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Dialect change in resident killer whales: implications for vocal learning and cultural transmission

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Variation in vocal signals among populations and social groups of animals provides opportunities for the study of the mechanisms of behavioural change and their importance in generating and maintaining behavioural variation. We analysed two call types made by two matrilineal social groups of resident killer whales, *Orcinus orca*, over 12–13 years. We used a neural network-based index of acoustic similarity to identify mechanisms of call differentiation. A test for structural modification of the calls detected significant changes in one call type in both groups, but not in the other. For the modified call type, the rate of divergence between the two groups was significantly lower than the rate of modification within either group showing that calls were modified in a similar fashion in the two groups. An analysis of structural parameters detected no strong directionality in the change. The pattern of call modification could have been caused by maturational changes to the calls or, if killer whale dialects are learned behavioural traits, cultural drift in the structure of the calls together with horizontal transmission of modifications between the two groups. Such vocal matching between members of different matrilines would suggest that vocal learning is not limited to vertical transmission from mother to offspring, which has important implications for models of gene–culture coevolution.

Vocal dialects represent complex and variable behavioural traits that are often relatively easy to quantify. Their study has therefore played an important part in identifying the processes involved in the evolution of behaviours (humans: Cavalli-Sforza & Feldman 1981; Barbujani 1991; Cavalli-Sforza 1997; songbirds: Slater 1986; Lougheed & Handford 1992; Lynch 1996; toothed whales: Whitehead 1998). The vocal dialects of the northern resident community of killer whales, *Orcinus orca* from the coastal waters of British Columbia have been studied extensively (Ford 1989, 1991). Resident killer whales live in stable social groups that are organized along maternal lines. The basic unit of their society is the matriline consisting of one to four generations of maternally related individuals. Dispersal of juveniles and adults from these groups appears to be absent in the resident communities (Bigg et al. 1990). Resident killer whales emit a variety of vocalizations, including echolocation clicks, tonal whistles and pulsed calls. The pulsed calls consist of individual pulses of sound that resemble echolocation clicks in their physical structure. The pulse 'tone' is dictated by the initial rise time of the click, and pulses are repeated at a certain frequency termed the pulse repetition rate. Both pulse tone and pulse repetition rate are modified in killer whale calls (Schevill & Watkins 1966). In addition, some pulsed calls have an independent tonal component termed the high-frequency component with a fundamental frequency of 4–12 kHz (Hoelzel & Osborne 1986).

The most common pulsed vocalizations of resident killer whales are 'discrete calls', which are highly stereotyped and can be divided into distinct call types (Ford 1987, 1989). All discrete call types of the northern resident community have an alphanumeric designation starting with the letter N (e.g. N1, N2, N4). Ford (1989, 1991) showed that groups of related matrilines called pods have unique vocal repertoires of 7–17 discrete call types and documented various levels of sharing of discrete call types between pods. The structure of shared calls often shows subtle variation between different matrilines within the same pods (Miller & Bain 2000). Ford (1991)

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Table 1. Composition of the A12 and A30 matrilines

Matriline	ID name	Sex	Mother	Born	Died
A12	A12	F	?	1941†	
A12	A31	M	A12*	1958†	1997
A12	A33	M	A12*	1971†	
A12	A34	F	A12	1975	
A12	A55	F	A34	1990	
A12	A62	F	A34	1993	
A12	A67	?	A34	1996	
A30	A02	F	?	1927†	1987
A30	A03	M	A02*	1952†	1979
A30	A30	F	A02*	1947†	
A30	A06	M	A30*	1964†	
A30	A38	M	A30*	1970–1971†	
A30	A39	M	A30	1975	
A30	A40	?	A30	1981	1983
A30	A50	F	A30	1984	
A30	A54	F	A30	1989	

From Bigg et al. (1990); Ford et al. (2000). F: female; M: male.
*Animal born before onset of Bigg et al.'s (1990) study. Mother determined from association behaviour.
†Year of birth determined from size at first observation or number and age of offspring.

found that the dialects of resident killer whales are rather stable at the level of the vocal repertoire, since he detected no differences in the call types used by certain groups over a 30-year period. So far no study has looked at modifications to the structure of discrete calls with time.

We compared the structure of calls made by two matrilines, A12 and A30, of the northern resident community (Bigg et al. 1990; Ford et al. 2000) over a period of 12–13 years. These groups are members of A Clan, one of three major acoustic groupings in this community. We chose these matrilines because, of all northern resident matrilines, they are the ones for which most recordings are available. Table 1 gives the composition and genealogies of the two groups. We used the method of Deecke et al. (1999) to describe the structure of discrete calls as a function of their pulse repetition rate and measured the similarity of samples of such pulse rate contours, using an artificial neural network.

The presence of different structural variants of call types shared by different matrilines suggests that the structure of discrete call types changes with time. Our first objective was to determine the rate of such structural change. If the structure of call types changes with time, a sufficiently sensitive measurement of acoustic similarity comparing samples of calls from the same group should give lower ratings of similarity, the further the samples are apart in time. The rate of decrease in the similarity index indicates the rate of change. Our second objective was to test for the divergence of call structure in the two groups. To do this, we determined the rate of vocal divergence between the groups by comparing their calls and measuring acoustic similarity at various times. If the structure of discrete calls changes in a similar fashion in the two groups, for example by vocal matching or because the same maturational processes affect the calls of both groups, we expect the rate of divergence to be significantly smaller than the rate of call modification.

Finally, we aimed to determine which structural parameters are important in neural network discrimination. Identifying these parameters and investigating their change with time can show whether modifications to the calls are directional, and whether certain structural parameters change in a similar fashion in both groups. Directional modifications resulting in monotonic changes in structural parameters may suggest maturational changes in the call types, whereas nondirectional change could suggest cultural drift (e.g. Mundinger 1980; Lynch 1996; Payne 1996) in the structure of calls if the calls are learned. Additionally, if calls are learned and structural modifications of the call types are transferred between the groups, structural parameters should show parallel trends in the calls of the two groups.

METHODS

Underwater recordings were made by us and by a number of other researchers using a variety of hydrophones and recording equipment from land-based and boat-based research platforms. All recording systems had a relatively flat frequency response from 0.1 to 7 kHz, although for some systems the range of the flat response extended up to 20 kHz. The recordings covered the period 1984–1998, were made between May and November, and came primarily from western Johnstone Strait, British Columbia. Whalewatching operators, research vessels and several shore-based research camps share information on whale movements in this area, so that the locations of all resident groups present in western Johnstone Strait are generally accounted for during the daylight hours.

The analysis was mostly restricted to recording sessions where only one matriline was within recording range, and was identified photographically or visually by an experienced observer. On the land-based platforms, Bushnell Spacemaster spotting scopes (Bushnell

Corporation, Overland Park, Kansas, U.S.A.) were used for identification. However, in eight of the 100 recording sessions analysed for this study, one of the two matrilines and another group belonging to a different acoustic clan were within recording range. By definition, members of different clans do not share any call types, and therefore these other groups would not produce any of the calls analysed in this study (Ford 1991). On rare occasions, resident killer whales appear to mimic the calls of other clans, but these imitations have distinctive tonal qualities, are readily identified by ear and are limited to specific behavioural contexts (Ford 1991).

Great care was taken to minimize disturbance of groups during fieldwork. When recordings and visual identifications were obtained from boats, effort was made to adhere to the British Columbia Whalewatching Guidelines (summarized in Ford et al. 2000) whenever possible. This involved maintaining a minimum distance of 100 m from the animals and never positioning the boat directly in the path of travelling groups. Photographic identification required approaches to within 25–30 m following the protocol of Bigg et al. (1986) and was done as part of an annual population census of the northern resident community. All research was done in collaboration with the Canadian Department of Fisheries and Oceans under valid research permits where required.

Although the calls of killer whales are often audible over long distances, signal quality deteriorates quickly because of reverberation in the fjords and inlets of the study area. Since the contour extraction algorithm described below requires calls to be clear, the distance at which analysable recordings can be obtained is generally much smaller than the visual range. Calls with acceptable signal-to-noise ratios were identified acoustically and visually from the recordings and digitized with the Canary 1.2.1 sound analysis software (Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A.). Sufficient sample sizes were available for the two most commonly used call types, N4 and N9 (Ford 1991). For the reasons outlined by Deecke et al. (1999), sample size required standardization, and was set to 24 calls/year for the N4 call type and 21 calls/year for the N9 call type. Calls were selected to maximize the number of independent recording sessions in each sample so as to include within-group and context-related variability. Recording sessions were considered independent if they were made on different days. Within each session, we selected calls so as to maximize the amount of time between calls in the sample. No sample contained calls from fewer than three independent sessions. Because too few N9 calls were available for the A12 matriline from 1986, this sample also includes two calls from 1984.

Spectrograms were computed from the calls and pulse rate contours were extracted from them as described in Deecke et al. (1999). Pulse rate contours consisted of 100 measurements of the pulse repetition rate evenly distributed throughout the call. Calls were therefore standardized for length, but call length was added as a separate variable into the analysis. To measure the similarity of samples of pulse rate contours, we used an artificial neural network. Neural network analysis is a method of pattern recognition that allows the classification of unknown patterns based on information from a known training set. Similar to discriminant function analysis, the performance of a neural network at correctly classifying unknown patterns depends on the amount of consistent variation between the pattern classes in the training set and can therefore be used as an index of similarity for these pattern classes.

We assessed the structural similarity of the calls for each pairwise comparison by combining the two samples of contours to be compared, removing a single contour, training a neural network to distinguish the remaining contours according to which sample they came from and using the neural network to classify the excluded contour. We repeated this procedure until each contour in the sample had served as test contour, so that 48 and 42 neural networks were trained and tested for comparisons of N4 calls and N9 calls, respectively.

The acoustic similarity index is the average error of all networks trained on one comparison. This measure of similarity is based on the premise that any discriminant analysis will perform better at discriminating between distinct than similar patterns. An index value of 0 would indicate that the neural network detected consistent structural differences between the call samples compared. Values as low as 0.003 have been obtained from comparisons of the same call types from different matrilines (Deecke 1998). A value of 0.5 suggests that the neural network detected no consistent variation and that discrimination was no better than random.

This acoustic similarity index was robust to sampling errors. Two replicate indices using call samples from independent recording sessions were generated for 28 comparisons. These replicates were highly correlated (Pearson correlation coefficient: $r_{26}=0.903$, $P<0.0001$) and differed on average by 0.049 (range 0.006–0.107). See Deecke et al. (1999) for details of the extraction of pulse rate contours and neural network analysis.

Test for Call Modification

To test whether the calls had been modified over the 12–13-year period, we measured acoustic similarity for all possible year-to-year comparisons for both groups and both call types. We used a linear regression model (Zar 1996) to determine the rate of call modification, expressed as the rate of decrease with time of the acoustic similarity index. By generating all possible pairwise comparisons between call samples from all years, we used n samples to generate $0.5n(n-1)$ comparisons. Since the correlation structure of this data set was unknown, we assumed that all data points generated with the same sample were correlated and used the number of samples (i.e. the minimum number of independent data points), rather than the number of comparisons, to obtain degrees of freedom for all tests of significance. A one-tailed t test was used to determine whether the acoustic similarity index showed a significant decrease with time. We used a one-tailed test, since comparisons of calls from the same group and consecutive years consistently gave similarity indices around 0.5 (i.e. discrimination is no better than

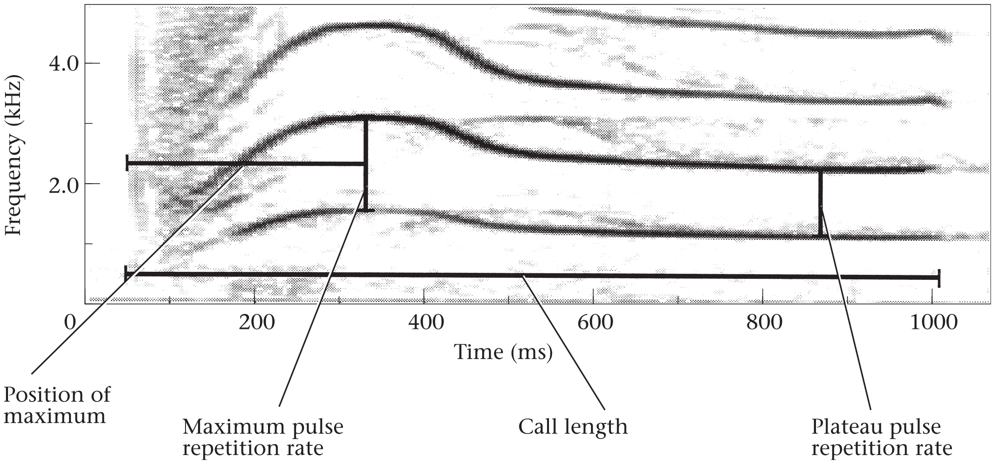

Figure 1. Spectrogram of an N4 call showing the parameters analysed in the comparisons of call structure.

chance). An increase in the similarity index was therefore logically impossible (see Kimmel 1957).

Test for Call Divergence

To determine whether the similarity of the calls of the two matrilines had changed over the study period, we trained neural networks to discriminate between the calls of the two groups for all years from which samples were available. Since no samples could be obtained from the A12 matriline in 1985, and from the A30 matriline in 1986, the call samples from A12 in 1986 were compared with the A30 samples in 1985. We determined the rate of acoustic divergence between the two groups by applying a linear regression model to the acoustic similarity indices and used a two-tailed *t* test to test whether this rate was significantly different from zero. To see whether the rate of divergence was significantly lower than the rate of call modification in the two groups, we used a one-tailed *t* test (Zar 1996). A one-tailed test was permissible here since a rate of call divergence that is either greater than or equal to the call modification rate suggests an absence of parallel changes in the calls of the groups (see Kimmel 1957). Again, to correct for possible autocorrelation in the within-group comparisons, we used the number of samples, not the number of comparisons, to obtain degrees of freedom.

Analysis of Call Structure

Since the test for call modification did not show any changes in the N9 call type, this analysis was limited to the N4 call type. We analysed change over time in four structural parameters for each group: pulse repetition rate at t=85% of call length (plateau pulse repetition rate); the duration of the call (call length); the highest pulse repetition rate in the call (maximum pulse repetition rate); and the relative position of this maximum in the call (position of maximum). We chose these parameters (Fig. 1) a priori by training a neural network to discriminate between the two earliest and latest samples from each group. To identify which parts of the pulse rate contours and call length information were important to neural network discrimination, we tested the neural network with pulse rate contours not used in training. One measurement of the test contour was substituted with the corresponding measurement from a contour belonging to the other category. We repeated the test with the modified contour and assessed the effect of the substitution by subtracting the discrimination error of the contour without substitution from the resultant discrimination error. One by one, the contribution of each measurement of the contour to neural network discrimination was examined in this way. Measurements that were important to neural network discrimination led to large increases in discrimination error when substituted. Plotting the change in discrimination error with reference to the pulse rate contours and finding the area of maximum increase in discrimination error allowed us to identify the relevant parameters visually.

Measurements for the four structural parameters analysed were extracted from the samples of pulse rate contours. Since it was not necessary to standardize sample size for this analysis, pulse rate contours not used in the neural network analysis were also included. We calculated mean values and 95% confidence intervals for the four parameters for each group and each year. We used a sign test (Zar 1996) on the differences between consecutive years to test for monotonic change in the structural parameters. To test for any parallel changes in the calls of the two groups, we calculated the cross-correlation coefficient without lag (Chatfield 1984) of the yearly means of the two groups.

RESULTS

Test for Call Modification

N4 call type

The acoustic similarity indices for the year-to-year comparisons of the N4 calls ranged from 0.23 to 0.55 for the A12 matriline and from 0.21 to 0.52 for the A30 matriline (Appendix Table A1; Fig. 2a, b). There was a significant decrease in discrimination error with increasing time

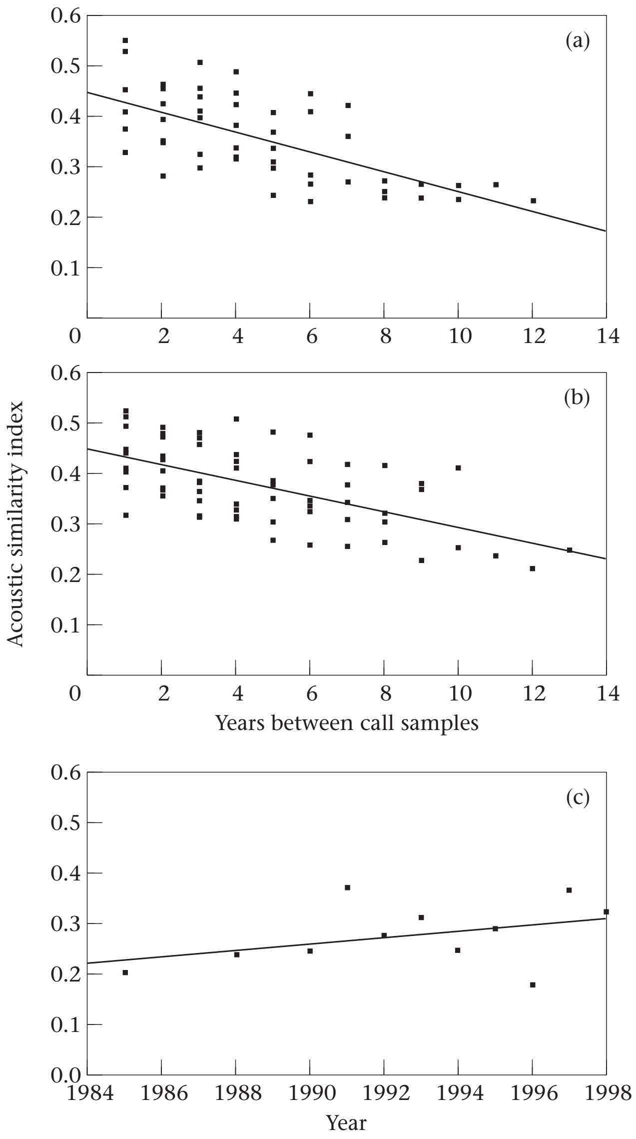

Figure 2. The rate of call modification for the N4 call type of (a) the A12 matriline, 1986–1998, and (b) the A30 matriline 1985–1998 and (c) the rate of acoustic divergence between the two groups.

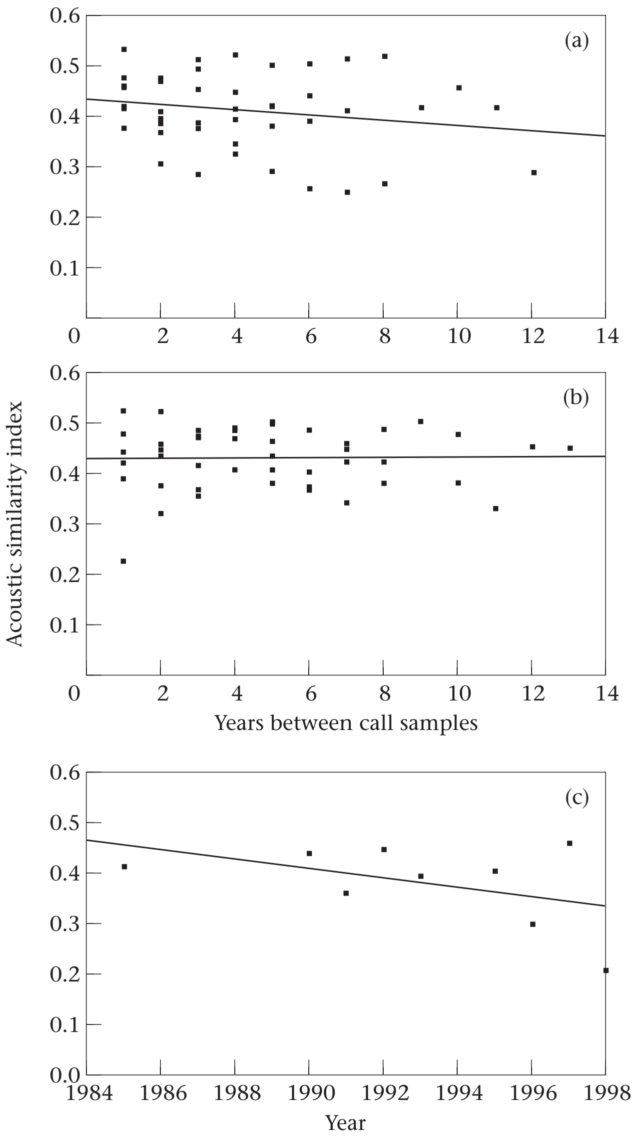

Figure 3. The rate of call modification for the N9 call type of (a) the A12 matriline, 1986–1998 and (b) the A30 matriline, 1985–1998 and (c) the rate of acoustic divergence between the two groups.

between the call samples (linear regression: A12 matriline: $F_{1,9}$=40.455, P=0.0001, R^2=0.43, Y=0.45–0.020X; A30 matriline: $F_{1,10}$=35.864, P=0.0001, R^2=0.36, Y=0.45–0.016X) and the rates of decrease were significantly lower than zero (one-tailed t test: A12 matriline: $t_9 = -2.621$, P=0.014; A30 matriline: $t_{10} = -2.367$, P=0.020). This shows that the variation between samples became more consistent with increasing time between them and is conclusive evidence that both matrilines modified the structure of their N4 call type over a period of 12–13 years.

N9 call type

Acoustic similarity indices for the comparisons of the N9 call type ranged from 0.25 to 0.54 for the A12 matriline and from 0.23 to 0.53 for the A30 matriline (Appendix Table A2; Fig. 3a, b). Unlike the N4 call type, the similarity ratings for the N9 call did not change with increasing time between call samples (linear regression: A12 matriline: $F_{1,8}$=1.579, P=0.244; R^2=0.04, Y=0.43–0.005X; A30 matriline: $F_{1,8}$=0.022, P=0.885, R^2=0.00, Y=0.43+0.000X). The structure of the N9 call type, therefore, did not change detectably over the period of study.

Test for Call Divergence

N4 call type

While the results show that the structure of the N4 call type changed in both groups, Fig. 2c suggests that the similarity of the N4 calls of the A12 and A30 matrilines did not change substantially between 1985–1986 and 1997. Similarity indices for the comparisons between groups ranged from 0.18 (1996) to 0.37 (1991) with an average of 0.28. The regression of between-group

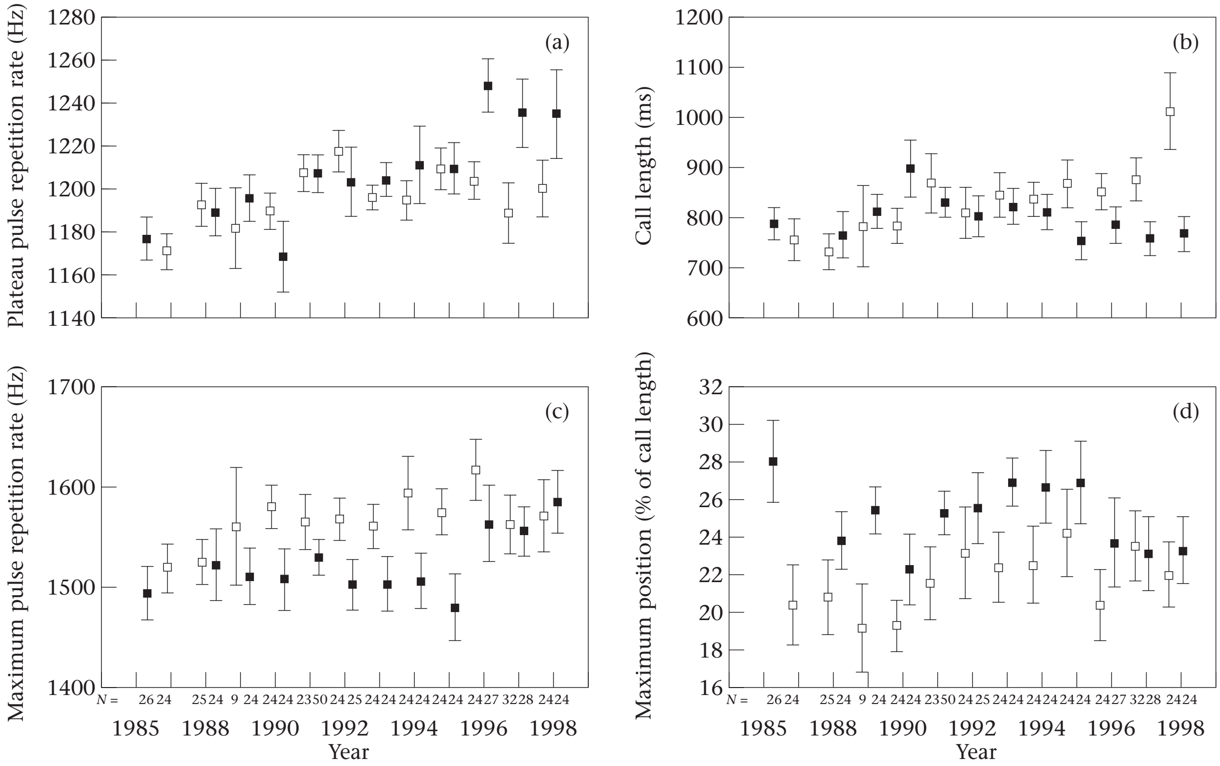

Figure 4. Means±95% confidence intervals for (a) plateau pulse repetition rate (at t=85% of call length), (b) call length, (c) maximum pulse repetition rate and (d) position of the maximum pulse repetition rate (as a percentage of call length) of the N4 call type of the A12 (□) and A30 (■) matrilines from 1985 to 1998. Cross-correlation coefficients (zero lag) for the yearly means of both groups: (a) 0.228, P=0.501; (b) −0.305, P=0.361; (c) 0.165, P=0.627; (d) 0.423, P=0.195.

similarity ratings against time gave a slight positive slope ($F_{1,9}$=1.720, P=0.222, R^2=0.16, Y=0.22+0.006X; Fig. 2c), suggesting that, if anything, the calls became more similar, but the relationship is not significant. Comparing the rates of call modification of the two groups with the rate of acoustic divergence between them shows that the rate of acoustic divergence was significantly lower than the rate of modification in the A12 matriline (one-tailed t test: $t_{18}=-2.136$, P=0.023) and in the A30 matriline ($t_{19}=-1.809$, P=0.043).

N9 call type

The discrimination errors between groups for the N9 call type ranged from 0.21 (1998) to 0.46 (1997) with an average of 0.38 (Fig. 3c). As for the N4 call type, the linear regression indicates that the difference between the groups did not change significantly with time ($F_{1,7}$= 1.852, P=0.216, R^2=0.209, Y=0.462–0.009X). For this call type, the differences in the rate of call modification in the two groups and the rate of vocal divergence between them were not significant (one-tailed t test: A12 matriline: t_{15}=0.294, P=0.387; A30 matriline: t_{15}=0.820, P=0.213).

Analysis of Call Structure

Mean values and 95% confidence limits for the measurements of plateau pulse repetition rate (Fig. 4a), call length (Fig. 4b), maximum pulse repetition rate (Fig. 4c) and position of maximum (Fig. 4d) for both groups show that some parameters of the N4 call type showed pronounced changes from one year to the next (e.g. plateau pulse repetition rate in A12 matriline 1992–1993; call length in A12 matriline 1997–1998, plateau pulse repetition rate in A30 matriline from 1990 to 1991 and from 1995 to 1996; maximum pulse repetition rate in A30 matriline from 1995 to 1996). None of the parameters showed a significant monotonic trend (sign test: P=0.274–0.500). Correlation coefficients for the measurements from the two groups in different years ranged from −0.305 (call length) to 0.423 (position of maximum). None of the correlations was significant.

DISCUSSION

The acoustic similarity of samples of N4 calls decreased consistently in both A12 and A30 matrilines with increasing time between them (Fig. 2a, b). This shows that the discrete calls of resident killer whales are not static behavioural traits, but are subject to change over time. Killer whale vocal dialects therefore change not only on the level of the call repertoire, but, as Ford (1991) suggested, also in the structure of individual call types. In contrast, the comparisons of N9 calls made by the same group in different years showed no change in the similarity index for either group. This implies that the rate of structural modification is not equal for all discrete call types.

The neural network index integrates the amount of variation between pattern classes over the entire pulse rate contour. The significant decrease in the acoustic similarity index with time for the N4 call type could therefore result from strong directional changes in a few structural parameters of the calls, or from the additive effect of multiple relatively minor modifications to the calls that may not be strongly directional. The absence of monotonic change in the structural parameters analysed supports the second scenario. Since the observed changes were small compared to the variation between call types in the parameters (see Ford 1987), the lack of directionality is not caused by physiological constraints.

Although both groups significantly modified their N4 call type, the neural network performed no better at discriminating between the calls of the two groups at the end of the study than it did at the beginning. Therefore, the structure of the calls of the two groups did not diverge even though it changed in both groups. This implies that at least some of this structural change was similar in the two groups. We did not detect any significant correlations for any of the parameters, but if the decrease in the acoustic similarity results from the additive effect of changes to multiple structural parameters, an analysis of each parameter independently will not detect such changes.

The vocal behaviour of animals can change because of genetic differences, maturational effects, or vocal learning (Janik & Slater 1997). The patterns of call modification we observed cannot be explained by genetic differentiation. Group membership did change during the study in both matrilines through births and deaths (Table 1). The genetic makeup of the groups therefore did not remain constant. However, the most pronounced year-to-year differences in the structural parameters happened between years in which the individual members of the group, and thus its genetic composition, remained the same. Furthermore, the acoustic similarity indices for the N4 calls of the A30 matriline showed a downward trend for 1990–1998 (Appendix Table A1), a period when no births and deaths took place in this group. The change observed is therefore not the result of changing group membership, but of structural modifications to the calls shared by all group members. Parallel changes in the groups would require genetic exchange between them if the structural variation was genetically coded, which can be tested with an analysis of paternity.

Maturational change in the vocalizations of animals is caused by anatomical or physiological changes to the structures involved in the production and reception of sound as the animals grow and age. Such maturational change has been demonstrated in some bats in which the frequency of echolocation signals changes with age (Jones & Ransome 1993; Scherrer & Wilkinson 1993). The structural changes we observed could be caused by the additive effect of maturational changes affecting the vocalizations of different group members. The two groups had a similar age structure (Table 1) which could explain the parallel changes in the calls. However, any physiological or anatomical changes to sound production or reception structures should affect all vocalizations equally. Maturational change alone therefore is not sufficient to explain the difference in the rate of change between the two call types. In addition, the patterns described by Ford (1991) of different groups with similar age and sex compositions sharing structurally distinct variants of the same call types are not easily explained by maturational change alone.

Cultural drift describes the modification of behaviours in a population and subsequent fixation of the new variants by behavioural matching (Lynch 1996). Behavioural change is introduced in the form of mutational change (Lynch 1996) or elemental improvisation (Marler & Peters 1982), by variation during copying or reproduction of behavioural patterns, and distributed within a group by behavioural matching between its members. Cultural drift therefore requires that behaviours have a learned component. Such vocal matching between relatives or members of a social group has been demonstrated in birds (e.g. Nowicki 1989; Wright 1996; Bartlett & Slater 1999), bats (Boughman 1997, 1998) and cetaceans (Sayigh et al. 1995).

Cultural drift combined with vocal matching between members of a matriline can explain the decrease in call similarity observed for the N4 call of the two groups. If the observed change was indeed caused by cultural drift, the different rates of change for the two call types would suggest that the cultural mutation rate (Lynch 1996) is not constant across call types. Since structural modifications are introduced by random processes, a model of cultural drift predicts that change is not strongly directional; our findings that none of the parameters changed in a monotonic fashion is consistent with this. If the observed changes in the N4 call type were due to cultural drift and vocal matching, then the lack of divergence in the call structure of the groups implies that matching is not limited to within the matriline, but occurs between groups as well.

The patterns of vocal change in this study, as well as the vocal variation between different matrilines of resident killer whales described by Ford (1991) and Miller & Bain (2000) are therefore most parsimoniously explained by cultural drift. A model of cultural drift does not rule out a genetic component to variation, since studies on acoustic variation in several species of songbirds have shown that learning acts in concert with genetic factors in generating and maintaining the patterns of variation observed (e.g. Marler & Sherman 1985; Mundinger 1995). While the ability to acquire new vocal patterns and to modify existing ones has been established for some odontocetes (Janik & Slater 1997), such vocal learning has yet to be demonstrated in controlled experiments for killer whales. Bain (1986) provided circumstantial evidence for vocal copying in captivity and Ford (1991) described what appear to be cases of vocal imitation in the wild.

Although the year-to-year comparisons for the A12 and A30 matrilines showed modifications to the N4 call type, the acoustic similarity index for the N9 call type did not change in either group (Fig. 3a, b). This means that not all call types accumulate modifications at the same rate and some therefore remain more stable than others. Ford

(1991) noted that the N3 call type, which is shared by a large number of matrilines in the northern resident community, shows very little structural variation among different groups. The structure of others, such as the N8 call type, on the other hand differs greatly from one social group to the next. Differences in the rate of modification for different call types can explain such different amounts of structural variation between groups.

Ford (1991) suggested that rates of acoustic differentiation can be used to reconstruct genealogies within acoustic clans of resident killer whales and to determine the timing of group divisions. In our study, the average acoustic difference between N4 calls of the A12 and A30 matrilines was 0.28. Assuming strictly independent modification, the observed rates of call modification (-0.016/year to -0.020/year) could generate such a difference in 11–14 years (or less than that, if effects of modifications on the index are cumulative). Bigg et al. (1990) suggested that the A12 and A30 matrilines are closely related but that any common female ancestor must have died before 1973. Furthermore, the two matrilines have been observed travelling apart as far back as 1979 (Bigg 1982). This apparent discrepancy between the date of separation predicted by the acoustic data and the observed date can be explained by parallel change in the structure of calls of the two groups; accounting for such parallel change is crucial when attempting to estimate the timing of group divisions.

Our study shows that behavioural traits in resident killer whales can evolve in parallel long after group-splitting events. The dialects of different groups may even converge under certain conditions. Such reticulate patterns of behavioural evolution have been proposed for songbird dialects by Mundinger (1980) and Payne (1996). If the change we observed was indeed caused by cultural drift, then this finding has important implications for current models of gene–culture coevolution in cetaceans. Cultural transmission outside of the immediate kin group (oblique or horizontal transmission, Lynch 1996) will weaken any correlations between a learned behavioural repertoire and genetic markers. Whitehead (1998) recently presented a model to explain the reduced variability in the mitochondrial DNA of toothed whales with matrilineal social structures by selection on culturally transmitted behavioural traits. However, the model requires the rate of nonmatrilinear transmission of behavioural traits to be lower than the genetic mutation rate and Whitehead (1998) showed that even an oblique transmission rate of 0.005 (i.e. 0.5% of daughters acquire a certain trait lacking in their mothers) is enough to halt a reduction in mitochondrial diversity. Our findings make such low rates of nonmatrilinear transmission unlikely, so that Whitehead's (1998) model needs to be revised if it is to be applicable to resident killer whales. The fact that distinct acoustic repertoires persist in the northern resident community in the form of acoustic clans, in spite of frequent prolonged acoustic contact between members of different clans, suggests that clan boundaries rather than boundaries between matrilines are the barriers to vocal matching and horizontal transmission.

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Appendix

Within-group comparisons of acoustic similarity for the test for call modification

Table A1. Triangular matrices giving acoustic similarity indices for the year-to-year comparisons of N4 calls by the A12 (upper right) and A30 (lower left) matrilines

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
1985	—	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1986	NA	—	NA	0.42	NA	0.42	0.24	0.23	0.27	0.27	0.24	0.26	0.27	0.23
1987	NA	NA	—	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1988	0.38	NA	NA	—	NA	0.39	0.33	0.32	0.30	0.28	0.27	0.24	0.27	0.24
1989	0.44	NA	NA	0.40	—	NA	NA	NA	NA	NA	NA	NA	NA	NA
1990	0.38	NA	NA	0.37	0.41	—	0.33	0.28	0.41	0.38	0.31	0.41	0.36	0.25
1991	0.42	NA	NA	0.38	0.49	0.32	—	0.53	0.46	0.40	0.45	0.41	0.45	0.42
1992	0.42	NA	NA	0.42	0.47	0.40	0.44	—	0.33	0.35	0.44	0.34	0.37	0.27
1993	0.42	NA	NA	0.39	0.51	0.36	0.47	0.51	—	0.55	0.46	0.46	0.49	0.34
1994	0.38	NA	NA	0.33	0.48	0.34	0.46	0.44	0.52	—	0.45	0.45	0.51	0.32
1995	0.41	NA	NA	0.38	0.48	0.38	0.41	0.48	0.48	0.45	—	0.41	0.52	0.30
1996	0.24	NA	NA	0.26	0.34	0.26	0.27	0.31	0.32	0.36	0.37	—	0.41	0.35
1997	0.21	NA	NA	0.23	0.32	0.25	0.34	0.35	0.33	0.35	0.37	0.44	—	0.38
1998	0.25	NA	NA	0.25	0.37	0.30	0.31	0.35	0.30	0.31	0.31	0.43	0.49	—

N=24 calls for each year. N/A indicates that the sample size from one or both groups was less than 24. Note the trend towards increasing similarity indices from the corners of both matrices (call samples are far apart in time) to their diagonals (call samples are from consecutive years).

Table A2. Triangular matrices giving acoustic similarity indices for the year-to-year comparisons of N9 calls by the A12 (upper right) and A30 (lower left) matrilines

	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
1985	—	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1986	NA	—	NA	NA	NA	0.42	0.42	0.39	0.52	0.52	0.42	0.46	0.42	0.29
1987	NA	NA	—	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1988	0.48	NA	NA	—	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
1989	NA	NA	NA	NA	—	NA	NA	NA	NA	NA	NA	NA	NA	NA
1990	0.38	NA	NA	0.44	NA	—	0.42	0.40	0.38	0.40	0.50	0.44	0.41	0.27
1991	0.37	NA	NA	0.41	NA	0.44	—	0.46	0.37	0.39	0.53	0.42	0.51	0.25
1992	0.42	NA	NA	0.47	NA	0.52	0.48	—	0.42	0.39	0.52	0.35	0.38	0.26
1993	0.49	NA	NA	0.51	NA	0.47	0.46	0.53	—	0.48	0.41	0.50	0.45	0.29
1994	NA	NA	NA	NA	NA	NA	NA	NA	NA	—	0.46	0.48	0.46	0.33
1995	0.38	NA	NA	0.34	NA	0.44	0.41	0.37	0.38	NA	—	0.42	0.47	0.29
1996	0.33	NA	NA	0.42	NA	0.37	0.41	0.49	0.49	NA	0.23	—	0.54	0.31
1997	0.45	NA	NA	0.50	NA	0.46	0.40	0.50	0.49	NA	0.32	0.42	—	0.38
1998	0.45	NA	NA	0.48	NA	0.38	0.45	0.49	0.47	NA	0.36	0.45	0.39	—

N=21 calls for each year. N/A indicates that the sample size from one or both groups was less than 21.