was distinct over a 27-yr period; however, both temporal stability and pod distinctiveness were strongly influenced by a subset of dominant call types within the repertoire of each pod. Some call types within the repertoires contain biphonation (two overlapping independently modulated tones) and have a higher estimated active space than call types containing just one tone. In multi-pod aggregations the relative production of the dominant call types of each pod decreased and the relative production of a subset of call types that are rarely recorded from single-pod groupings increased. The majority of these contained biphonation. The data suggest a distinction between a subset of dominant call types that may function to identify the pod and a subset of less common call types including several call types containing biphonation that are more commonly produced during inter-pod affiliations.

## Introduction

Stable, shared, group-specific learnt repertoires of 'contact' or 'monitoring' calls are found in a number of species that live in stable social groups (e.g. Boughman 1997; Brown & Farabaugh 1997; Hausberger 1997; Price 1998). A function of calling in these species is to inform others of the signaller's location, but often calls have an additional function of conveying social identity and signal affiliations between individuals, enabling the distinction between a subset of conspecifics and all other conspecifics (e.g. Brown & Farabaugh 1997; Hausberger 1997; Price 1998; Boughman & Wilkinson 1998). Species that form multi-layered social groups often have a repertoire of contact signals, where different signals identify different types of affiliation, e.g.

intra- and inter-group signals (Pola & Snowdon 1975; Waser 1975; Brown & Farabaugh 1997; Hausberger 1997; Price 1998; Wilkinson 2003). The physical characteristics of vocalizations can be important in determining the social context in which they are used. For example, calls with a lower active space may be used between individuals in close contact, while those with a higher active space are used over longer distances (Pola & Snowdon 1975; Waser 1975).

Fish-eating resident killer whales of the North Pacific live in highly stable matrifocal groups known as pods, from which there is no natal dispersal by either sex (Bigg et al. 1990). Inter-pod associations are characteristic of a fission–fusion social structure and associations between pods can change over periods of hours and pods can travel

separately for days or weeks at a time (Bigg et al. 1990). Pods can be further split into intra-pod groups commonly and hereafter in this paper referred to as matriline, which typically consist of a female and two to four generations of her direct offspring (Bigg et al. 1990).

Resident killer whales call at a high rate across a range of contexts (Hoelzel & Osborne 1986; Deecke et al. 2005). Each pod has a repertoire of seven or more highly stereotyped call types (Ford & Fisher 1982; Hoelzel & Osborne 1986; Ford 1991). There is strong evidence that the usage and production of call types are learned (Deecke et al. 2000; Yurk et al. 2002; Foote et al. 2006). The relative call type production varies between pods; some call types are shared with other pods while others are pod-specific (Ford & Fisher 1982; Hoelzel & Osborne 1986; Ford 1991). It has been suggested that inter- and intra-pod variation in the relative production of call types may evolve passively due to stochastic processes (Ford 1991; Miller & Bain 2000) or actively due to selection (Yurk et al. 2002). Ford (1991) previously found that particular killer whale stereotyped call types remained in a pod's repertoire for periods of up to 28 yr (approximately one generation) and that the relative production of call types was stable over a 6-yr period. Based on their physical characteristics these stereotyped call types can be placed into two broad categories; those which contain biphonation, e.g. contain two independently modulated, overlapping tones ('two-voiced' call types) and those that do not ('single-voiced' call types; Hoelzel & Osborne 1986). Two-voiced call types have a higher mean source level and an estimated active space ( $12.4 \pm 4.3$  km) almost double that of single-voiced call types ( $6.8 \pm 3.1$  km) (Miller 2006). The low frequency component of two-voiced call types is relatively omni-directional, while the high frequency component shows stronger forward facing directionality (Miller 2002). Both components are significantly group-specific in structure (Miller & Bain 2000).

In this study, we analyse recordings collected over three decades to address two hypotheses. First, we investigate the stability over time and group distinctiveness of call repertoires. This extends earlier work by Ford (1991) by looking in detail at the relative frequency of call production over a longer time-frame, and considering different categories of calls separately. Second, we test the hypothesis that call usage differs between single- and multi-pod groupings. We further consider possible inference about the role of call structure in its contextual usage and

discuss implications for the function of such diverse call type repertoires.

## Methods

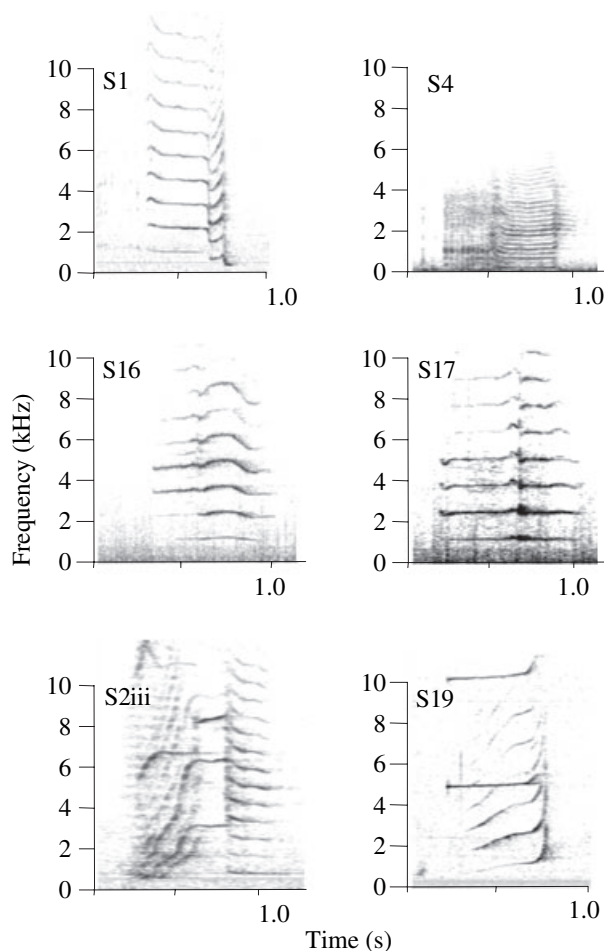
### Study Population

The three pods (J, K and L) of the Southern Resident population of killer whales are found in the nearshore waters of Washington State and British Columbia. The population comprised 86 individuals in 2003 (Van Ginneken et al. 2005), the last year recordings were made. However, L pod, which contained 42 individuals and 12 matriline in 2003 (compared to 23 and 21 individuals and four matriline each in J and K pods, respectively, Van Ginneken et al. 2005), may have a level of association between some of its constituent matriline of less than the 50% required to be classified as a true pod (Bigg et al. 1990).

### Acoustic Analysis

Recordings and visual identification of the Southern Resident population were made using the methodology described in Foote et al. (2004). All vessel-based recordings were made with the engine shut down and the approach was slow and gradual to minimize impact on the whales. Spectrograms were produced for all vocalizations detected in a given recording using CANARY 1.2.4 software with a filter bandwidth of 88.24 Hz, fast Fourier transformation size of 1024 and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz (Fig. 1). Recording sessions were only used when all calls were of high enough amplitude to be distinguished easily. Vocalizations were then classified into categories of discrete call types by aural recognition and inspection of the spectrograms. All call type classifications were carried out by the lead author to ensure consistency. It has been experimentally demonstrated that human observers using pattern recognition give biologically meaningful categorization of natural signals (Janik 1999). Categorization of calls from each recording session was done without reference to notes on groups present to avoid observer bias (see Janik 1999). We used the alphanumeric categories of Ford (1987) as a reference.

We only used recordings collected when all of the pods present had been visually identified. In order to control for possible differences in call production during different behaviours (e.g. Hoelzel & Osborne 1986; Ford 1989), we used only recordings where



**Fig. 1:** Spectrograms of two most common call types of each pod; S1, S4, S16, S17, S2iii and S19. S2iii and S19 are 'two-voiced' call types that contain biphonation. Spectrograms were created using a fast Fourier transformation size of 1024 samples, a filter bandwidth of 88.24 Hz and 87.5% overlap, resulting in a grid resolution of 5.752 ms and 21.73 Hz.

the pods were travelling directionally. We also chose relatively long sampling periods (>20 min) to allow for sufficient sample sizes to reduce short-term sampling bias.

### Statistical Analysis

Miller et al. (2004) found that resident killer whales call bouts were short (mean duration 6.3 s), and matching with the same call type within these bouts occurred only 20% more than expected by chance. The length of recording sessions meant that they typically contained several independent bouts. Therefore, relative call type production should be statistically comparable between contexts and groups (e.g. Ford 1989, 1991; Miller & Bain 2000; Weiß et al. 2007). Pearson's product moment correlation coefficient was used to test if there was a linear relationship between the relative production of call types in time period 2 (2001–2003) compared with time period 1 (1977–1981). We compared call type production between pods for both time periods using a chi-square test. We also used a Student's t-test (or a Mann–Whitney U-test when the number of recording sessions for a given period was <20) to compare the mean relative production of particular call types per recording session between the two time periods. In this case we compared only the two most common call types to ensure an adequate sample size from both time periods.

To estimate the effect of multi-pod recordings on the relative production of call types, we combined the call type production of each pod recorded individually for approx. 1000 min. We compared these estimated proportions with the actual call type production from recordings of all three pods together.

**Table 1:** A comparison of the call type production between pods in two time periods (1971–1981 and 2001–2003)

Pods	Call types	1977–1981		2001–2003	
		$\chi^2$ (df)	p	$\chi^2$ (df)	p
J and K	All	1027.4 (24)	<0.001	872.3 (23)	<0.001
	Common	836.8 (1)	<0.001	750.0 (1)	<0.001
	Rare	176.3 (20)	<0.001	121.8 (19)	<0.001
J and L	All	2089.8 (27)	<0.001	1186.6 (27)	<0.001
	Common	1656.8 (1)	<0.001	840.6 (1)	<0.001
	Rare	417.1 (23)	<0.001	333.9 (23)	<0.001
K and L	All	1533.8 (23)	<0.001	760.6 (20)	<0.001
	Common	1073.1 (1)	<0.001	510.4 (1)	<0.001
	Rare	453.2 (19)	<0.001	238.3 (16)	<0.001

Common call types are the two most commonly produced call types, and rare call types are the remaining call types in each pods repertoire.

These analyses were done using recordings from all years 1977–2003.

## Results

We analysed over 114 h from 278 recording sessions of the Southern Residents, recorded between 1977 and 2003 and classified 16 153 calls into 28 call types. Calls that did not fit the 28 recognized types ('variable' calls, Ford 1989) were not included in the analysis, these accounted for 7% of the vocal output.

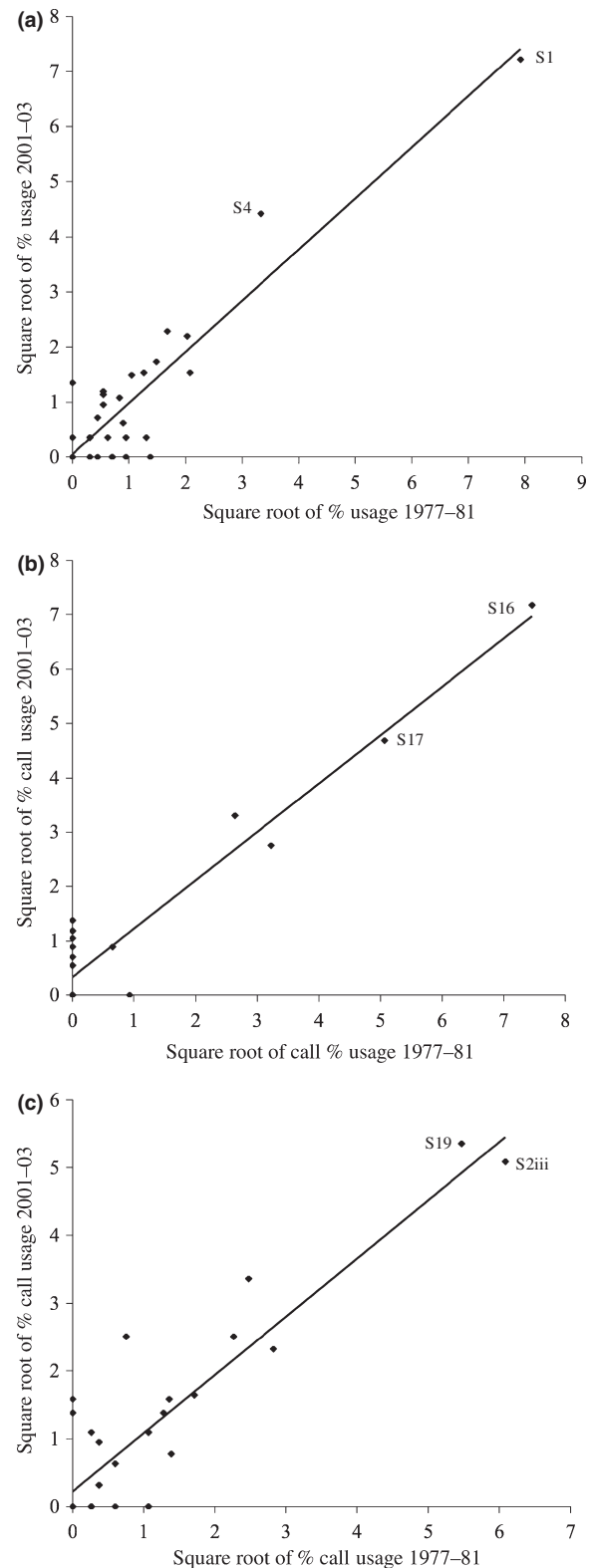
### Single-Pod Call Production

Although each pod shared a number of call types with the other two, the relative production was highly distinctive among pods in both time periods (see Table 1). The relative production of each call type by each pod was strongly correlated between the two time periods (Pearson's correlations for J pod:  $r_{25} = 0.979$ ,  $n_1 = 993$  calls, 23 recording sessions, 493 min,  $n_2 = 767$  calls, 35 recording sessions, 756 min,  $p < 0.001$ ; K pod:  $r_{16} = 0.991$ ,  $n_1 = 230$  calls, six recording sessions, 172 min,  $n_2 = 368$  calls, 15 recording sessions, 445 min,  $p < 0.001$ ; L pod:  $r_{23} = 0.956$ ,  $n_1 = 1403$  calls, 13 recording sessions, 586 min,  $n_2 = 672$  calls, 26 recording sessions, 547 min,  $p < 0.001$ ; Fig. 2). This suggests that there is overall stability in the relative production of call types within each pod's repertoire. However, the correlation results were in each case inflated by outlying data points (from the most common call types; see Fig. 2). Therefore, we removed the data-points for the two most common call types of each pod in case they were driving the trend. This resulted in weaker correlations, though they remained significant for each pod (J pod:  $r_{23} = 0.716$ ,  $p < 0.01$ ; K pod:  $r_{14} = 0.936$ ,  $p < 0.01$ ; L pod:  $r_{21} = 0.826$ ,  $p < 0.01$ ) (Table 2).

L pod produced a significantly higher total proportion and mean proportion per recording session of two-voiced call types than either J pod ( $\chi^2 = 3345.71$ ,  $p < 0.0001$ ;  $U = 1537.0$ ,  $p < 0.0001$ ), or K pod ( $\chi^2 = 2164.22$ ,  $p < 0.0001$ ;  $U = 938.0$ ,  $p < 0.0001$ ; Table 3, Fig. 3a–c), though this is primarily due to the fact that their common call-types are two-voiced.

### Multi-Pod Call Production

In multi-pod aggregations the relative production of nine call types increased significantly (chi-square



**Fig. 2:** A plot of the square root of relative call type production in time period 1977–1981 compared against time period 2001–2003 by (a) J Pod; (b) K Pod; (c) L pod.

**Table 2:** Call type production ( $\pm 1$  SD) for the two most common call types in each pod's repertoire for the two time periods

Pod	Call type	1977–1981		2001–2003		t ( $u^a$ )	p
		Number of that call type recorded (#recording sessions)	Mean relative production per recording session (%)	Number of that call type recorded (#recording sessions)	Mean relative production per recording session (%)		
J	S1	623 (23)	55.6 $\pm$ 32.8	400 (27)	48.5 $\pm$ 31.1	0.648	0.521
J	S4	150 (23)	8.7 $\pm$ 11.3	110 (27)	19.7 $\pm$ 31.6	1.53	0.136
K	S16	128 (6)	66.8 $\pm$ 25.5	190 (15)	44.5 $\pm$ 28.8	40.0 <sup>a</sup>	0.313
K	S17	59 (6)	19.6 $\pm$ 11.8	81 (15)	17.3 $\pm$ 10.9	33.0 <sup>a</sup>	0.792
L	S19	420 (13)	38.1 $\pm$ 27.1	193 (26)	23.4 $\pm$ 29.1	1.41	0.170
L	S2iii	519 (13)	27.8 $\pm$ 27.8	174 (26)	26.9 $\pm$ 33.3	0.0714	0.944

<sup>a</sup>Indicates Mann–Whitney U-test was used rather than Student's t-test due to the number of recording sessions (see Methods).

**Table 3:** Percentage of two-voiced call types from recordings of each pod and multi-pod aggregations

Pod(s) and context	Total number of stereotyped calls	Number of recording sessions	Total recording time (min)	Mean relative production of two-voiced call types per recording session (%)	Total relative production of two-voiced call types (%)
J	2588	59	1475	16	11
K	866	34	1050	9	8
L	2612	49	1288	85	91
Multi-pod aggregations of J, K and L	4510	33	1331	65	88

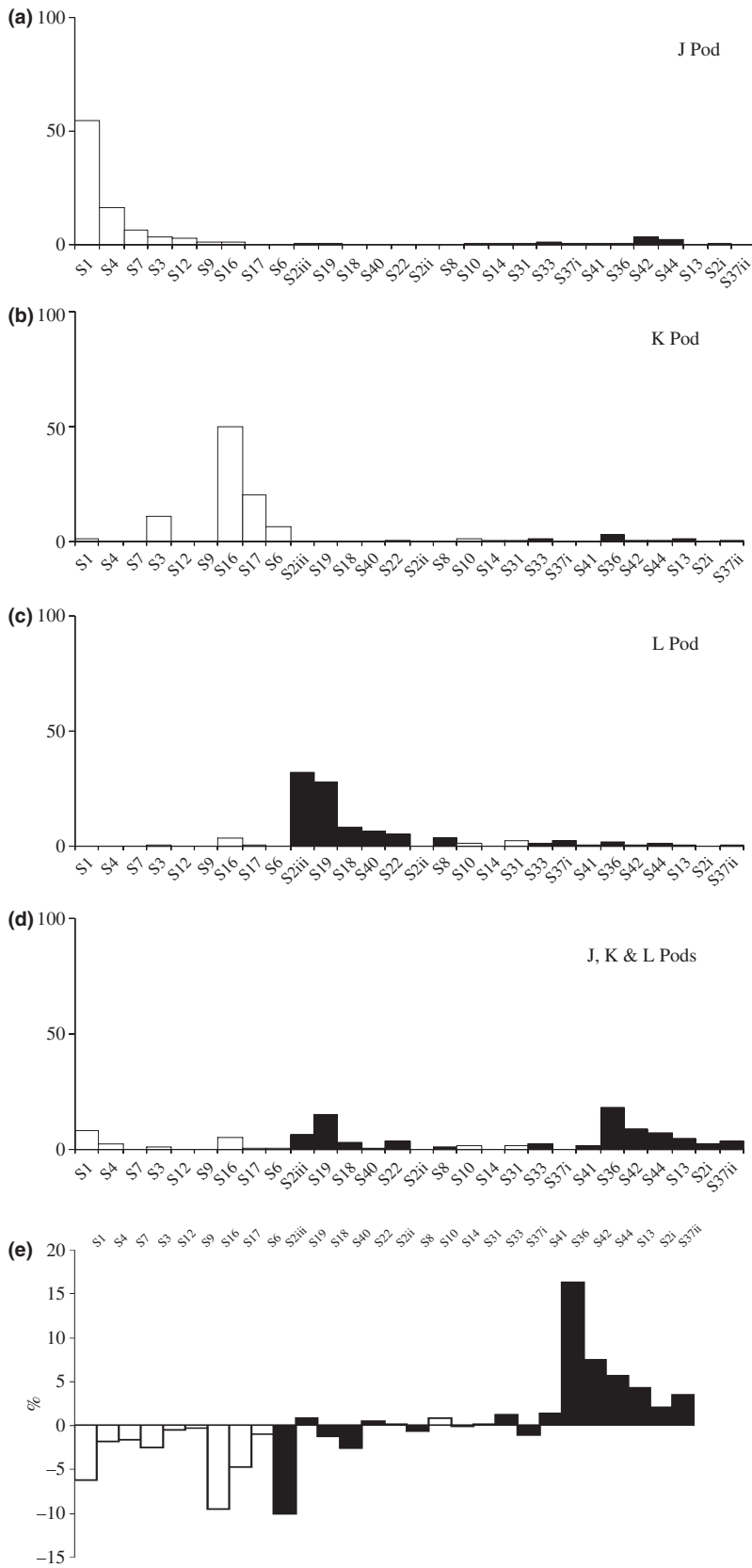
test:  $p < 0.05$ ) more than expected, and of these eight contained biphonation (Fig. 3d, e). There were 12 call types that were produced significantly less than expected (chi-square test:  $p < 0.05$ ), of these five contained biphonation. Three call types decreased more than 5% compared to that expected in multi-pod aggregations. These were the primary call type (S1, S16 and S2iii) of each pod (J, K and L, respectively; Fig. 3d, e). Six call types (three two-voiced and three single-voiced), did not differ significantly (chi-square test:  $p > 0.05$ ) from our expected values in their observed production.

## Discussion

The group specificity of killer whale call repertoires has led to earlier suggestions that they could function to maintain distinct social groups (Ford 1989, 1991). Our results support and extend previous findings by Ford (1989, 1991) that proportional call production in these repertoires are conserved over time, and show that this extends over a period of more than 30 yr. However, we also show a distinction between a stable dominant subset of each pod's repertoire and the less commonly produced

call types. Common call types are consistent in their relative production for single-pod groupings over time, and may therefore function at least in part in signalling pod affiliation, rarer call types seem less suitable for this as they are less group distinctive. This suggests an alternative function that may vary with context. Earlier studies have shown that the diversity and relative production of call types varied between 'social' and 'milling' behavioural contexts (Hoelzel & Osborne 1986; Ford 1989). Additionally Weiß et al. (2007) reported subtle variation in relative call production between the contexts of single- and multi-matriline groups. However, there are few data so far correlating specific call types to specific functions in Pacific resident killer whales. One possible exception is from the work of Ford (1989) who found that certain pods from the Northern Resident population produce the N2 two-voiced call type predominantly during inter-matriline convergence.

Although we were unable to determine the relative contribution by each group our comparison of vocal behaviour in single- vs. multi-pod groupings clearly shows a change in call production between these two social contexts. Each single-pod's main call



**Fig. 3:** Call type production of (a) J pod; (b) K pod; (c) L pod; (d) multi-pod aggregations of J, K and L pods; (e) percentage differences in actual call type production of multi-pod aggregation of J, K and L pods compared to expected call type production based upon each pod's call type call production when recorded individually. □, 'Single-voiced' call types; ■, 'Two-voiced' call types.

types were produced significantly less than expected and most of the call types that became more common compared to expectations in multi-pod groups were two-voiced call types. One possible explanation would be an increase in the usage of calls that are structurally suited to long-distance propagation, under the assumption that multi-pod groupings during travel would be spread out over larger distances (though this has not been quantified, and may not always be the case). The higher active space of call types containing biphonation (Miller 2006) could be advantageous for signalling over longer distances.

Biphonation occurs in the vocalizations of a variety of taxa using a variety of sound production mechanisms (e.g. the syrinx of birds, Fee et al. 1998; the larynx of terrestrial mammals, Fitch et al. 2002; the nasal complex of odontocetes, Tyson et al. 2007) suggesting adaptive significance (Fitch et al. 2002). An experiment with emperor penguins (*Aptenodytes forsteri*) manipulated two-voiced calls (removing one of the two components in playback trials) to illustrate their use in individual recognition, and characteristics of the call (the beat generated by the interaction of two fundamental frequencies) were shown to propagate well through obstacles (such as other penguins; Aubin et al. 2000). This type of experimental manipulation may provide further resolution of this question for killer whales, but it would be logistically very difficult in the wild, and for now the lack of this information means that we cannot interpret this aspect of the study further. However, we can show that the repertoire of each pod changes substantially during multi-pod groupings. Further, the calls that become rarer in these groupings are those that are dominant when the pods are alone, reinforcing the idea that these calls support intra-pod cohesion. The data also support the contention that the remaining calls serve a different function such as inter-pod affiliations, since many of them become significantly more common in multi-pod groups.

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