



Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*

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Pod-specific calling behaviour of resident killer whales has been shown to include: discrete call types not shared among pods, different production rates of shared call types, and differences in the detailed structure of shared call types. To investigate the mechanisms leading to pod-specific calling, we compared the repertoire and structure of calls produced by three different matrilineal units within the same pod, and described call features encoding matrilineal-unit distinctiveness. The three matrilineal units had different production rates of shared calls, including one call type used almost exclusively by one matrilineal unit. Cross-validated discriminant function analyses revealed matrilineal-unit distinctive structure in five of the six shared call types examined, with duration of the terminal component being the most distinctive feature for all call types containing a terminal component. Calls generally consist of low- and high-frequency components that may follow different time-frequency contours. In our sample, a particular high-frequency contour was consistently paired with a particular low-frequency contour, both contours had roughly equal overall variability, and each contained independent matrilineal-unit distinctive information. The only call type that did not differ structurally between matrilineal units is reportedly used more in interpod meetings than in intrapod contexts. The differences in calling behaviour between matrilineal units were similar in form to previously described differences between pods, although more subtle. These results suggest that pod-specific calling behaviour in resident killer whales arises primarily as a consequence of accumulated drift or divergence between highly cohesive matrilineal units as they gradually separate into different pods.

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Several recent studies have shown that certain features of communication signals are shared within socially interactive groups due to a process of vocal convergence (e.g. D-note in chick-a-dee calls, Nowicki 1989; spectra of greater spear-nosed bat, *Phyllostomus hastatus*, screech calls, Boughman 1997; time-frequency contours of bottlenose dolphin, *Tursiops truncatus*, signature whistles, Smolker 1993). These group-distinctive behaviour patterns result from the combination of a mechanism for vocal convergence and social interactions that promote group stability (Snowdon & Hausberger 1997). As a practical matter, identifying the actual group among which vocal convergence occurs can be difficult because sharing on a fine scale can result in larger-scale patterns as a by-product or 'epiphenomenon' (Andrew 1962). For example, chaffinch, *Fringilla coelebs*, song dialects (Slater

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et al. 1980; Williams & Slater 1990) and colony-distinctive screech calls in greater spear-nosed bats (Boughman 1997) may reflect differences between groups composed of neighbours or harems, respectively. Our goal here is to investigate group-specific calling behaviour in resident killer whales, a case where the groups are composed of matrilineal units. Specifically, we explore whether differences in calling behaviour exist among matrilineal units that compose pods, and identify which call features encode distinctiveness.

Natural markings on killer whales (shape of the dorsal fin, shape of the grey patch below the fin known as the saddle, wounds and scars) allow for photographic and visual identification of individuals (Bigg et al. 1990; Olesiuk et al. 1990). Based on extensive behavioural and genetic evidence, killer whales in the northeastern Pacific have been classified into two subtypes: 'residents', which primarily prey upon fish, and 'transients', which primarily prey upon marine mammals (Bigg et al. 1987;

Ford et al. 1998; Hoelzel 1998). This study only addresses the vocal behaviour of resident killer whales (hereafter killer whales).

Killer whale social structure is typified by a nested hierarchy of stable interactions. The basic unit of social organization is the 'matrilineal group', which consists of a mother, all of her male offspring and young female offspring (Bigg et al. 1990). Surface association patterns of killer whales show that offspring of both sexes travel with their mothers more often than with an unrelated individual throughout their lives, and dispersal from a matrilineal group has not been documented in 20 years of intensive observation (Bain 1988; Bigg et al. 1990; Ford et al. 1994). Males remain in close association with their mothers throughout life, but females with offspring of their own gradually spend more time away from their mother, eventually forming their own matrilineal group. Matrilineal groups associate on a temporary basis, and 'pods' consist of one to nine matrilineal groups observed together on 50% or more of observation days (mostly in the summer; Bigg et al. 1990). The pod level of association is fairly stable, but increased observer effort in the summer biases association data towards pod associations as killer whale aggregations appear to be particularly large in the summer compared to the rest of the year (D. B., personal observation). On a still wider scale, pods that have been observed to interact socially are considered to be part of the same community (Bigg et al. 1990). In this study, we use the term 'matrilineal unit' (MU) to refer to a matrilineal group plus any surviving members of the mother's natal matrilineal group.

Killer whales produce whistles and echolocation clicks, but pulsed calls dominate their vocal behaviour (Schevill & Watkins 1966; Diercks et al. 1971; Steiner et al. 1979; Ford 1989). Calls have a complex structure consisting of multiple parts in time and frequency (Fig. 1). All calls contain a low-frequency component (LFC), which appears to be a burst-pulse sound with sidebands ranging to 10 kHz or higher (Watkins 1967; Ford & Fisher 1982). The LFC is composed of multiple temporal parts separated by shifts in the pulse repetition rate, which ranges from 80 to 2400 Hz (Ford 1987). A feature of some calls is the 'terminal note', which is a relatively short feature at the end of the call separated by a discontinuity in slope or frequency of the LFC. Many calls also contain a high-frequency component (HFC), which consists of a fundamental ranging from 2 to 12 kHz and multiple harmonics ranging to 100 kHz or more (Hoelzel & Osborne 1986; Bain & Dalheim 1994). Although a beampattern has not been measured, the HFC appears to be significantly more directional than the LFC (Schevill & Watkins 1966; Bain & Dalheim 1994). Stereotyped calls are composed of distinctive combinations of low- and high-frequency components, which researchers have used to classify calls into discrete types by visual inspection of spectrograms and aural recognition (Bain 1986; Ford 1987). Call type classification has relied primarily upon inspection of the entire LFC and portions of the HFC below 8 kHz (Ford 1987), and it is unknown if the entire HFC is stereotyped within each call type.

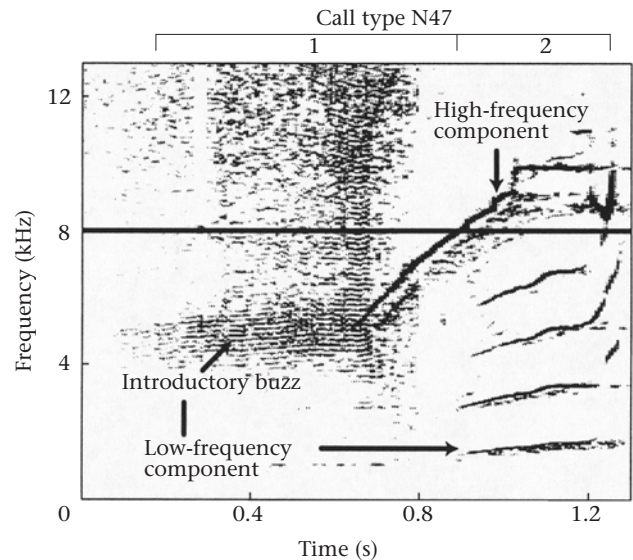


Figure 1. Spectrogram of a killer whale call with an effective filter bandwidth of 40 Hz. This exemplar shows the presence of two different contours, the low- and high-frequency components. The low-frequency component is divided into two parts, part one (the introductory buzz) and part two, based upon the shift in the pulse repetition rate (Watkins 1967; Ford 1987). The high-frequency component starts at roughly 0.6 s and 5 kHz, then rises to 10 kHz. Reverberation is present and is particularly apparent in frequency-modulated portions of the call. The line at 8 kHz marks the upper frequency limit of Ford's (1987) spectrographic analyses of killer whale calls.

Ford (1987, 1989, 1991; Ford & Fisher 1982) recorded calls from identified pods and described pod-specific repertoires of 7–17 call types per pod (Ford & Fisher 1982; Ford 1991). Repertoire differences among pods are of two forms: call types not shared (different call types), and call types that are shared but differ consistently in some structural variable (different call subtypes). Structural differences in the terminal note of shared calls accounted for almost all of these call subtypes (Ford 1987, 1991). Ford (1991) grouped pods that shared any call types or subtypes into acoustic clans, and identified four different acoustic clans off Vancouver Island, three of which socially interact. Pods within clans have varying degrees of repertoire similarity and Ford (1991) suggested that repertoire similarity reflects matrilineal relatedness. Pods also differ in relative production rates of shared calls.

Ford (1991) proposed that the pattern of pod-specific calling is a product of cultural drift that results from the appearance of errors and innovations in vocal learning and transmission of these changes across generations (Slater 1989). There is convincing evidence for vocal learning in bottlenose dolphins and humpback whales, *Megaptera novaeangliae*, and growing evidence that killer whales also learn their vocalizations (Janik & Slater 1997). A young Icelandic killer whale produced the calls of an older British Columbia whale after being placed in a pool with it, although these were not part of her natal repertoire (Bain 1988). In another captive study, a young killer whale produced calls that matched those of its mother, but not those of its father's pod to which it had

Table 1. Identity, sex, estimated birth year and relatedness of the individuals in A1 pod at the time of the study

Matrilineal unit	Individual	Sex	Estimated birth year (range)*	Live offspring
A12	A12	F	1936 (1935–1945)	A31, A33, A34
A12	A31	M	1959 (1957–1961)	
A12	A33	M	1971	
A12	A34	F	1975	
A30	A02	F	1912 (1911–1934)	A30
A30	A30	F	1951 (1949–1952)	A06, A38, A39, A50
A30	A06	M	1965 (1963–1966)	
A30	A38	M	1970	
A30	A39	M	1975	
A30	A50	F	1984	
A36	A36	F	1950 (1942–1951)	A32, A37, A46
A36	A20	M	1953 (1952–1956)	
A36	A32	M	1965 (1963–1966)	
A36	A37	M	1977	
A36	A46	M	1982	

*Individuals whose birth year was observed are not given a range. See Bain (1988) and Bigg et al. (1990) for determination of estimated age and relatedness.

never been exposed (Bowles et al. 1988). Members of pods occasionally produce sounds from other pods' repertoires, which may be an example of vocal mimicry (Ford 1991, page 1476). Two resident MUs appear to have made similar alterations to the LFC of one call type over a 12-year period, consistent with some degree of horizontal learning across MUs (Deecke et al. 2000). However, because members of pods are related, and evidence exists that killer whales are highly inbred (Hoelzel 1998), some researchers have pointed out that Mendelian genetic inheritance of calls is consistent with pod-specific calling behaviour (Janik & Slater 1997). A genetic transmission mechanism seems unlikely, however, as the pattern of call sharing observed by Ford (1991) would break down unless call structure was genetically coded in an unusual manner (mtDNA), or the mating system was highly restrictive.

In this study we explore the mechanisms of pod-specific calling by comparing the repertoires and the structure of calls produced by MUs from the same pod. MUs naturally separate by distances sufficient to obtain recordings from a single MU without employing acoustic localization techniques (e.g. Miller & Tyack 1998). A finding that differences in calling behaviour exists between MUs would provide new evidence to support the model that pod-specific calling is a consequence of the gradual accumulation of errors and innovation in intergenerational transmission of vocal traits. Alternatively, a finding of no differences between MUs would suggest that pod-specific calling arises from rare but large changes in the vocal behaviour of the entire pod. No differences between MUs would also be evidence that vocal convergence occurs at the level of the pod, possibly as a consequence of horizontal learning from other pod members (Cavalli-Sforza & Feldman 1981).

We assess whether potential differences between MUs parallel differences among pods, as this would provide

stronger support that MU differences eventually lead to pod-level differences (Ford 1991). Thus, we compare relative rates of call type usage, especially exploring whether any call types are not shared between MUs. We test for structural differences in shared call types, and assess whether similar structural features of calls differ between MUs and pods (Ford 1991). An additional aim of the structural analyses is to measure and describe the variability in the HFC because most analyses of killer whale calls have not considered the entire HFC.

METHODS

The subjects for this study were the members of the three MUs that make up pod A1 (Bigg et al. 1990). Pod A1 is most similar acoustically to pods A4 and A5, and is the most commonly observed pod in the study area, Johnstone Strait and the adjacent waters off Vancouver Island, British Columbia (Ford 1991). At the time of this study, pod A1 consisted of three MUs, named A12, A30 and A36 (Table 1). Association measures of these three units from data collected annually from 1973 to 1987 show that A30 and A36 were more affiliative to each other than either was to A12 (Fig. 2). Association levels may also reflect matrilineal relatedness between the MUs (Bigg et al. 1990).

Recordings were made in 1984 and 1985 from each of the three MUs on an opportunistic basis when they were acoustically isolated from other pod members. Whales were approached briefly for visual recognition by standard markings, and photographed for later confirmation of field identifications. The research vessel (a 5.5 m C-Dory) was stopped approximately 400 m in front of the isolated MU, a hydrophone array was deployed, and recordings were made with a Brüel & Kjaer (B&K) 8104 hydrophone connected to a B&K 2635 charge amplifier and a Hewlett-Packard 3968A tape recorder

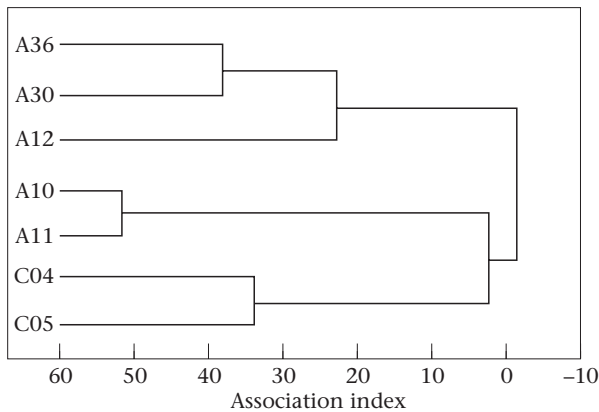


Figure 2. Association dendrogram of the MUs (A12, A30 and A36) in pod A1 based upon data collected from 1973 to 1987 (Bigg et al. 1990). The nearest neighbouring clusters to pod A1 (containing matrilineal units A10, A11, C04 and C05) are also shown. Note that A12 is the relative outlier of the three MUs in A1 pod.

(flat ± 3 dB, 500 Hz–64 kHz). We reidentified and tracked whales visually when they surfaced near the array using standard and nonstandard marks, such as bends in and relative heights of the dorsal fins, or right-side saddle patterns. To decrease the probability that our sample was dominated by one vocalizing individual, we conducted multiple recording sessions of each MU. In addition, John Ford provided two recordings (both of the A12 subgroup) from 1979 and 1981 made with equivalent field techniques.

We transferred recordings to cassette (flat ± 3 dB, 100 Hz–15 kHz) for analysis of call type usage and acoustic structure. We performed spectrogram analysis on a Kay Sonagraph Model 5500 (frequency limit of 16 kHz, fast Fourier transform (FFT) bandwidth of 113 Hz, and dynamic range of 48 dB). We identified call types by visual inspection of the spectrogram contours and aural comparison to known call types following the methods and naming system devised by Ford (1987). We assigned any calls that were not clearly a member of a defined call type and any whistles to type 0. To test whether calls were used in the same relative proportions by each subgroup, we performed a chi-square analysis. We used post hoc analyses to determine which call types were most likely to be responsible for any differences found (Zar 1984).

We carried out the structural analysis of shared calls by measuring multiple time-frequency variables of the six call types (N1, N2, N4, N5, N7 and N9) for which we had an adequate sample from all three MUs (Fig. 3). We had three primary goals in choosing which time and frequency variables to measure from call spectrograms. The first was to choose points that would roughly describe the LFC and HFC contours. The second was to choose points previously measured by Ford (1987). The third goal was to take several measures of the pulse-repetition rate of the LFC and the fundamental of the HFC at the same point in time. We obtained LFC pulse-repetition rates by measuring the sideband interval (SBI; Watkins 1967) while we measured HFC frequency points on the fundamental. We computed variables to estimate the slope of the HFC

from the difference between successive HFC frequency measures. To describe the stereotypy of calls, we compared the coefficient of variation (CV) of time versus frequency and SBI measures as well as the CVs of LFC and HFC variables.

To test for differences among MUs in the structure of the six shared call types, we measured the probability that an excluded or 'jackknifed' call would be correctly classified to its source MU based upon a prediction rule created from the other calls (Smith et al. 1982; Efron 1983). We conducted a separate analysis for each call type using the variables measured for that type. We generated the prediction rule using stepwise discriminant function analysis (DFA) carried out with SPSS for Windows Release 6.0. Stepwise DFA reduces the number of variables used to create the discriminant function, which improves the accuracy of the prediction rule (Lachenbruch & Mickey 1968; Smith et al. 1982). Tolerance was set to 0.001, *F*-to-enter was 3.84, and *F*-to-remove was 2.71. The algorithm selected the variable with the greatest *F* score (above 3.84) for use in the DFA and continued to select variables until all that were acceptable were included. The DFA used the components identified above to create two uncorrelated linear functions consisting of variable coefficients that minimized Wilks' lambda (also known as the *U* statistic), so that the function scores of calls from different MUs differed as much as possible.

After classifying calls to MU, we statistically tested whether the matrix of predicted versus actual source MU was better than that expected by chance (Efron & Gong 1983). Jackknifing and other forms of cross-validation, which remove and predict blocks of data based upon the remaining data, is necessary to reduce the well-known bias (on the order of n^{-1}) which results when the same data points are used to construct and evaluate a discriminant prediction rule (the 'resubstitution estimator'; Lachenbruch & Mickey 1968). Jackknifing reduces the bias of the resubstitution estimator to order n^{-2} , so for $N=10$, the bias is reduced from $\sim 10\%$ to $\sim 1\%$ (Efron 1983). Jackknifing of single data points is preferred over removing large blocks of data by some statisticians because the combined discriminant function is more similar to each function used to classify cases, and jackknifing is more robust in cases where sample sizes are small (Lachenbruch & Mickey 1968). When a priori grouping is possible, the DFA prediction method is more powerful than principal components analysis (PCA) at testing for differences between groups, particularly when differences are subtle and only occur on a subset of the variables measured.

To assess which call features encode MU distinctiveness for each call type, we calculated the stepwise discriminant functions using all replicates of that call type and examined the importance of each function and the correlation between the variables and functions (Norusis 1986). We compared the intrapod variability we observed with the interpod variability reported by Ford (1987) to assess whether certain call features tend to be particularly important in the development of group-specific calling behaviour. To assess more directly the relative MU distinctiveness of the LFC and HFC, we also conducted

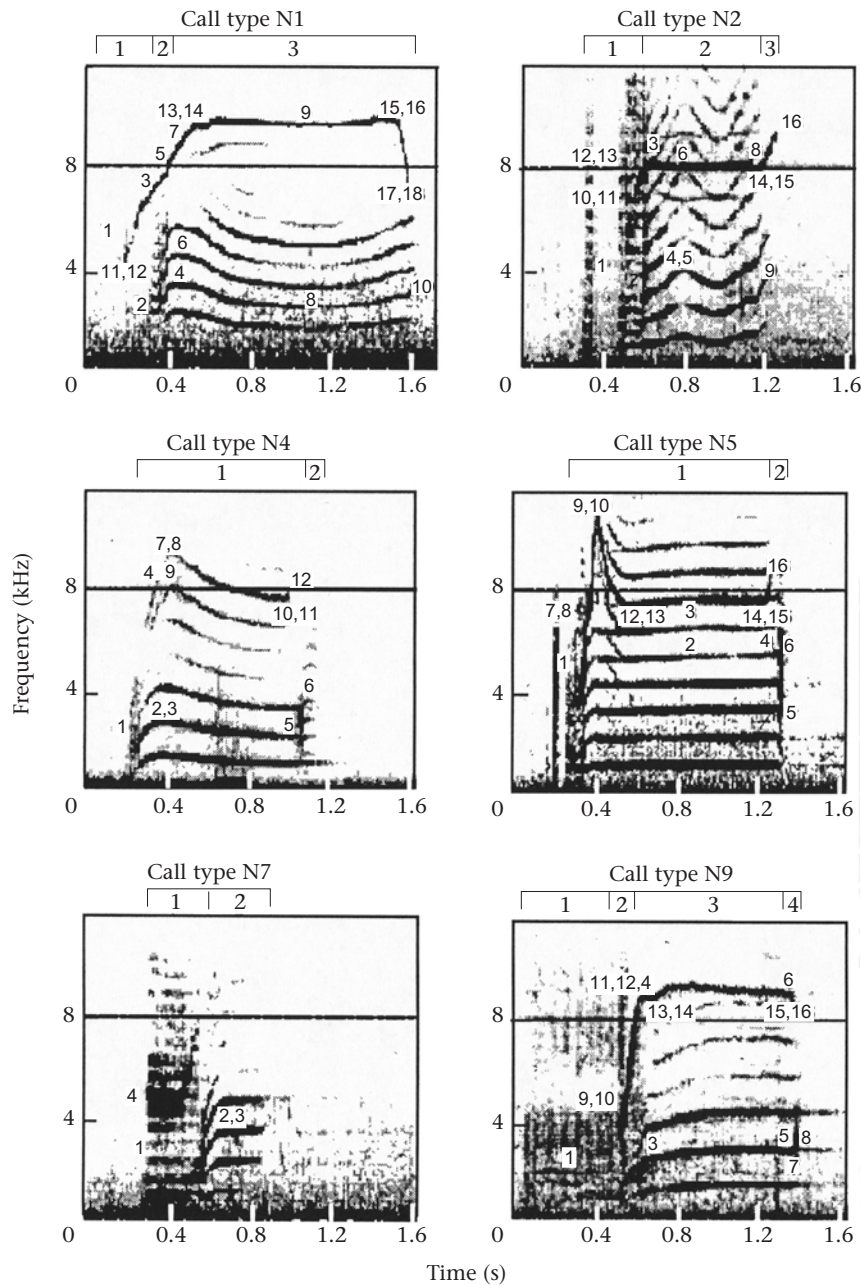


Figure 3. Structural variables measured for six call types shared by the MUs within pod A1. Spectrograms have an effective filter bandwidth of 113 Hz, and the line at 8 kHz marks the upper frequency limit of Ford's (1987) spectrographic analyses of killer whale calls. Numbers on the spectrogram show where measures were taken in addition to duration measures of the call and each low-frequency component part (boundaries shown above each spectrogram). Single numbers are frequency (high-frequency component) or sideband interval (low-frequency component) measures only, except variable 9 of call type N4 and variable 11 of call type N5, which are both measures of the sharpness of the HFC peak. Pairs of numbers are frequency and time measures, respectively. Descriptions of the numbered variables are given in the Appendix. See text for details.

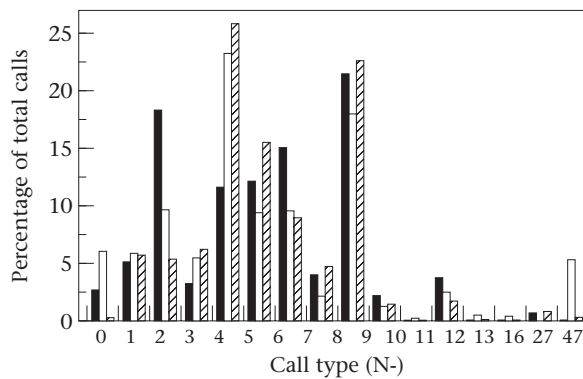
stepwise DFA using measures from only one contour. For each call type, we calculated the percentage correctly classified using measures from the LFC, the HFC and the LFC and HFC together. When no discriminant function was formed because no variables were entered using the stepwise criteria, we used the percentage correct expected by chance (33.3%). We compared the MU distinctiveness of each component using the percentage of calls correctly classified from each data subset across all call types.

RESULTS

We analysed over 18 h of active sound production. Of 1784 calls identified to type, structural variables of 516 calls were clear enough to be measured. A total of 412 calls were used in the DFA as not all variables could be measured from each of the 516 calls. In particular, the HFC of calls was occasionally missing from the spectrogram, possibly due to greater directionality of the HFC. Each measured call type occurred at least once in a mean

Table 2. The number of measured calls and recording sessions (in parentheses) by call type and matrilineal unit (MU)

Call type	MU		
	A30	A36	A12
	Calls (sessions)	Calls (sessions)	Calls (sessions)
N1	18 (8)	9 (4)	15 (7)
N2	20 (7)	13 (5)	27 (9)
N4	50 (10)	33 (6)	22 (11)
N5	21 (9)	35 (6)	34 (11)
N7	23 (9)	23 (4)	35 (12)
N9	40 (8)	49 (7)	49 (12)

**Figure 4.** Histogram of call type usage by the three MUs in pod A1. Call type 0 is an 'other' category that includes whistles and calls that did not clearly fall into one of the types defined by Ford (1987). $N=491$, 717 and 576 for MUs A12 (■), A30 (□) and A36 (▨), respectively.

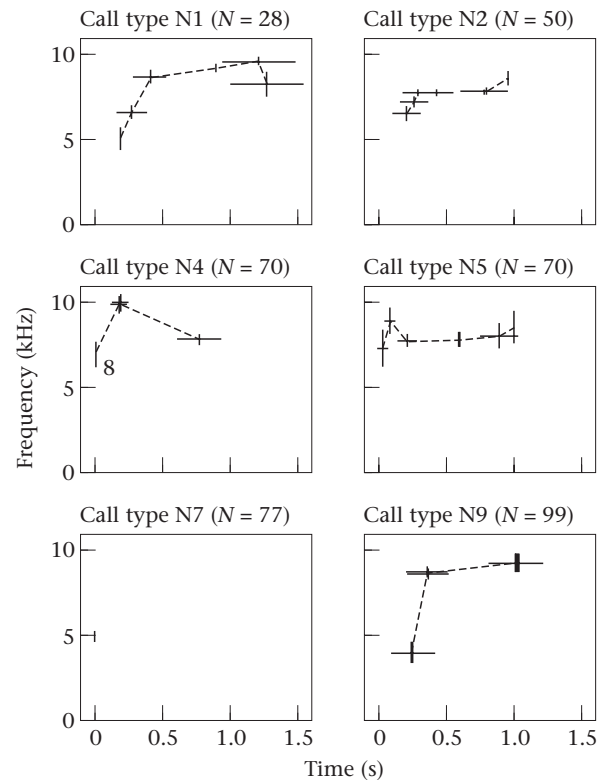
of 8.06 (minimum of four) separate recording sessions from each MU, providing a reasonably representative sample (Table 2).

Call Usage

As a group, A1 pod's call usage closely matched that observed by Ford (1991). Discrete stereotyped calls dominated the sound production of each MU with the 0 category of whistles and nonstereotyped calls accounting for less than 5% of sound production overall (Fig. 4). There were significant differences in call usage between the three subgroups ($\chi^2_{30}=195.8$, $P<0.001$). A large contribution to this difference may be from call types N2, N4, N5, N7, N47 and the 0 category, although the remaining calls showed significant variability as well ($\chi^2_{18}=31.6$, $P<0.05$). One call type (N47) was made almost exclusively by MU A30. Although the other MUs were observed to make this call rarely, it does not appear to be a common call in their repertoire.

Call Structure

Within a given call type, the contour of the HFC was highly stereotyped (Fig. 5) and could be used as an accurate means of identifying call type. Using measures

**Figure 5.** Stereotypy by call type of the high-frequency component of killer whale calls. The middle of each bar is the mean of the time and frequency variables measured on the high-frequency component contour, and the length of the bar is ± 1 SD for time measures (horizontal bars) and ± 2 SD for frequency measures (vertical bars). Sample sizes are given above each box, except one variable noted within the N4 box. The dashed line connects the time-frequency means to roughly recreate the high-frequency component contour. Note the combination of stereotypy within each call type and distinctiveness across call types.

from both the LFC and HFC, the CVs of time variables were greater than those of SBI/frequency variables ($\bar{X}_{\text{time}}=39.2$, $\bar{X}_{\text{frequency}}=12.4$; $t_{64}=5.84$, $P<0.001$). The CVs of time variables did not differ significantly between the LFC and HFC ($\bar{X}_{\text{LFC}}=36.7$, $\bar{X}_{\text{HFC}}=42.8$; $t_{39}=0.74$, $P=0.46$, power=50%), nor did the CVs of SBI/frequency variables ($\bar{X}_{\text{LFC}}=17.8$, $\bar{X}_{\text{HFC}}=8.9$, $t_{31}=1.91$, $P=0.07$, power=82%), although the latter approached significance. This result suggests that the HFC is at least as stereotyped as the LFC.

A total of 21 variables were entered into the DFA using the stepwise procedure (Table 3), 11 of which came from the LFC (five SBI and six time variables) and 10 of which came from the HFC (eight frequency and two time variables). For call types N1, N4, N5, N7 and N9, stepwise DFA correctly predicted source MU of jackknifed calls above random accuracy, but did not do so for call type N2 (Table 4). For all call types except N1, calls produced by MU A12 were most likely to be assigned to the correct group. Figure 6 is a two-dimensional plot of all cases according to their values from the discriminant functions.

Terminal note duration was the most important variable in predicting source MU for the three call types with such a note (N4, N5 and N9; Table 5). SBI variables were

Table 3. The mean, coefficient of variation (CV) and sample size of all variables included in the discriminant function analysis

Call type Variable (number)*	Matrilineal unit											
	A12			A30			A36			Combined		
	\bar{x}	CV	N	\bar{x}	CV	N	\bar{x}	CV	N	\bar{x}	CV	N
N1												
SBI start part 3 (4)	893.3	10.1	15	847.5	8.1	16	622.9	22.2	7	824.2	16.2	38
Freq 1st turn of HFC (13)	9074	3.5	14	8544	3.4	15	8493	4.4	6	8749	4.7	35
N2												
SBI (×2) end LFC (9)	3474	10.3	26	3200	9.7	13	3316	18.0	11	3368	12.5	50
N4												
Duration part 2	5.7	169.4	22	15.7	114.6	50	52.3	63.8	32	24.8	118.0	104
SBI peak part 1 (2)	1471	5.0	22	1432	4.3	50	1370	8.3	33	1421	6.4	105
Duration part 1	704.8	13.9	22	831.1	15.9	50	795.4	26.6	32	793.4	20.4	104
Freq upsweep end HFC (12)	8053	4.3	18	8388	4.9	25	8018	4.3	24	8166	4.9	67
Freq. end HFC (10)	7760	1.6	19	7874	3.8	30	7897	4.3	28	7854	3.6	77
N5												
Duration part 2	5.5	139.0	34	18.7	113.3	19	36.8	73.7	35	20.8	117.5	88
Duration part 1	891.9	8.2	34	941.0	22.0	19	1016.5	15.4	35	952.1	16.1	88
Time peak HFC (10)	79.3	33.1	29	162.2	155.1	12	97.9	34.2	30	101.2	106.1	71
Freq. peak HFC (9)	9136	9.4	29	8633	5.7	12	8728	8.3	30	8878	8.7	71
Freq. end-f. turn HFC (14–12)	191.7	180.2	29	220.0	260.0	12	490.0	164.2	32	327.1	192.4	73
N7												
Time to parallel LFC (3)	91.6	30.2	35	130.7	31.2	23	118.1	36.0	23	110.2	35.9	81
SBI at parallel LFC (2)	1249	10.4	35	1203	9.9	23	1332	6.5	23	1260	9.9	81
N9												
Duration part 4	25.6	93.3	48	34.2	36.2	37	39.0	70.3	46	32.7	71.1	131
SBI (×2) end LFC (8)	3528	11.4	48	3828	15.4	36	3627	14.2	46	3646	14.0	130
Freq. end-f. turn HFC (15–13)	629.0	52.0	48	595.7	58.4	37	690.9	74.3	47	641.6	63.4	132
Freq. end HFC (15)	9408	4.3	48	9139	3.5	39	9469	8.0	48	9352	5.9	135
Freq. HFC start part 3 (4)	8784	3.4	49	8474	4.0	39	8773	4.6	49	8629	4.3	137
Time start HFC (10)	325.1	25.7	48	268.1	48.1	37	145.1	106.4	46	245.8	59.6	131

All time or durations measures are in ms, frequency or sideband intervals (SBI) measures are in Hz. HFC: high-frequency component; LFC: low-frequency component.

*Numbers in parentheses are the variable numbers from Fig. 3 and the Appendix.

the most important for call types N1 and N2, and the duration of the upsweep was the most important feature for call type N7. Because each call type used a unique variable set in the DFA, we tested whether the number of variables measured from the call influenced classification success. We found no correlation between the percentage of calls correctly classified and the number of variables measured ($r=0.27$, $N=6$, $P>0.5$, power=0.87), suggesting that distinctiveness of call structure was not strongly influenced by the number of variables measured.

We compared the structural differences among MUs within pod A1 with those among pods A1, A4 and A5 reported by Ford (1987). As mentioned above, terminal note duration was the most important classification variable for all three calls with terminal notes (N4, N5 and N9), matching Ford's (1987) extensive use of terminal note variation to define different call subtypes. Because Ford's (1987) spectrogram analysis cut off at 8 kHz, only 12 of the 21 variables included in the DFA were also measured by Ford. Overall, nine of the 12 variables entered into the DFA (75%), but only 19 of 42 variables not entered (45%), differed across pods.

There was no difference in MU distinctiveness between the LFC and HFC based upon stepwise DFA of the par-

tioned data set (Fig. 7). Across the six call types, the percentage of correctly classified calls using measurements from single contours was the same (paired t test: $t_5 = -0.543$, NS). We therefore averaged these single component results and compared the average to the percentage correct using both components together. The combination of both contours was more effective at predicting source MU than the average of the single contours alone (paired t test: $t_5 = 9.677$, $P < 0.001$). This strongly suggests that both the LFC and HFC are group distinctive, and that at least some of the distinctiveness in each contour is independent of that in the other.

DISCUSSION

These findings strongly support the hypothesis that pod-specific calling behaviour in killer whales results from differences between matrilineal units that accumulate over time. Differences between MUs resulted from apparently gradual changes in call structure and changes in call repertoire (Ford 1991). Five of the six call types we analysed had MU-specific structural features (Table 4), suggesting that details of call production are somewhat flexible but are MU distinctive. Differences in call usage rates were apparent for many call types, and call type N47

Table 4. Results of the jackknife predictions for each call type

Call type	Predicted unit			%Correct	
	Actual unit	A12	A30		A36
N1					
A12		10	3	1	71.4
A30		1	11	1	84.6
A36		0	0	4	100.0
Total % correct=80.6%, $G_4=29.57$, $P<0.001$					
N2					
A12		17	6	3	65.4
A30		6	6	3	40.0
A36		2	7	2	18.2
Total % correct=48.1%, $G_4=8.213$, $P<0.10$					
N4					
A12		16	2	0	88.9
A30		4	19	3	73.1
A36		2	3	17	77.3
Total % correct=78.8%, $G_4=61.93$, $P<0.001$					
N5					
A12		25	4	0	86.2
A30		4	0	6	0.0
A36		8	6	16	53.3
Total % correct=59.4%, $G_4=16.23$, $P<0.005$					
N7					
A12		23	5	7	65.7
A30		9	10	4	43.5
A36		8	4	11	47.8
Total % correct=54.3%, $G_4=12.93$, $P<0.025$					
N9					
A12		37	3	2	88.1
A30		8	16	7	51.6
A36		8	11	21	52.5
Total % correct=65.5%, $G_4=57.12$, $P<0.001$					

was used primarily only by MU A30 (Fig. 4). It is unclear whether N47 is an entirely new call that was created within the A30 lineage, a major modification of another existing call, such as call type N9 (see Figs 1, 3), or an ancestral call that was dropped by the other MUs.

The differences in call usage and structure between MUs in pod A1 are more subtle than the differences between pods described by Ford (1991), but are qualitatively similar. The very rare production of call type N47 by the other MUs in pod A1 is similar to the rare production of other pods' calls observed by Ford (1991). Terminal note duration was the most important structural variable distinguishing MUs for all three call types with a terminal note (N4, N5 and N9), which matches Ford's (1991, page 1478) finding that terminal notes are consistently the most important variable defining different call subtypes, especially among pods A1, A4 and A5. Other variables that differed among MUs within A1 pod did not vary as consistently among pods A1, A4 and A5 (six did, three did not), suggesting that other parts of calls may be more stable than the terminal note. Higher variability has also been observed in terminal components of song for several bird species (e.g. song sparrows, *Melospiza melodia*, Horning et al. 1993). The qualitative similarity of MU differences and pod differences add support to our conclusion that pod differences

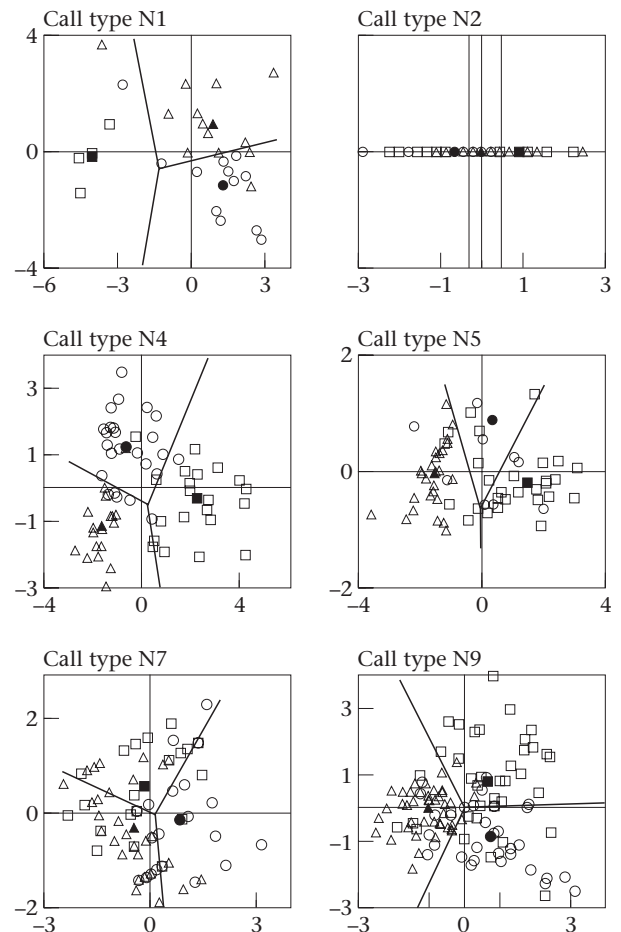


Figure 6. Discriminant function plots. This figure displays the discriminant function scores of each call from which structural measures were taken. Call scores (Δ : A12; \circ : A30; \square : A36) and each MU's centroid (mean discriminant score; \blacktriangle : A12; \bullet : A30; \blacksquare : A36) are shown. The two-dimensional field is broken into three regions, which are the territories for each MU. Correctly classified calls are in the same territory as the MU's centroid, while misclassified calls are in the territory of a different centroid. Note that call type N2 has only one discriminant function, so the plot is divided into three one-dimensional territories.

result from differences on the MU level that accumulate over generations until matrilineal dissociate into pods (Bigg et al. 1990; Ford 1991).

We found that MU A12 was the most vocally distinct and the outlier in terms of association within pod A1 over the course of the study (Table 4, Fig. 2). Since Bigg et al. (1990) found that association levels correlate with matrilineal relatedness, the A12 lineage may have had more generations to accumulate vocal distinctiveness. Alternatively, the more frequent association of the MU A30 with MU A36 may have led to greater vocal similarity due to horizontal cultural transmission between MUs (Cavalli-Sforza & Feldman 1981). The possibility of cultural transmission between MUs is also supported by Deecke et al.'s (1999) finding that association patterns of MUs correlate with acoustic similarity of the LFC of call type N4 based upon a neural net prediction technique. Similarly, Deecke et al. (2000) report that two MUs (A12

Table 5. Importance of acoustical variables in the discriminant function analysis

Call type Variable	%Variance		Correlation	
	Function 1	Function 2	Function 1	Function 2
N1	75.06	24.94		
SBI start part 3 (4)			0.9999*	0.0077
Freq. 1st turn HFC (13)			0.3966	0.9180*
N2	100.00			
SBI (×2) end LFC (9)			1.0000*	
N4	73.33	26.67		
Duration part 2			0.7806*	-0.2085
SBI peak part 1 (2)			-0.2860*	-0.2297
Duration part 1			0.1719	0.4596*
Freq. upswing end HFC (12)			-0.0896	0.4065*
Freq. end HFC (10)			0.0794	0.1140*
N5	93.72	6.28		
Duration part 2			0.5804*	-0.2761
Duration part 1			0.2805*	0.0321
Time peak HFC (10)			0.0883	0.8856*
Freq. peak HFC (9)			-0.2036	-0.4329*
Freq. end-freq. turn HFC (14-12)			0.0551	-0.2287*
N7	68.11	31.89		
Time to parallel LFC (3)			0.7777*	0.6286
SBI at parallel LFC (2)			-0.3857	0.9226*
N9	64.11	35.89		
Duration part 4			0.5326*	-0.0012
SBI (×2) end LFC (8)			0.2639*	-0.1867
Freq. end-freq. turn HFC (15-13)			0.1422*	0.1239
Freq. end HFC (15)			0.0990	0.5988*
Freq. HFC start part 3 (4)			-0.2732	0.5443*
Time start HFC (10)			-0.4811	-0.5049*

The relative importance of each variable can be assessed as a combination of the percentage of variance explained by each function and the correlation between the variable and the functions. Thus, the first variable listed is the most important for discriminating subgroups. Numbers in parentheses are the variable numbers from Fig. 3 and the Appendix. SBI: sideband interval; HFC: high-frequency component; LFC: low-frequency component. *Correlation values were statistically significant.

and A30) altered the LFC of one call type in a matching fashion across a 12-year period, which is consistent with horizontal cultural transmission.

Repertoires of sounds may be particularly efficient for encoding information about multiple levels of social affiliation (Hausberger 1997). In this study, call type N2 was the only type that we found to have no MU distinctiveness. This same call type was shown previously to be used more often during meetings between pods than in any other context (Ford 1989). Use of stable, shared calls when pods meet may serve to signal group size, spatial distribution and emotional state to members of other pods, as in Australian magpies, *Gymnorhina tibicen*, which increase caroling during intergroup interactions apparently to signal their group size and willingness to act in concert (Brown & Farabaugh 1991). Increased production of stable call types in large diverse groups could provide a feedback mechanism to reduce drift of stable call types relative to more variable, distinctive call types which are produced more in small groups. In this case, the range of MU distinctiveness across different call types may provide a highly accurate 'badge' of relatedness or affiliativeness to each group (Ford 1991), and the functional use of the badge in different social settings supports its stability.

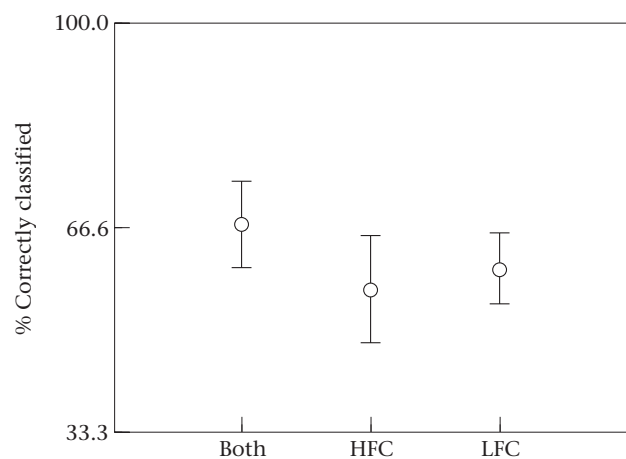


Figure 7. Mean±SE percentage of calls correctly classified to matrilineal unit depending on which component was used in the discriminant function analysis (see text). Percentage correct was the same for high-frequency component (HFC) only and low-frequency component (LFC) only (paired t test: $t_5 = -0.543$, NS). Across all call types, percentage correct was significantly higher when both contours were used together than when the mean of the two single component scores was used ($t_5 = 9.677$, $P < 0.001$).

The contour of the HFC was highly consistent within each call type, with overall variability in time and frequency similar to that of the LFC. Audiograms of killer whale hearing ability suggest that the most sensitive frequencies for hearing in killer whales (15–20 kHz) are approximately the same as the range of the second harmonic of the HFC, which may contain more energy than the fundamental (Hall & Johnson 1972; Symanski et al. 1999). Carefully designed playback experiments are needed to test perception and function of the group-distinctive nature of killer whale calls.

In some calls the HFC did not appear in the spectrogram with the LFC, which is consistent with previous observations of greater directionality of the HFC than the LFC (Schevill & Watkins 1966; Bain & Dalheim 1994). Different levels of directionality in the LFC and HFC could provide a cue communicating the orientation of a signalling animal relative to the receiver, which may be helpful for maintaining group cohesion in this mobile species (Hunter et al. 1986; Miller 2000).

These results provide some support for the hypothesis that killer whales learn the detailed structure of their calls and that group specificity is due to cultural evolution. Although we do not rule out a genetic mechanism to explain similarities within and differences between MUs, the restrictions this would place on the mating system would be more extreme than that postulated for pod-specific calling, and are inconsistent with what is believed about the life history of the species. MU distinctiveness is more parsimoniously explained by learning, where vocal similarity arises as a consequence of exposure to the sounds of tutors. Stable MUs provide a setting where development of learned vocal traits can be shaped by exposure to sounds produced by other members of the MU, and where affiliative interactions support call sharing and vocal similarity (Snowdon & Hausberger 1997).

It is not known why resident killer whale MUs are so stable, with no cases of dispersal by either sex over a 20-year period (Ford et al. 1994). The lack of male dispersal is particularly unusual in mammals (Dobson 1982; Rose 1992). Transient killer whales occur in smaller groups with less matrilineal stability, suggesting that prey type and distribution may be an important influence on group size (Bain 1988; Baird & Dill 1995; Nichol & Shackleton 1996; Ford et al. 1998). Members of kin groups of killer whales might also mutually benefit from alloparental care or other reciprocal activities (Waite 1988; Ford 1991). Vocal similarity seems to be correlated with the multilayered structure of killer whale society, and ultimately to the social interactions that contribute to the stability of the social structure.

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Appendix

Table A1. Description of the numbered variables measured from each call type

Call type	Variable number*	Description
N1	1	SBI part 1
	2	SBI part 2
	3	Freq. HFC start part 2
	4	SBI start part 3
	5	Freq. HFC start part 3
	6	SBI peak part 3
	7	Freq. HFC peak part 3
	8	SBI middle part 3
	9	Freq. HFC middle part 3
	10	SBI end part 3
	11	Freq. start HFC
	12	Time start HFC
	13	Freq. 1st turn HFC
	14	Time 1st turn HFC
	15	Freq. 2nd turn HFC
	16	Time 2nd turn HFC
	17	Freq. end HFC
	18	Time end HFC
N2	1	SBI part 1
	2	SBI end part 1
	3	Freq. HFC end part 1
	4	SBI peak part 2
	5	Time peak part 2
	6	Freq. HFC peak part 2
	7	SBI end part 2
	8	Freq. end part 2
	9	SBI ($\times 2$) end LFC
	10	Freq. start HFC
	11	Time start HFC
	12	Freq. 1st turn HFC
	13	Time 1st turn HFC
	14	Freq. 2nd turn HFC
	15	Time 2nd turn HFC
	16	Freq. upsweep end HFC
N4	1	SBI start part 1
	2	SBI peak part 1
	3	Time peak part 1
	4	Freq. HFC peak part 1
	5	SBI end part 1

N5	6	SBI part 2	
	7	Freq. peak HFC	
	8	Time peak HFC	
	9	Δt at 320 Hz below peak HFC	
	10	Freq. end HFC	
	11	Time end HFC	
	12	Freq. upsweep end HFC	
	1	SBI start part 1	
	2	SBI middle part 1	
	3	Freq. HFC middle part 1	
	4	SBI end part 1	
	5	Δf 1st peak of 3rd sideband	
N7	6	SBI part 2	
	7	Freq. start HFC	
	8	Time start HFC	
	9	Freq. peak HFC	
	10	Time peak HFC	
	11	Δt at 560 Hz below peak HFC	
	12	Freq. turn HFC	
	13	Time turn HFC	
	14	Freq. end HFC	
	15	Time end HFC	
	16	Freq. upsweep end HFC	
	N9	1	SBI part 1
		2	SBI at parallel LFC
		3	Time to parallel LFC
		4	Freq. HFC in part 1
	N9	1	SBI part 1
2		SBI part 2	
3		SBI start part 3	
4		Freq. HFC start part 3	
5		SBI end part 3	
6		Freq. HFC end part 3	
7		SBI part 4	
8		SBI ($\times 2$) end LFC	
9		Freq. start HFC	
10		Time start HFC	
11		Freq. peak HFC	
12		Time peak HFC	
13		Freq. turn HFC	
14		Time turn HFC	
15		Freq. end HFC	
16		Time end HFC	

SBI: sideband interval; HFC: high-frequency component; LFC: low-frequency component.

*See Fig. 3.