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Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit

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ABSTRACT

The vocal repertoires of group-living animals may communicate individual or group identity. Female and juvenile sperm whales live in long-term social units that can be assigned to vocal clans based on the pattern of clicks in coda vocalizations. An unusual set of circumstances allowed us to record the vocalizations of photo-identified individuals within a single social unit over a 41 d period. Using click interpulse intervals, we were able to assign codas to individuals and investigate coda production at the individual level within a social unit for the first time. Adult females in the unit vocalized at approximately equal rates. A calf and juvenile, both male, vocalized less often than the adult females. Repertoires were indistinguishable for all unit members apart from a mother and her calf, which possessed significantly different repertoires—even from one another. We suggest that similarity among the coda repertoires of most unit members indicates a function in advertising unit identity. In contrast, the distinctive repertoires of the calf and its mother may facilitate reunions between these whales. We hypothesize that sperm whales may be able to vary their vocal repertoires as their reproductive status alters the trade-off between the benefits of individual and group identification.

Key words: sperm whale, *Physeter macrocephalus*, vocal repertoires, vocalizations, communication.

In social animals the acoustic signaling of individual identity can be important in the establishment and maintenance of social relationships between individuals (*e.g.*, Caldwell *et al.* 1990, Tooze *et al.* 1990, Nousek *et al.* 2006). However, the advertisement of group identity can also be important, thus causing selection for group-specific rather than individual-specific vocal repertoires (Schusterman *et al.* 2000, Nowicki 1983, Hile and Striedter 2000). In species where visual and olfactory cues are of limited value, a lack of individual-specific vocal repertoires may indicate that members of a species do not have strong individual-specific relationships. Studying the vocal production of social marine mammals thus provides the opportunity to examine the correlations between levels of variation in vocal repertoires and vocalization rates, communicative function, and social structure (Tyack 1986, Tyack and Sayigh 1997), with general implications for the evolution of complex communication. One such highly social and vocal species is the sperm whale, *Physeter macrocephalus*.

In the Pacific, where most current data originate, females, calves, and juveniles of both sexes live in long-term social units, containing on average 11 individuals, that persist for decades (Christal *et al.* 1998); these units themselves form temporary associations with other units that last for up to 10 d (Whitehead 2003). Acoustic recordings of sperm whale social units show that they vary in their usage repertoires of short stereotyped patterns of clicks termed "codas" (Watkins and Schevill 1977, Weilgart and Whitehead 1997, Rendell and Whitehead 2003*b*). In the Pacific, units preferentially associate with other units possessing similar coda repertoires, such that these repertoire dialects appear to signal a higher-order social structure, termed the vocal clan (Rendell and Whitehead 2003*b*).

A better understanding of this system has, however, been impeded by a lack of data on the coda production of known individual whales. Despite evidence that whales share some coda types within a social unit (Moore *et al.* 1993, Rendell and Whitehead 2004), it is still unknown whether sperm whales possess individual-specific coda repertoires or whether individuals make codas at different rates. If these were the case, then some observed repertoire variation between units could result from differences in coda repertoires and/or production rates between individuals, calling into question previous interpretations of group-specific repertoires (Freeberg 2001, Tyack 2001). Some have suggested that codas may function in individual identification, and that codas might be used in a manner similar to that suggested for bottlenose dolphin "signature whistles," to allow individual recognition in a social context (Watkins and Schevill 1977, Watkins *et al.* 1985, Caldwell *et al.* 1990, Janik *et al.* 2006). Conversely, if individuals in a unit do not possess individual-specific coda repertoires, then coda production may function instead primarily to signal unit or clan affiliation.

Data on the coda production of individual sperm whales is therefore crucial. The lack of such data until the present study largely reflects the difficulty of studying the individual vocal behavior of free-ranging cetaceans (Janik *et al.* 2000). To address this problem here, we used a feature of sperm whale clicks, the interpulse interval (IPI; Fig. 1), to assign codas to individuals. Because the IPI of a click is related to the length of the sound-producing organ, and hence the size of the vocalizing whale (Gordon 1991), the IPIs of well-defined click waveforms are consistent for an individual whale (Zimmer *et al.* 2005)—so long as the length of its spermaceti organ does not increase greatly between recordings. Using the similarity between the IPIs of usual (*i.e.*, echolocation) and coda (*i.e.*, communication) clicks made by the same whale, we were able here for the first time to assign codas to known individual whales. This technique, combined with a fortuitous series of encounters with a single social

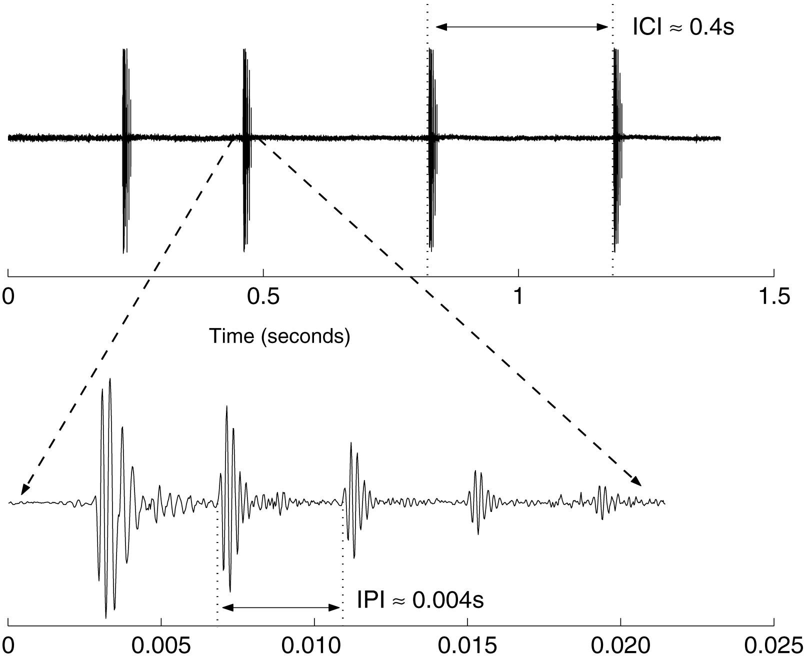


Figure 1. The IPI of sperm whale clicks. Top panel shows waveform of a single coda containing four clicks; bottom panel shows a single click at high resolution (after Rendell and Whitehead 2004).

unit, enabled us to collect a unique data set to investigate individual coda production in a known sperm whale social unit.

METHODS

Field Methods

A unit of seven sperm whales (five adult females, one juvenile male, and one male calf) was observed for a total of 41 d between 16 January and 26 March 2005 off the coast of the Commonwealth of Dominica (including on 100% of our 30 d at sea between 16 January and 20 February). This unusual residency pattern is rare among sperm whale units and provided us with a unique opportunity to study coda production at the individual level. In addition, no other whale apart from the seven unit members was ever observed on any of the days on which any of the recordings we analyze here were made (despite being able to do so with ease whenever a second group entered the area). As a result, we have a very high confidence that all the vocalizations we report here were made by one of these seven whales. We tracked the animals visually during the day and acoustically at night using a directional hydrophone (Whitehead and Gordon 1986). When a whale dived alone, a photograph was taken of its fluke (tail) for photo-identification (Arnbom 1987) and the first loud, usual (*i.e.*, echolocation) clicks produced by the diving whale (Gordon 1991) were recorded and assigned to the photographed whale (henceforth “first clicks”). Sloughed skin samples were collected from the water behind individual whales for genetic analyses (Whitehead *et al.* 1990). The results of DNA analysis to determine the sex and genetic relatedness of the seven individuals in the unit have been previously published, as have details of their social affiliations (Gero *et al.* 2008). In addition to usual clicks, we also recorded codas whenever we heard them. Recordings were made on a Fostex VF-160 multi-track recorder (44.1 kHz sampling rate) via a custom-built towed hydrophone (Benthos AQ-4 elements, frequency response: 0.1–30 kHz), and analyzed using Rainbow Click software (see Gillespie 1997, Leaper *et al.* 2000, Jaquet *et al.* 2001, Rendell and Whitehead 2004).

Our field protocols were pre-approved by the Dalhousie University Committee on Laboratory Animals (http://animalethics.dal.ca/) and were designed to minimize disturbance by approaching whales slowly from behind whenever possible and using minimum required engine power for maneuvering. The research vessel never approached whales to within 30 m under power, although occasionally whales would approach the vessel of their own accord when it was drifting, behavior over which we had no control.

IPI Analysis

The validity of this study rests on our ability to assign codas to known whales by measuring the IPIs of the clicks. We analyzed IPIs from two types of click sequences: (1) codas (one coda being one sequence), recorded either from behind a cluster of whales logging at the surface or in the time between a cluster beginning a deep dive and their first production of usual clicks, and (2) trains of first usual clicks, recorded immediately after a singleton whale (that is, a cluster containing one whale and one whale only) began a foraging dive. A cluster was defined as one or more animals swimming within three body lengths of each other and showing coordinated behavior. The pulse structure of the two types of clicks is different, and in both of them the pulsed structure of the received click varies considerably with the relative aspect of the whale to the recording hydrophone (Zimmer *et al.* 2005). Usual clicks typically show relatively few pulses as most acoustic energy is directed into the main forward pulse of the echolocation beam (Møhl *et al.* 2003). However, the technique of recording usual clicks immediately after a single animal dives means that recordings are made from directly behind the whale, and thus "on-axis" at an aspect most favorable to the accurate reception of pulse structure (Zimmer *et al.* 2005), and several authors report accurate and repeatable measures of IPI using this technique (Gordon 1991, Goold 1996, Teloni *et al.* 2007). Coda clicks in contrast are marked by an extended reverberation pattern, typically containing four or more distinct pulses, depending on the signal-to-noise ratio (Madsen *et al.* 2002). This pattern also changes with recording aspect (Schulz *et al.* 2009). Based on the currently available literature, it is relatively straightforward to ascertain by visual inspection of the click waveform the likelihood that it was recorded on or off the main anterior–posterior acoustic axis of the whale. In addition, we used a technique, described below, that allowed us to quantify the extent to which the pulse structure in a click was clear and therefore likely to return an accurate IPI estimate.

We calculated the IPIs of clicks using a modified version of the custom-written MATLAB routines (version 6.1) described in Rendell and Whitehead (2004) and Marcoux *et al.* (2006). The first step was to remove clicks that were obviously recorded off-axis and clicks for which an obvious nonbiological transient (wave noise or hydrophone knocking) had corrupted the pulse structure. Next we calculated the lagged cross-correlation function for each click. Exploratory analyses showed that for clicks with a clear multipulse structure the time delay that results in the best overlap between adjacent pulses, and thus corresponds to the true IPI, results in a maximum cross-correlation peak in the center of a symmetrical peak distribution. Thus for each click in a sequence, we extracted three estimates of the IPI: (1) the time-delay giving the maximum waveform cross-correlation, (2) the median time-delay among those giving the five largest positive cross-correlation values, and (3) the time-delay associated with the cross-correlation peak closest to the midpoint among peaks at least 30% of the height of the maximum peak. If the cross-correlation peak genuinely was the central peak in a symmetrical distribution, then these three values should be identical. Thus, the degree of congruence between these three methods is a quantitative measure of the clarity of the pulse structure in a given click. We calculated the single mode over all three measures for all the clicks analyzed in a given click sequence. If at least 50% of clicks in a sequence were within 0.05 ms of the mode then we took that mode to be the true IPI of that individual. If this condition was not met, the sequence was discarded from further analysis. All IPI analyses described thus far were carried out blind to the identities of whales visually observed at the time of recording.

For the first click sequences, each sequence was assigned an IPI value equal to the mode of all the IPI values assigned to clicks in that sequence. As we analyzed only recordings taken from singleton clusters, we could then associate each first click recording with a photo-identified individual. Each whale in the group (except the calf, which did not fluke) was then assigned a "first click IPI" by taking the mode of the IPIs assigned to each of its first click recordings. Henceforth, we refer to these data as "usual click IPI data."

We made 15 recordings of codas produced by these same whales. Coda recordings were made either from behind clusters of whales while they rested at the surface between foraging dives or in the period between a cluster diving to initiate a foraging dive and the commencement of usual click production (Watkins and Schevill 1977); thus in general recordings were made from directly behind the animals and thus likely on their acoustic axes. As photo-identification data were taken from every encountered cluster, we were able to retrospectively ascertain which whales were in a given cluster (typical clusters contained 1–4 animals). By definition, members of a cluster were usually within a few body lengths of one another, but GPS data showed that clusters were generally hundreds to thousands of meters apart. Thus, typically only members of one cluster would be within 400 m of the hydrophone, and thus available for recording codas (which are only clearly audible through near-surface hydrophones at ranges of a few hundred meters or less). Each recorded coda was assigned an IPI by taking the single mode over all three IPI measures (described earlier) for all the clicks in that coda. We next assigned some codas to individuals based on the similarity of the IPIs assigned to the codas and the first click IPIs of the whales present while the recording was being made (Fig. 2). This was done for a subset of eight coda recordings in which the first click IPIs of the whales present were known to be at least 0.20 ms different, a conservative criterion given that codas with IPIs greater than 0.10 ms in difference are likely not produced by the same whale (see Appendix A for our method of determining this figure, developed by examining the IPIs of coda clicks recorded in situations we knew contained only two whales). Subsequently, we calculated the modal coda click IPI for each fluking whale (*i.e.*, excluding the calf) as the modal IPI of its assigned codas. The remaining unassigned

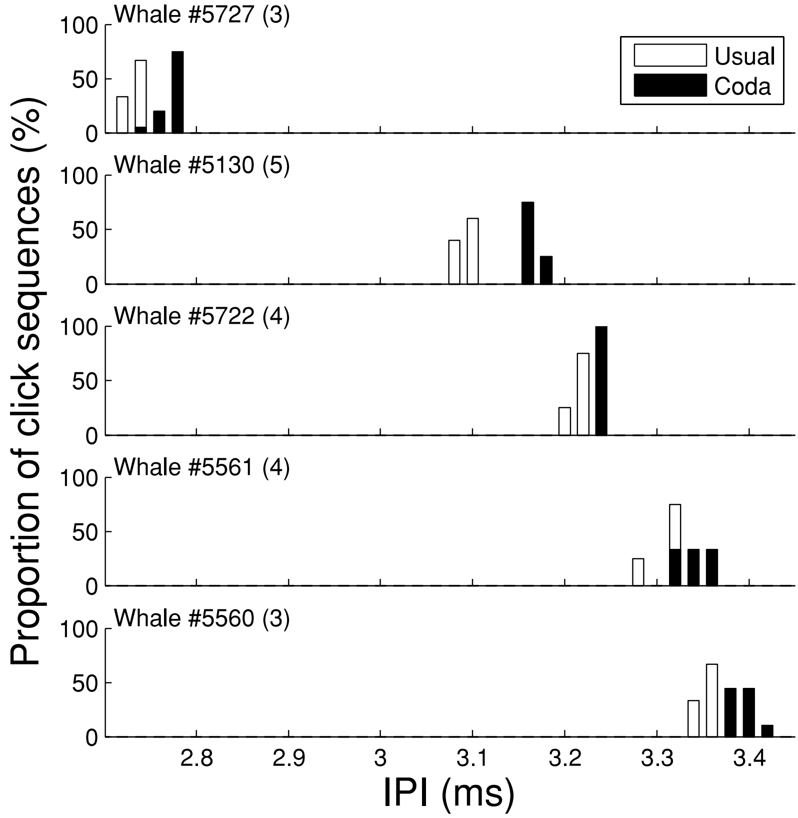


Figure 2. Distributions of modal IPI values for usual click sequences (white bars) and codas (black bars) for five of the whales in the Group of Seven. The IPI distributions are given in terms of percentage of total usual click sequences (the number of usual clicks sequences is given in brackets after the whale ID) or percentage of total codas obtained for each whale.

codas were then assigned to an individual whale if its modal IPI was within 0.05 ms of the modal coda click IPI of that whale, given that it was present at the time of recording, and at least 0.10 ms dissimilar to the modal coda click IPI of every other whale present during the recording (see Appendix A for justification).

We needed two further steps to complete our assignment of codas to individuals. First, we found that the modal coda click IPIs of whales #5561 and whale #5560 ascertained from recordings when one of the pair were present were within 0.05 ms of one another, introducing potential confusion in the assignment of further codas. However, in recordings in which only one of these two whales was present (and thus the identity of the vocalizing whale was unambiguous), the modal IPI of codas produced by whale #5561 were always shorter than 3.36 ms ($n = 10$ codas) and the modal IPI of codas produced by whale #5560 were always longer than 3.36 ms ($n = 43$ codas). In these recordings, the other whale was not sighted for at least 2 h before or after the recording in question, on days during which the sea state averaged 1.3–1.8, hence our confidence in assigning these codas to the whale that was present.

Codas in recordings where both these whales were present were thus assigned to one of these whales using this criterion in addition to the assignment criterion described earlier. The use of this criterion was further corroborated when we used it to analyze 35 pairs of overlapping codas recorded from these whales (Schulz *et al.* 2008). The two codas in each overlapping pair were always assigned to different whales (#5560 and #5561) and never to the same whale.

Second, we could not calculate a modal coda click IPI for whale #5563 due to the fact that it was present during only one recording, a recording that did not meet the criteria for the unambiguous assignment of codas to whales. However, because its modal usual click IPI was very similar to that of another whale (#5130), it was assigned the same modal coda click IPI as that whale, and since there were no recordings in which both whales were present this did not result in any ambiguity in which animal made the recording.

The calf (whale #5703) was never observed initiating a foraging dive, and we never recorded usual clicks with IPIs less than 2.7 ms, so we assume that it did not make usual clicks. The IPIs of the other whales were all longer than 2.7 ms, so codas with clear IPIs of less than 2.0 ms recorded while the calf was present were assumed to have been made by the calf.

Coda Production Rate Analysis

As we did not record all the time that animals were observed during the study period (*cf.* Soltis *et al.* 2005) and did not record during regularly spaced intervals, we could compare only the relative rates with which individuals produced codas in these opportunistic recordings when recorded in the presence of at least one other whale. To determine whether a whale produced relatively more or fewer codas in recordings than expected (given the number of recordings for which it was present and the rates of coda production within each recording), we used permutation tests (Manly 1997) that randomly reassigned the numbers of codas produced by whales within recordings, thereby keeping constant both the number of recordings in which each whale was present and the total number of codas produced in each recording (Appendix B). To control for the influence of recordings that may have high overall rates of coda production, we also repeated these permutation tests using the percentage of codas produced by a whale in a recording rather than the absolute number of codas produced by a whale in a recording. We compared the observed mean number of codas produced by each whale in recordings for which it was present to the expected mean from 10,000 permutations (see Appendix B for details).

Coda Repertoire Analysis

We assigned codas to categorical type using *k*-means cluster analysis methods described in Rendell and Whitehead (2003*a*, *b*, 2004). Each coda type was given a descriptive name based on the pattern of clicks. For example, "5R" denotes a coda with five regularly spaced clicks, while "5 + 1" signifies five regularly spaced clicks followed by a longer gap before the sixth click (Weilgart and Whitehead 1997).

We used both categorical and continuous measures to examine differences between coda repertoires. For the categorical method, two codas were considered similar (categorical similarity = 1) if they were assigned to the same type and dissimilar (categorical similarity = 0) if they were assigned to different types. Additionally, two continuous measures of similarity were calculated for each pair of codas. For these, each coda was represented by the intervals between adjacent clicks (interclick intervals), either using absolute time intervals or proportions relative to total coda length. The multivariate similarity of two codas with the same number of clicks was measured using the infinity-norm distance between the interclick intervals (ICIs) as in Rendell and Whitehead (2003*a*, *b*), that is, the maximum time difference between two ICIs in the coda. The multivariate similarity of two codas containing different numbers of clicks was zero. We also calculated average similarities between sets of codas assigned to pairs of whales and entered these similarities into an average linkage cluster analysis (Manly 1994). We tested the robustness of the resultant clustering using jackknifed resamples omitting each recording in turn. For a given branch we counted the number of jackknife resamples in which the branch contained exactly the same groups as the original clustering.

Finally, we tested whether coda repertoires correlated with genetic relationships by using Mantel tests (Mantel 1967, Schnell *et al.* 1985) and matrix correlation coefficients to examine the relationship between the similarities of the coda repertoires from different whales and their genetic relatedness. Mantel tests were carried out using SOCPROG (2.2, H. Whitehead, Dalhousie University, NS, Canada) in MATLAB.

RESULTS

A total of 318 codas from 15 recordings (on 14 different d over a 45-d period) were assigned to individuals, comprising 76% of all the codas recorded from the unit over this period (Table 1, Fig. 3). Codas were categorized into 16 types with two types ("1 + 1 + 3" and "5R") making up more than 50% of the recorded codas. However, neither the calf, nor its mother (whale #5722), ever produced these two most prevalent coda types. In contrast, all the other whales produced repertoires dominated by these two types. The coda type that was produced most often by the group ("1 + 1 + 3") was the most prevalent in two of the whales' coda repertoires (#5130, #5563), while "5R" codas were most prevalent for #5560 and #5561; the juvenile male produced the most prevalent and second most prevalent coda types with equal frequency.

Most of the codas we recorded were produced by adult females. When all the whales in the unit were included in the production rate analysis, the calf produced 77% fewer codas and the juvenile produced 66% fewer codas in recordings than expected under the null hypothesis of equal production rates (calf: observed mean = 1.5 codas/recording, expected mean = 6.6, SE 2.2 codas/recording, P = 0.007; juvenile: observed mean = 2.7 codas/recording, expected mean = 8.0, SE 2.7 codas/recording, P = 0.044). The calf's mother and the mother of the juvenile male produced more codas in recordings than expected (calf's mother: observed mean = 14.4 codas/recording, expected mean = 9.9, SE 2.2 codas/recording, P = 0.027; juvenile's mother: observed mean = 9.0 codas/recording, expected mean = 3.7, SE 2.4 codas/recording, P = 0.019). Moreover, even when the calf's mother was excluded from the analysis, the calf produced fewer codas than expected (observed mean = 2.0 codas/recording, expected mean = 6.9, SE 2.5 codas/recording, P = 0.045).

When the calf was excluded from the analysis, the juvenile male still produced fewer codas than expected but the calf's and juvenile's mothers did not produce

Table 1. The number of codas produced by each whale in each recording for which it was present; a zero means the individual was present but did not make any codas, and empty cells means the individual was not present.

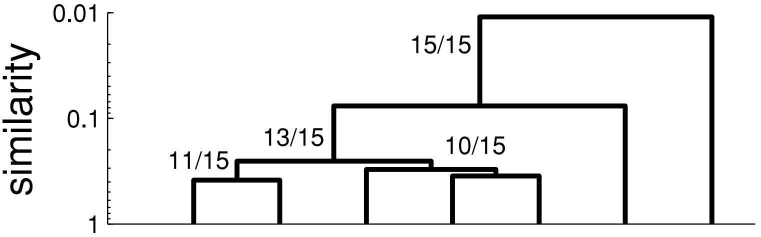
			Individual						
Recording date and time (2005)	% codas assigned to individual	In rate analysis?	#5130 Adult female	#5563 Adult female	#5727 Juvenile male	#5561 Adult female	#5560 Juvenile's mother	#5722 Calf's mother	#5703 Calf
23 January 15:26	73	Y		32	6	24	27		12
26 January 13:50	67	Y			8				0
1 February 09:51	90	Y	22				23		
2 February 11:37	75	Y	6			3			
3 February 10:04	75	Y			1	21	18		0
7 February 11:55	100	Y	4				5		0
7 February 12:49	62	Y	3		0		13		
11 February 08:12	50	Y						2	0
15 February 14:00	100	Y	1					7	0
17 February 13:00	78	Y			0	7	11		
18 February 15:29	44	N[a]			2	0			17
27 February 09:48	100	Y				0		7	0
2 March 17:30	100	Y			0		4		
6 March 18:17	45	N[b]			5				
9 March 08:23	79	Y				7		20	0
		Total	36	32	22	62	101	36	29

[a] The presence of an unidentified member of the group in this cluster meant that relative rates of known individuals from this recording could not be included, although all recorded codas were assigned so the repertoire data were unaffected.

[b] Only one animal was present during this recording, so we could not calculate any relative rates of coda production from this recording.

significantly more codas in recordings than expected ($P = 0.004$, $P = 0.056$, and $P = 0.125$, respectively). Finally, when limiting analysis to just the adult females, the hypothesis that all whales produced codas at the same rate was not rejected (all $P > 0.052$). When we repeated these tests, but used the percentage of total coda output produced by each whale in a recording instead of the absolute number of codas, the results were qualitatively identical (in terms of direction of trends and statistically significant results) with one exception: when just the calf was excluded from the analysis, not only did the juvenile still make fewer codas than expected but the juvenile's mother made a greater percentage of the codas in recordings than expected ($P = 0.009$).

Cluster analysis of the similarities between individual repertoires showed that the repertoires of the calf and its mother, whose repertoire contained only one coda type ("1 + 3"), were the least similar to those of the other whales in the unit (Fig. 3). The branch containing the other group members was robust, being reproduced in every jackknife resample (15 of 15; Fig. 3). Matrix correlation and Mantel tests showed no significant correlations between genetic relatedness and repertoire similarity measured using relative ICIs (Mantel test matrix correlation = 0.131, $P = 0.366$), absolute ICIs (Mantel test matrix correlation = 0.269, $P = 0.171$), or category types (Mantel test matrix correlation = 0.405, $P = 0.118$).



	whale ID:	**#5130 (AF)**	**#5563 (AF)**	**#5727 (JM)**	**#5561 (AF–B)**	**#5560 (AF)**	**#5722 (AF–M)**	**#5703 (C)**	
	usual IPI:	3.11	3.08	2.74	3.31	3.36	3.22	–	
	coda IPI:	3.15	3.15	2.79	3.33	3.4	3.24	–	**TOTAL**
coda type	**2+1**	–	–	2	–	–	–	–	**2**
	4R	–	–	–	1	–	–	1	**2**
	1+3	**11**	1	–	3	–	**36**	–	**51**
	2+1+1+1	–	**6**	1	–	3	–	**4**	**14**
	1+1+3	**24**	**18**	**8**	**24**	**34**	–	–	**108**
	5R	–	**4**	**8**	**34**	**41**	–	–	**87**
	5+1	–	–	–	–	–	–	**12**	**12**
	6R	–	–	1	–	–	–	1	**2**
	7R	1	–	1	–	6	–	–	**8**
	6+1	–	1	–	–	–	–	**4**	**5**
	6+1+1	–	–	1	–	–	–	1	**2**
	1+1+6	–	–	–	–	3	–	–	**3**
	8R	–	1	–	–	7	–	1	**9**
	1+1+7	–	–	–	–	1	–	–	**1**
	9R	–	1	–	–	5	–	**3**	**9**
	9+1	–	–	–	–	1	–	2	**3**
	TOTAL:	**36**	**32**	**22**	**62**	**101**	**36**	**29**	**318**
	Recordings:	5 (14)	1 (0)	5 (42)	5 (45)	7 (38)	4 (26)	2 (26)	

Figure 3. Coda type repertoires of individual sperm whales compared using average categorical similarity (top) and *k*-means classification methods (bottom). Numbers next to dendrogram branches indicate the number of jackknife resamples in which that branch was recreated (out of 15 recordings). Numbers in the top portion of the table indicate whale identification number, modal usual click IPI, and modal coda click IPI. Letters denote the individual's age class and/or relationship with the calf: C, calf; AF-M, mother; JM, juvenile male; AF, adult female; and AF-B, "babysitter" (the adult female most often escorting the calf when the mother was absent; see Gero *et al.* 2008). Numbers in the classification table indicate the frequency with which each individual produced each coda type. Bold, grayed numbers indicate that the coda type comprises at least 10% of the whale's coda production. The code "R" indicates a coda with regular ICIs and the code "+" indicates a gap between clicks. Numbers below each column are the number of codas recorded from each whale and the number of recordings made of each whale with the time interval (in days) between the first and last recording of that whale in parentheses.

DISCUSSION

This is the first study to track coda production by identified individual sperm whales. The combination of these data with relatedness data for the individuals involved provides a unique view of the relationship between communication signals and social structure for this unit. Our results constitute an interestingly complex answer to the question of whether sperm whales use codas in individually distinctive ways. The repertoires of most individual whales were statistically indistinguishable from each other in the recordings we made, which does not fit with the notion that codas are generally used for individual identification. In contrast, however, we found that both the calf and its mother had highly distinctive repertoires, suggesting that these particular animals could be using codas to signal their identity either individually (*cf*. Watkins and Schevill 1977, Watkins *et al*. 1985, Tyack 1999) or to their age-class or reproductive status (*i.e.*, mother or calf). We caution against premature generalization of our findings given that they concern just a single social unit, but note that as care of calves is considered a major driver of sperm whale social evolution in general (*e.g.*, Whitehead 2003), it is plausible that the patterns we report with respect to mother-calf repertoires would also be generally valid.

Our results also confirm previous findings that adult females produce the majority of codas within sperm whale social units (Marcoux *et al*. 2006). Of the 318 codas made in the 15 recordings (excluding those made by the calf) the adult females produced 89% of the recorded codas, a number that corresponds well with the finding by Marcoux *et al*. (2006) that adult females made 95% of codas in analyzed recordings from the Pacific. The calf in the present study produced far fewer codas than expected, apparently silent in seven of the nine recordings for which it was present. This demonstrates, as suggested by Marcoux *et al*. (2006), that adult females are more vocal in sperm whale social units than are younger animals. The higher rates of coda production by the adult females relative to the calf and juvenile, as well as the high rates of coda overlapping amongst adult females (Schulz *et al*. 2008), suggest that codas have an important function amongst adult females, perhaps most plausibly in order to establish and/or maintain social bonds. In contrast, the lower rates of coda production by the calf and juvenile male suggest that this function is less important or not necessary for these individuals.

We found that, in general, adult and juvenile sperm whales do indeed share a coda repertoire, as suggested by our previous studies (Rendell and Whitehead 2003*b*, 2004), such that the repertoires of most individuals are statistically indistinguishable. The similarities in coda repertoires between unit members in this study, and between units of the same clan, coupled with the dissimilarities in coda repertoires between units from different acoustic clans (Rendell and Whitehead 2003*b*), are compatible with the hypothesis that shared coda repertoires could function to signal clan and/or unit membership. An alternative possibility is that shared codas are signals primarily to other unit members, to indicate affiliation and maintain social bonds (Schulz *et al*. 2008), and that clan or unit specificity is a functionless by-product. Sperm whale social units are highly cooperative, with good evidence for both alloparenting (Whitehead 1996, Gero *et al*. 2009) and communal defence (Pitman *et al*. 2001), and the shared vocal repertoires we document here may be important signals associated with this cooperation.

Our findings suggest that the need for the mother to localize, reunite with, and transfer milk to her calf necessitates an obvious means of individual identification, or at least distinctive features in the communication system, compared with other unit members. The use of individually distinctive vocal features in parent–offspring recognition is not unusual and has been widely reported (*e.g.*, Jones *et al.* 1987, McCulloch and Boness 2000, Charrier *et al.* 2001). What is more unusual is the possibility that flexibility in the coda repertoires of sperm whales permits individuals to switch between repertoires depending on the context and need to broadcast individual and/or group identity. The focal unit of this study contained a juvenile male. We found that the repertoires of the juvenile male and its mother (whale #5560 Gero *et al.* 2008) are similar to the coda repertoires of the other adults in the unit (Fig. 3). The juvenile male was never observed attempting to suckle during our observations. This implies that if sperm whale mothers do use individually distinctive repertoires during lactation, they can also revert to their unit repertoire postlactation. However, our data concern only one social unit, and only during one field season, so while we can raise the hypothesis that females can and do switch repertoires depending on their reproductive status, the data we present cannot confirm or reject it.

Clearly, further longitudinal studies are needed on individual whale repertoires within social units, especially as calves are born and mature. We can make predictions about what such studies will reveal if our suggestions concerning the function of the repertoire variation are correct. Specifically, we predict that births of new calves would be accompanied by shifts in coda usage by mothers toward a more individually distinct repertoire. Likewise, as maturing calves begin to forage on their own, the necessity for mother-calf localization should decrease, and eventually be outweighed by the need to advertise clan/unit identity or affirm social bonds, so we predict that their repertoires will become more similar to the repertoires of the other unit members.

It is worth noting that while the mother's coda type repertoire is significantly dissimilar to that of the other whales, the sole coda type produced by the mother ("1 + 3") is acoustically similar to the most prevalent coda type in the unit repertoire ("1 + 1 + 3"), differing by the subtraction of just one click. More data are needed on repertoires of lactating females in relation to those of their social units to understand whether this similarity is coincidental.

Our data also provide some insight into the ontogenetic development of coda repertoires. The dissimilarity between the coda repertoire of the calf and those of the other whales could well be a consequence of its high coda diversity rather than a result of selection for individuality *per se*. In species where social factors influence vocal development, young often show more varied and less stereotyped vocal production than adults, a phenomenon sometimes termed "babbling" (McCowan and Reiss 1997, Goldstein *et al.* 2003, Catchpole and Slater 2008), and this seems to fit well with what we observe of the calf's repertoire in this study. The fact that the repertoire of the older, juvenile, male was more similar to that of the adult females than was the repertoire of the younger male calf suggests that at some stage between infanthood and adolescence, sperm whales develop a coda repertoire that is similar to that of their natal unit. We found no relationship between relatedness and vocal repertoire, which is consistent with learning having a greater role in vocal development than genetic factors.

Mature sperm whales are highly sexually dimorphic, both physically (*e.g.*, Whitehead 2003) and behaviorally (Whitehead and Weilgart 2000). Male sperm whales leave their natal units during maturation, move into temperate and high latitudes, and upon social maturity return alone to the tropics to rove between female groups searching for mating opportunities (Whitehead and Weilgart 2000). Mature male sperm whales appear to make very few codas in social contexts (Marcoux *et al.* 2006). There is some, relatively weak, evidence that mature males prefer to associate with females from particular vocal clans (Rendell *et al.* 2005), but it is otherwise completely unknown what significance, if any, coda repertoires hold for mature males. In this study, the juvenile male in the focal unit not only made several codas types, but also produced a coda repertoire very similar to that of the adult females with which it associated. Therefore, it appears that young male sperm whales are familiar with, and able to reproduce, the coda repertoire of their natal unit, so it is not unfeasible that these repertoires could also be important when it comes to mate choice, as they apparently are for killer whales (Barrett-Lennard 2000).

Adult females produced codas at relatively equal rates, suggesting that adult females contribute equally to the coda production of a unit. Thus, while Freeberg (2001) and Tyack (2001) speculated that observed differences in coda repertoires between units might be an artifact of differences in coda production rates and repertoires between individuals, the equivalence in the rates with which adults produced codas in this unit and the general similarity in the coda repertoires of adults suggest that recordings of social units represent a reasonable representation of the coda repertoire of the adults in the unit. Moreover, the lack of asymmetry in rates of coda production suggests that adults do not use vocal production to assert dominance (see Tobias *et al.* 2004) or aggression (see Hau *et al.* 2000). Among females within units, we have found little evidence for much leadership in diving (Whitehead 2003), preferred positions within foraging formations (Whitehead 1989), individually specific vocal repertoires, or asymmetric coda-overlapping rates (Schulz *et al.* 2008). This all seems to indicate a fairly egalitarian society.

The correlation we have found in this unit between vocal repertoire similarity and the apparent necessity for effective individual or group identification illustrates the relationship between a communication signal and its function, and furthermore highlights how cetaceans can contribute important data toward our understanding of the relationship between social evolution and the evolution of vocal communication (Tyack and Sayigh 1997). In sperm whales, a complex social structure is linked to a complex and apparently flexible system of vocal variation. We now need to expand on this study with further long-term tracking of vocal repertoire changes across changes in unit composition to properly understand how this repertoire system functions.

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APPENDIX A: DETERMINING THE CRITERIA FOR ASSIGNING CODAS TO WHALES USING IPIS

In this Appendix, we explain the process by which we determined that codas with IPIs that differ by more than 0.1 ms as measured by our methods are made by different whales. To determine the IPI criteria with which two codas could be assumed to have been made by similarly sized whales, and so potentially the same whale, or different-sized and thus different whales, we examined the distribution of the differences in IPIs between codas in four recordings in which we are confident from both visual observation and acoustic detection that only two whales were present in the area at the time of recording. Two two-whale recordings were made off of Dominica in February 2005 (recordings #020101 and #020703), one was made in the Sargasso Sea on 10 June 2005 (#20050610-1610b), and another was made in the Mediterranean Sea on 20 July 2005 (#20050720-0020). Codas were recorded using a custom-made towed hydrophone array (frequency response: 0.1-30 kHz) connected to a FOSTEX VF-160 multi-track recorder, or via a Creative Audigy PCMCIA soundcard to a laptop computer upon which recordings were made in the sound editing software ISHMAEL (Mobysoft). Recordings were made at a sampling frequency of 44.1 kHz or 96 kHz. Recordings were initially analyzed using Rainbow Click. We analyzed only codas that could be clearly identified aurally. We found that the IPI analysis method described in the main paper best resulted in a clear bimodal frequency distribution of IPI differences between codas within recordings (see Fig. A1). The first peak corresponds to the differences in IPIs between codas made by the same whale while the second broader peak corresponds to the differences in IPIs between codas made by different whales. Figure A1 demonstrates that intra-whale differences in IPIs were less than 0.05 ms, indicating that if two codas have IPIs within 0.05 ms of one another in a recording, it is possible that the two codas were made by the same whale. Furthermore, the intra-whale differences clearly did not exceed 0.10 ms, indicating that recorded codas with IPI differences of 0.10 ms or greater were likely not made by the same whale. All IPI analysis was conducted in custom-written routines in MATLAB® (version 6.1).

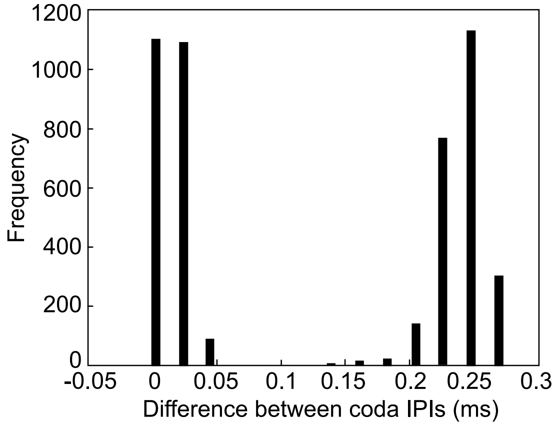

Figure A1. The distribution of the IPI differences between codas within four recordings in which only two whales were present at the time of recording.

APPENDIX B:

Table B1. Depiction of a single permutation, randomizing the number of codas produced by each whale within a recording. The permutation maintains the number of codas produced within a recording and the number of recordings for which each whale was present. The numbers in the tables represent the number of codas in each recording assigned to each whale that was present at the time of recording. The total number and average number of codas produced by each whale over all the recordings for which it was present were calculated for both the observed data (on the left) and sets of randomized data (as on the right).

Recording	#5703	#5727	#5130	#5563	#5722	#5561	#5560		Recording	#5703	#5727	#5130	#5563	#5722	#5561	#5560
012301	12	6		32		24	27		012301	27	6		12		24	32
012601	0	9							012601	0	9					
020101			22				23		020101			23				22
020205			6			3			020205			6			3	
020302	0	1				21	18		020302	21	1				0	18
020703	0		4				5	→	020703	0		4				5
020704		0	3				13		020704		0	13				3
021101	0				2				021101	0				2		
021501	0		1		7				021501	1		0		7		
021705		0				7	11		021705		0				7	11
022702	0				7	0			022702	0				0	7	
030202		0					4		030202		4					0
030901	0				20	7			030901	0				20	7	
Total	12	16	36	32	36	62	101		Total	49	20	46	12	29	48	91
Average	1.5	2.7	7.2	32.0	9.0	10.3	14.4		Average	6.1	3.3	9.2	12.0	7.3	8.0	13.0