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# Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurement

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Group-specific communication signals are found in many group-living species. One example is group variation in the production of codas, which are short stereotyped patterns of clicks produced in social contexts, by sperm whales, *Physeter macrocephalus*. However, little is known about how codas are used by groups and individuals. We used the multipulse structure of sperm whale clicks to estimate the size of animals producing codas. Recordings of a single social unit containing nine largely unrelated animals made over a 1-month period yielded 879 codas of 32 distinctive types. We used an automatic technique to measure the interpulse interval of the clicks in these codas because the interpulse interval is closely related to the size of the animal. Ninety-four codas had sufficiently accurate measurements to be included in further analysis. Modes in the distribution of these measurements showed that more than one animal was producing codas. Comparing the measurements within coda types revealed that several coda types were produced by more than one animal. Thus, the codas recorded from these animals represent a shared repertoire, whereby coda production is not limited to a single animal and coda types are shared between individuals within the unit.

Many animal species that live in groups also have group-specific communication signals, on which group members often converge through learning. Such phenomena have been reported in birds (e.g. Mammen & Nowicki 1981; Feekes 1982), bats (e.g. Boughman 1998), primates (e.g. Marshall et al. 1999) and cetaceans (Ford 1991). In some cases it has been shown that animals use these signals to identify groupmates (Nowicki 1983; Boughman & Wilkinson 1998; Hopp et al. 2001), suggesting that these signals serve as group signatures. The link between communication signal and social structure is particularly clear in cetaceans; individual, group or population specificity of signals often reflects the social system of the species in question (Tyack 1986; Tyack & Sayigh 1997). For example, 'resident' killer whales, *Orcinus orca*, show group-specific pulsed call repertoires (Ford 1991), and live in highly stable matrilineal groups that forage cooperatively and share food (see Baird 2000). Conversely, bottlenose dolphins, *Tursiops truncates*, apparently show individual-specific tonal 'signature whistles' (Caldwell et al. 1990; but see McCowan & Reiss 2001), and live in a fission–fusion society within which associations between individuals are labile in the short term, but can form the basis of long-lasting relationships (Connor et al. 2000). Thus, cetacean vocal variation parallels underlying social structure. Group-specific dialects may be important signatures for individuals seeking the advantages of group living (Tyack & Sayigh 1997; Connor et al. 1998); they may also play a role in mate choice (see Barrett-Lennard 2000). However, they may also be the results of selectively neutral cultural drift, the gradual accumulation of transmission errors (Cavalli-Sforza & Feldman 1981; Slater 2001). As a group, the Cetacea offer exciting opportunities to further explore these issues comparatively in species that live in stable social groupings. One such species is the sperm whale, *Physeter macrocephalus*.

Sperm whale social structure is complex. Females, calves and immature animals of both sexes, found in subtropical and tropical waters, live in relatively stable social 'units,' containing on average 11–12 animals, that persist for decades; however, these units typically form 'groups' with one or more other units that persist for several days, and so at sea one generally encounters these groups that are temporary associations of stable units (Whitehead et al.

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1991; Christal et al. 1998; Whitehead & Weilgart 2000); we will retain these meanings of the terms ‘group’ and ‘unit’ throughout this paper. Results of genetic studies initially suggested that these social units might be matrilines (Richard et al. 1996). However, more recent work has shown that these units may not generally be strict matrilines; specifically, observations of social units containing large proportions of unrelated individuals (Christal et al. 1998; Mesnick 2001), and of membership changes in social units (Christal et al. 1998), have produced a more complex picture. In contrast to females, males disperse from their natal units at a mean estimated age of 6 years, whence they migrate slowly into higher latitudes prior to attaining sexual maturity at 18–21 years (Whitehead & Weilgart 2000). This broad pattern of female philopatry and male dispersal is reflected in high variability and a lack of geographical structure in nuclear DNA relative to mitochondrial DNA (mtDNA, Lyrholm et al. 1999). The benefits of group living for females include, but may not be limited to, communal care of young and defence against predation (Whitehead & Weilgart 2000; Pitman et al. 2001).

Sperm whales make repeated stereotyped sequences of 3–40 broadband clicks lasting generally less than 3 s. These have been termed ‘codas’ (Watkins & Schevill 1977). Coda production in sperm whale groups is strongly linked to social behaviour; they are much more likely to be made when animals are together socializing at the surface than during foraging bouts when they are more dispersed (Whitehead & Weilgart 1991). For this reason, codas are presumed to have a social function such as reaffirming bonds after foraging bouts (Whitehead & Weilgart 2000), although there is no direct evidence regarding the role of these vocalizations. Communication systems based primarily on rhythm are unusual in mammals; the best example is the drumming of alarm signals by kangaroo rats, *Dipodomys* spp. (Randall 1997), and other possible examples include drumming by chimpanzees, *Pan troglodytes* (Boesch 1996), and the use of clicks by Hector’s dolphins, *Cephalorhynchus hectori* (Dawson 1991).

Codas can be classified into types according to the number and temporal pattern of the clicks they contain. For example, ‘2+3’ is a coda containing two regularly spaced clicks followed by a longer gap before three more clicks while ‘5R’ is a coda with five regularly spaced clicks. This classification makes intuitive sense because coda types as defined by patterns of clicks are more or less discrete (Moore et al. 1993; Weilgart & Whitehead 1993), but in no case has the significance of a classification to the animals been tested using playbacks; some studies have classified codas visually (e.g. Moore et al. 1993), others using numerical techniques (e.g. *k*-means cluster analysis, Weilgart & Whitehead 1997). In a study of sperm whales in the southern Pacific Ocean, Weilgart & Whitehead (1997) found that the sperm whale groups they encountered had distinctive dialects in coda usage based on analyses of interclick intervals (ICIs), the time intervals between clicks in a coda, standardized to total coda length. Specifically, the same groups recorded on different days produced very similar proportions of the 30 identified coda types, whereas proportional use of coda types differed between groups. A further study combining genetic and coda data from six sperm whale groups revealed a clear link between mtDNA and coda repertoire; groups with similar mtDNA tended to have similar coda usage dialects (Whitehead et al. 1998). This result implies that coda usage is transmitted between generations in a parallel fashion to mtDNA (i.e. matrilineally). Whitehead et al. (1998) suggested vertical cultural transmission (offspring learn codas from their mothers) as the best explanation for this pattern. This led us to suggest that sperm whale coda dialects were an example of cetacean culture, if culture is broadly defined (Rendell & Whitehead 2001). Since then, we have described variation in group coda usage in more detail, showing that sperm whale units and groups in the South Pacific can be assigned to one of five vocal ‘clans,’ broadly similar to clans in killer whales (Rendell & Whitehead 2003a). However, others have objected that the recording methods used to collect the data on vocal dialects cannot distinguish between group and individual behaviour (Freeberg 2001; Tyack 2001). Freeberg (2001) suggests that one cannot know from these recordings whether observed differences are really between units or between individuals that may be particularly vocal and thus consistently dominate recordings of groups, questioning the existence of unit-specific dialects in sperm whales.

Here we attempt to address these concerns using a fortuitous acoustic feature of sperm whale clicks, the interpulse interval (IPI). Sperm whale clicks have a multipulsed structure (Fig. 1), thought to arise from reverberations of the initial click along the length of the spermaceti organ within the whale’s head (Norris & Harvey 1972; Møhl 2001). In agreement with this theory, it has been shown that the IPI is directly related to body length (Gordon 1991). Here we apply a method developed by Goold (1996), which automatically measures IPIs, to

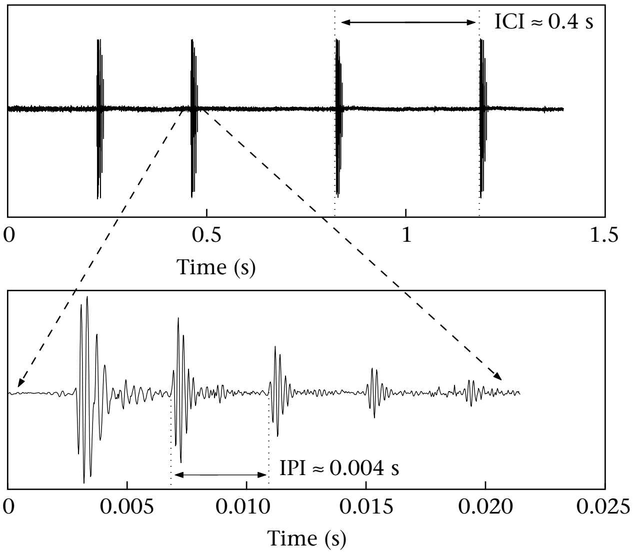

**Figure 1.** Illustration of interclick intervals (ICI) of a sperm whale coda and the interpulse interval (IPI) in a single click. The coda illustrated is a 2+2 type recorded from the focal social unit of this study.

multiple recordings of codas from a single sperm whale social unit. Thus, we estimate the length of the animal that produced any given coda and so examine the diversity of coda production by animals of various sizes within a single social unit. In this way we can investigate whether coda repertoires really are shared attributes or the persistent output of one or two individuals, and also determine whether coda types are shared within social units.

## METHODS

### Unit T

Unit T is a social unit of nine female and immature sperm whales that we followed during four encounters for a total of 17 days (10–20 March, 28–31 March, 6 April and 9–12 April 1999) around the Galápagos Islands. We tracked the animals visually during the day and followed them acoustically at night using a directional hydrophone (see Whitehead & Gordon 1986). We took identification photographs of the tails whenever possible and rated the quality, *Q*, of each picture from 1 to 5 based on the size of the tail in the frame, how focused the image was, and other factors (Arnbom 1987), which revealed the presence of nine animals in the group. All nine animals were repeatedly identified in a total of 379 identifications with $Q \geq 3$ (see Whitehead 2001). Photo-identification records from previous work around the islands revealed that all nine had been identified together 1 year previously; hence we considered them to be a long-term social unit (Christal et al. 1998). During the follows, the only other sperm whales seen were mature males on two separate days; hence in contrast to the normal pattern of a group consisting of more than one social unit, here we are confident that we were following a single social unit. Sloughed skin samples yielded genetic material from five of the nine unit T members (see Whitehead et al. 1990). Genetic results indicated that the five unit members sampled were largely unrelated, with *r* values of −0.23 to 0.17 from nine microsatellite loci, and two mtDNA haplotypes present (Mesnick 2001; Whitehead 2003).

### Coda Analysis

During the encounters with unit T, we made 21 recordings, but none on the days males were seen. Thus, we are sure that only the nine members of unit T were present during recording, giving a unique opportunity for insight into the diversity of a single unit's repertoire and to examine the question of coda sharing using interpulse intervals. To make the recordings, we used an Offshore Acoustics hydrophone (frequency response: ±3 dB; range 6 Hz–10 kHz) connected to a Sony TC-D5M cassette recorder (frequency response: 30 Hz–17 kHz). We subsequently digitized these recordings at 44.1 kHz onto a standard desktop PC and analysed them using a dedicated software package called Rainbow Click (see Gillespie 1997; Leaper et al. 2000; Jaquet et al. 2001). The program detects sperm whale clicks (with user supervision) and stores them in a separate data file; the user can then mark clicks as belonging to a coda. Once the user has marked codas, the software outputs the timing of clicks within the codas in seconds (e.g. a regular four-click coda could be represented as 0.180, 0.178, 0.182 s). We only analysed codas that could be clearly identified aurally; the recordings yielded 879 codas of sufficient quality for further analysis (Table 1). These data were then standardized by

**Table 1.** Recordings of sperm whale unit T during March and April 1999

| Date | Start time | Duration (minutes:seconds) | Latitude | Longitude | Number of codas recorded | Number of codas IQR < 0.02 ms |
|---|---|---|---|---|---|---|
| 10 March | 1019 | 01:50 | 0.19°S | 90.36°W | 26 | 0 |
| | 1052 | 02:34 | 0.19°S | 90.36°W | 35 | 1 |
| | 1118 | 00:59 | 0.19°S | 90.36°W | 8 | 0 |
| 13 March | 1255 | 02:49 | 0.14°S | 90.33°W | 79 | 8 |
| 14 March | 1018 | 01:51 | 0.32°S | 90.17°W | 22 | 0 |
| | 1040 | 04:21 | 0.32°S | 90.17°W | 75 | 4 |
| | 1508 | 01:29 | 0.27°S | 90.26°W | 10 | 2 |
| 15 March | 0920 | 09:38 | 0.23°S | 90.29°W | 194 | 17 |
| 16 March | 1105 | 02:23 | 0.27°S | 90.27°W | 29 | 3 |
| | 1310 | 01:54 | 0.28°S | 90.32°W | 13 | 0 |
| 18 March | 1145 | 05:58 | 0.09°S | 90.45°W | 76 | 14 |
| | 1251 | 01:16 | 0.12°S | 90.46°W | 16 | 5 |
| | 1259 | 02:19 | 0.12°S | 90.46°W | 33 | 8 |
| 19 March | 1141 | 04:56 | 0.06°S | 90.94°W | 69 | 5 |
| | 1307 | 01:29 | 0.05°S | 90.96°W | 24 | 2 |
| 20 March | 1116 | 05:06 | 0.07°S | 90.93°W | 60 | 15 |
| | 1257 | 01:37 | 0.06°S | 90.94°W | 8 | 1 |
| 28 March | 1537 | 01:58 | 0.41°S | 90.11°W | 30 | 1 |
| 6 April | 1505 | 02:41 | 0.17°S | 90.34°W | 36 | 7 |
| 6 April | 1630 | 01:40 | 0.17°S | 90.34°W | 21 | 1 |
| 10 April | 1240 | 01:48 | 0.24°S | 90.29°W | 15 | 0 |
| Total | | 60:36 | | | 879 | 94 |

IQR: interquartile range.

coda length and classified into types using *k*-means cluster analysis in a divisive clustering algorithm using Duda & Hart's (1973, pp. 239–243) ratio criterion as a stopping rule to determine the number of clusters, or coda types. This criterion compares the reduction in the ratio of the within- and between-group sum of squares obtained by splitting a given cluster into two with the range of ratios expected under the null hypothesis of splitting a single multivariate normal population; if the obtained ratio falls outside a given proportion of the expected null range, then the null hypothesis is rejected and the two resultant clusters are accepted. Here we set the critical level at 95%, and clustered the codas as follows. For codas with a given number of clicks (e.g. four-click codas), we clustered the data using iterative *k* means with $k = 2$ (repeated 10 times, selecting the solution with the lowest within-group sum of squares); each split was then accepted or rejected according to the Duda & Hart criterion, and the resultant clusters were again split and tested, with division continuing until all possible splits were rejected (for more details, see Rendell & Whitehead 2003b).

## IPI Analysis

Repeated broadband pulses cause 'ripples' in the log magnitude spectrum of a signal, with a frequency equal to the time between pulses; because the multiple pulses of a sperm whale click are broadband signals, they cause ripples in the spectrum of a click with a frequency equal to the IPI of the click (Goold 1996). This frequency can be measured automatically by extracting peaks from the spectrum (termed the cepstrum) of a click (Goold 1996). The software package Rainbow Click also outputs the digitized sound data for each click in each coda, and we used these data for the IPI analysis. We wrote MATLAB (v12.0, with Signal Processing Toolbox) routines to automatically analyse large numbers of clicks by extracting the maximum value from the cepstrum, following precisely Goold's (1996) method.

We then calculated the median and interquartile range for IPI measurements from all the clicks in each coda, and selected from this set those codas with IPI interquartile ranges of less than 0.02 ms, the minimum time resolution at a 44.1-kHz sampling rate (typical IPI estimates ranged from 3.7 to 4.5 ms). This last step can be justified under the assumption that the 'true' IPI is identical for every click in a given coda, and thus large interquartile ranges are indicative of measurement error (e.g. due to overlapping clicks, wave noise or poor recording conditions) rather than a genuine variation in IPI. Interpulse intervals from a given individual are expected to vary with pressure (i.e. depth) and temperature, because these factors affect the speed of sound through spermaceti oil and hence within the spermaceti organ (Goold et al. 1996). However, 99% of the codas analysed were less than 3 s long; the potential for these factors to change significantly during the emission of a coda was thus rather limited, given that all the codas were recorded from whales at the surface. Hence we assumed identical IPIs.

## RESULTS

The *k*-means cluster analysis grouped the codas into 32 types. A 'discovery curve' of the number of types heard plotted against the number of codas recorded reached an asymptote after approximately 400 codas (Fig. 2). The seven most common types accounted for over 75% of the codas heard, with the two most common types accounting for 40% (Fig. 3). However, there were many rare types; 19 of the 32 clusters each made up less than 1% of the codas recorded (Fig. 3).

Of the 879 codas recorded from unit T, 94 (~11%) had IPI measurements with interquartile ranges of less than 0.02 ms, and these had median IPIs between 3.7 and 4.2 ms (see also Table 1). Using Gordon's (1991) equation to calculate estimated body length from IPI, our results indicated that the animals we recorded were between 10.20 and 10.92 m in length, which is the range expected for female and immature sperm whales (Rice 1989) and concurs with actual measurements of other whales in the same area (Waters & Whitehead 1990). There were clear modes in the distribution of median IPIs, showing that a number of differently sized animals were vocalizing (Fig. 4).

For a number of types, in particular 3R, 1+2 and 2+2, there were again clear clusters in the data, showing that these coda types were made by a number of animals that differed in size (Fig. 5). A similar picture emerged when we measured their proximity in multivariate space. We selected the 46 three-click codas from unit T with IPI measurements having an interquartile range of less than 0.02 ms. For each pair of codas in this set, we plotted the absolute difference in median IPI against the Euclidean distance between the two codas calculated from the standardized ICIs of the codas (Fig. 6). A number of differently sized animals were recorded, because most of the pairs of codas had median IPIs that differed by more than 0.02 ms, and on several occasions, different animals (indicated by a large difference in median IPI) made similar

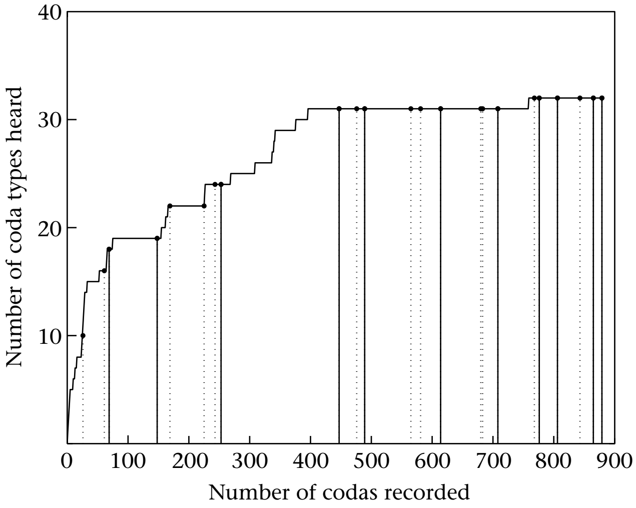

**Figure 2.** Discovery curve of coda types heard plotted against codas recorded from unit T. Solid vertical lines separate recording days and dotted vertical lines separate recordings.

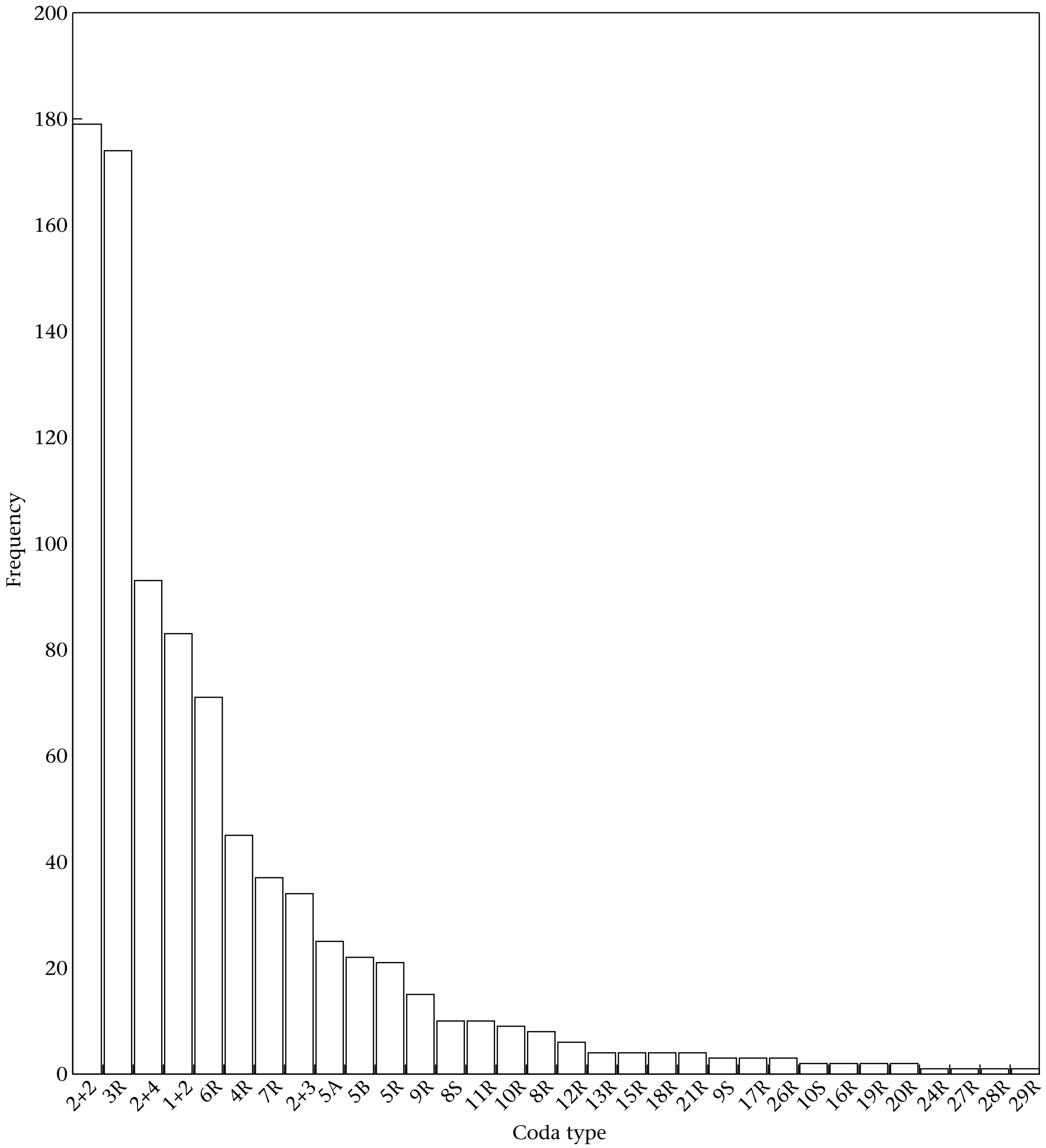

**Figure 3.** Frequency distribution of coda types heard from unit T.

codas, as evidenced by points occurring in the top left sector of the plot in Fig. 6.

## DISCUSSION

In this study we investigated whether coda types are shared across individuals, and whether coda repertoires recorded from sperm whale social units are genuinely unit repertoires, in that they are an attribute of the unit as a whole rather than of one or two vocal individuals. The data presented here show that, for unit T at least, the answer to both these questions is yes. Our results showing that unit T's repertoire differs from the repertoires of other units are presented elsewhere (Rendell & Whitehead 2003b). The results of the IPI measurement were inconsistent with a scenario in which vocalizations recorded from unit T were produced by a single individual. Instead, they are consistent with several animals vocalizing, given the modes present in the data. Similarly, a given coda type can be produced by more than one animal; sperm whales in unit T share at least some of their coda types. This conclusion is robust to varying coda classification because it holds true when no classifications were made; very similar codas were recorded with IPI estimates that clearly indicated that they were made by different animals. Also, different codas were recorded with IPI estimates close enough (i.e. median differences of less than 0.02 ms) to be from the same individual (Figs 5, 6). While this suggests that individual sperm whales have repertoires containing

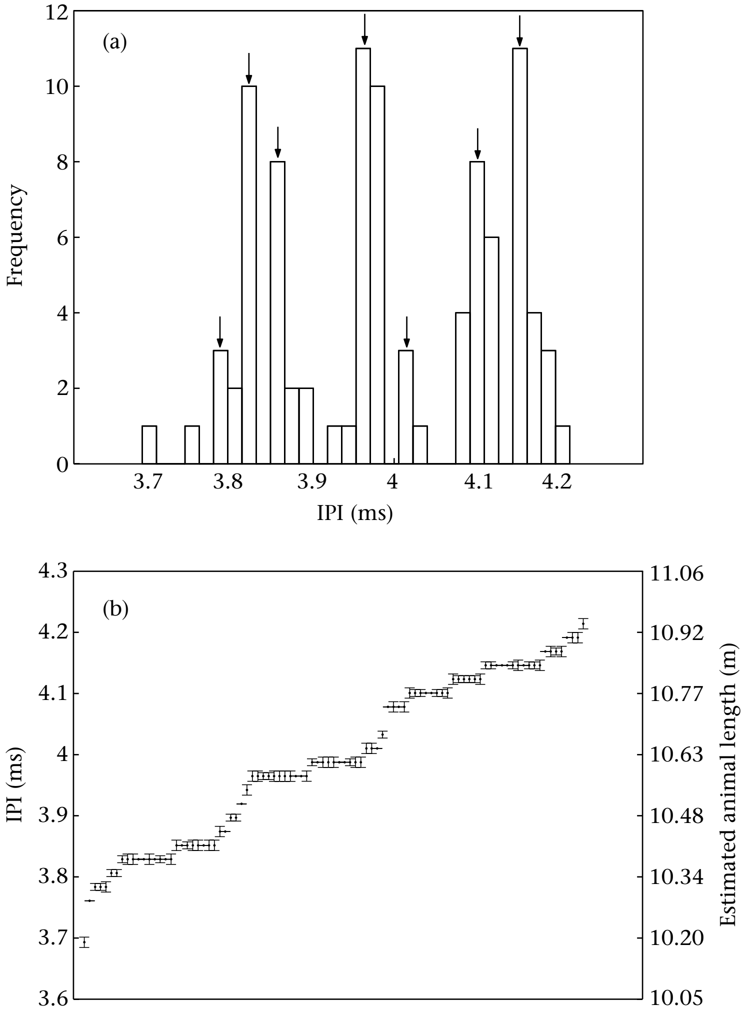

**Figure 4.** IPI measurements from the 94 codas recorded from unit T having interquartile ranges of less than 0.02 ms. (a) Histogram of the median IPI for each coda; the seven peaks in the distribution are marked. (b) IPI measurements are ordered by increasing duration and corresponding animal length, derived from Gordon's (1991) equation. Points are medians with interquartile ranges represented by bars.

several coda types, we cannot eliminate the possibility that the different codas could have been made by different whales of very similar size. However, because only nine animals were present and 32 coda types were recorded, at least one animal must have made more than one coda type.

Although our conclusions are based on the assumption that the true IPI of the clicks we measured in this study did not change during any given coda, we believe that this assumption is justified. Consider a click with a 4-ms IPI (i.e. in the middle of our range of estimates), and assume that the spermaceti is at 33 °C (as measured from a recently killed sperm whale; Clarke 1978). Using Goold's (1996) empirically derived equations relating sound velocity to temperature and pressure in spermaceti oil, a 4-ms IPI at 33 °C and 101 kPa (1 atmosphere) gives a 5.59-m travel distance for the sound pulse (sound velocity: 1397 cm/s), equating to a head size of 2.79 m, because each pulse is thought to travel twice through the spermaceti before leaving the head (Norris & Harvey 1972). Increasing the pressure to 1013 kPa (10 atmospheres), representing a dive to 100 m, results in a decrease of 0.011 ms in the travel time (and hence IPI). Maximum observed dive rates for sperm whales are 4 m/s (Watkins et al. 1993), so it would take at least 25 s for an animal to reach that depth. Because the longest of the 94 selected codas lasted 3.4 s, and because we made all our recordings while the group was socializing at the surface, it seems unlikely that variation in IPI due to pressure would be a significant factor here. Temperature also affects sound transmission in spermaceti. However, temperature would need to fall by 1.5 °C from 33 °C at atmospheric pressure to produce a 0.02-ms change in the IPI, again using Goold's (1996) equations; it is impossible that this could occur in the 1–3 s required to produce a coda (see Clarke 1978). One further potential source of within-coda IPI variation is alteration of the shape of the spermaceti sac using the maxillonasalis muscle (Goold 1996). If sperm whales use the maxillonasalis muscle to alter the shape of the spermaceti sac, then IPIs from the same whale would vary unpredictably. Studies using acoustic tags (Madsen et al. 2002; P. Madsen, personal communication), however,

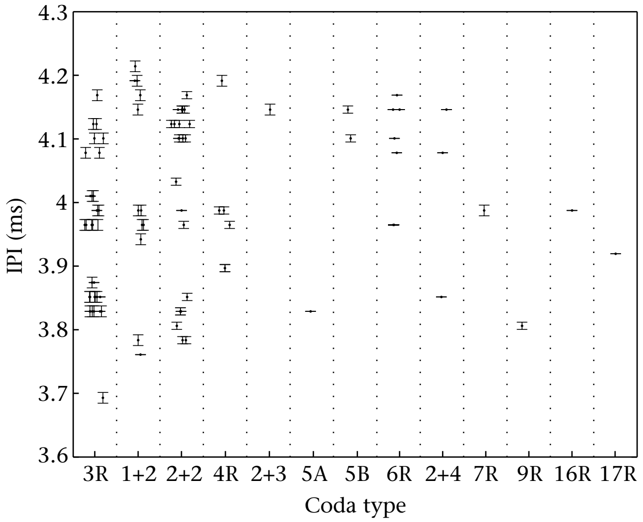

**Figure 5.** IPI measurements from unit T plotted by coda type. Each column contains one coda type. Points are medians with interquartile ranges represented by bars, and are jittered horizontally to illustrate codas having identical median IPIs.

show that within-coda IPI variation is less than ±0.02 ms for codas recorded in the upper 250 m of the water column, and studies of solitary male sperm whales show that IPIs in regular clicks remain stable over periods of minutes (Rhinelander 2001). Hence, we are confident in our assumption that large variation in within-coda IPI values was due to measurement error and not to changes in the true IPI of the clicks. It is unfortunate that we were forced to reject large numbers of codas from our original data set, probably because the recordings in the present study suffered from overloading problems. Although other recordings that were made with better equipment and without overloading yielded much higher proportions of usable IPI estimates (>30%, L. Rendell, unpublished data), we used the recordings of unit T because they were made from a clearly defined set of animals, crucial for the present study.

Variation between codas made by the same animal is another possible source of confound; because the animals were always at the surface, pressure due to depth is an unlikely source of variation. However, we can be less confident regarding temperature, mainly because we do not know how the spermaceti temperature in a sperm whale's head may vary over periods of days; it may not vary at all, but probably does at least to some extent. We measured the sea surface temperature every 3 h while at sea; the temperatures nearest to each recording were between 26.0 and 31.8 °C, a range of 5.8 °C. Taking a conservative approach by assuming that the spermaceti temperature in the recorded animals oscillated as much as the sea water temperature (i.e. 5.8 °C) around a mean of 33 °C (i.e. as much as 2.9 °C either above or below 33 °C) would result in a maximum change in IPI of 0.06 ms between the coolest and warmest conditions according to Goold's (1996) equations. This could account for some of the spread in our data, but is not of sufficient magnitude to significantly alter our conclusions, because the gap between most of the clusters exceeded 0.06 ms (Fig. 5). In addition, it is unlikely that spermaceti temperature varies as freely as this. Given that the primary function of the spermaceti organ is thought to be sound transmission (see e.g. Cranford 1999), it seems reasonable to expect the temperature to be maintained around some optimum for this function, perhaps 33 °C as measured by Clarke (1978). Finally, the elimination of codas with variable IPI estimates could introduce bias in our results if it meant only codas from one or two recordings were retained. However, this was not the case here; the highly accurate measurements came from 17 different recordings on 10 different days and represent an essentially random sample of the group's total output (Table 1).

This study characterizes the coda repertoire of a single social unit. The discovery curve of coda types (Fig. 2) gives us some confidence that, with 32 coda types identified, most of the repertoire diversity of unit T was captured. Most of the diversity was present in approximately the first 500 codas recorded, giving a useful cue for future studies that seek to characterize unit coda repertoires in sperm whales. However, these patterns themselves may be group specific, so care should be taken in generalizing. Codas were recorded in very similar behavioural contexts (socializing or resting at the surface), but then codas are generally heard from sperm whales in these contexts (Whitehead & Weilgart 1991). Given that our recordings spanned 1 month, we are confident that the repertoire of unit T was well characterized. It is noteworthy that relatively few types dominated the coda output, particularly 2+2 and 3R codas (Fig. 3); these types may be a 'unit signature' similar to the discrete calls of killer whales (see Ford 1991), but more work is needed on the repertoires of other known social units before conclusions can be drawn. Some have suggested that coda types may function as individual signatures (Watkins & Schevill 1977; Watkins et al. 1985; Tyack 1999); if this were the case, then one would expect nine coda types to be prevalent in the repertoire of these nine animals, but there was no indication of this (Fig. 3).

The five genotyped individuals showed no close relations, and possessed two mtDNA haplotypes; therefore, this unit is not a strict matriline. Given that we only sampled five individuals, it is possible that first-order relationships (sibling, or mother–offspring) existed in unit T but were not sampled. The most extreme case possible would be that the four individuals not sampled were all first-order relatives of one of the five that were sampled. We simulated sampling, without replacement, of five individuals at random from nine animals with four, three, two and one first-order relationships; the percentages of 10 000 samples that contained no relationships were 12.9, 28.3, 47.5 and 72.8, respectively; it is therefore possible that one or two close genetic relationships were missed, but rather unlikely that more were present. Given that coda types were shared within unit T, and that unit T members appeared largely unrelated, the most parsimonious explanation for these patterns is that coda sharing is a result of social learning rather than common genetic descent. This could take the form of contextual learning, where the context of producing sounds is learned but the

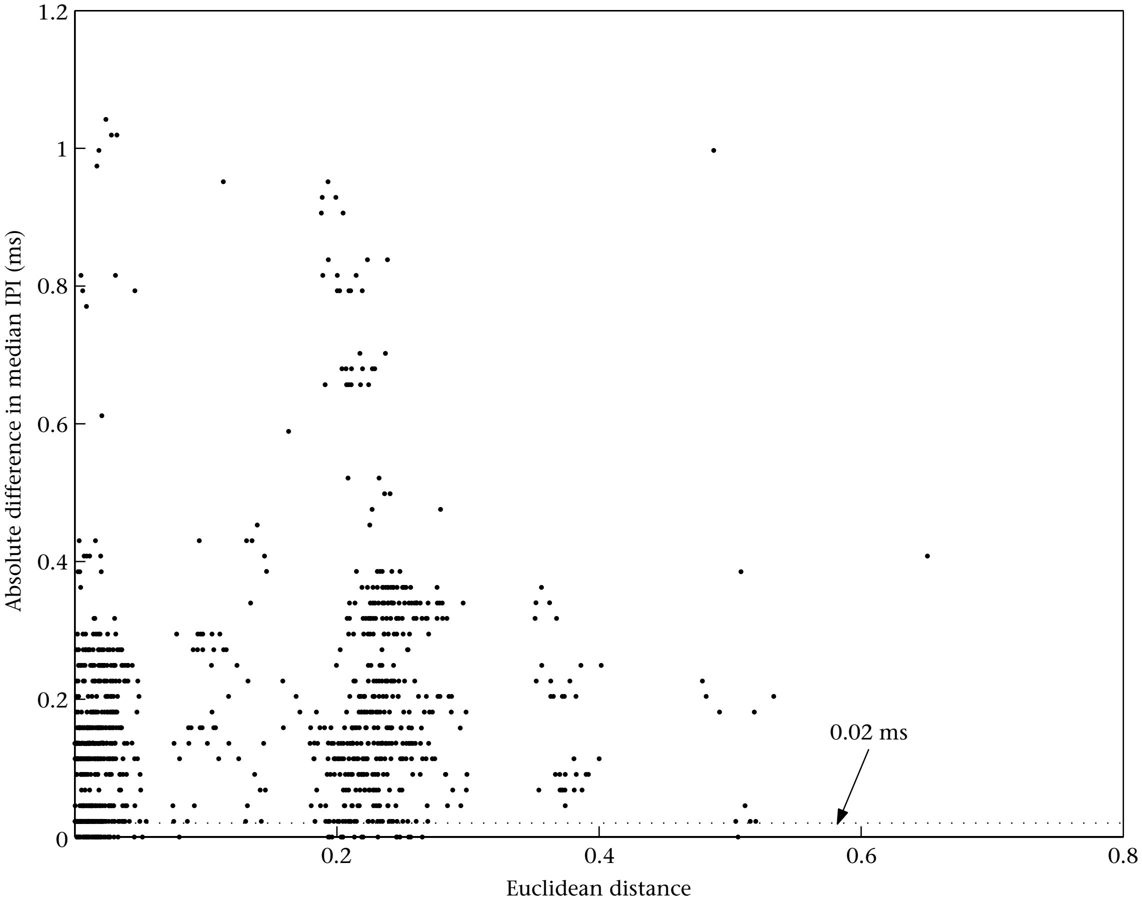

**Figure 6.** Absolute difference in median IPI plotted (high values indicate vocalizing animals of increasingly divergent size) pairwise against Euclidean distance (high values indicate increasingly different coda rhythms) for three-click codas from unit T. The horizontal dotted line represents a difference of 0.02 ms in median IPIs; points above this line represent pairs of codas that were probably made by different animals.

sounds themselves are not (i.e. learning the timing of clicks in a coda), or production (vocal) learning, where the form of the sound itself is learned (i.e. the entire coda is learned as a single unit; see Janik & Slater 2000). The difference depends critically on what the minimum unit of production is for sperm whale social sounds, which remains unknown (Janik & Slater 2000).

The initial impetus for this study was given by Freeberg's (2001) and Tyack's (2001) suggestions that what Weilgart & Whitehead (1997) labelled group dialects could equally have been differences between individuals in those groups; these suggestions also presumably apply to our description of vocal clans (Rendell & Whitehead 2003b). Here we have shown that coda types are shared within a social unit, and that several whales produced codas during social periods. Whether this holds true on a wider basis remains to be seen, but the implication is clear: repertoire differences between recordings of different units (Rendell & Whitehead 2003a) represent real differences in the repertoires and are not the result of individuals biasing the unit output, provided that the unit has been sufficiently sampled. Similar studies of other units are clearly desirable so we can move forward to study how this communication system fits into the wider context of group-specific signals in social animals regarding the relationship between coda dialect and social structure. We still need to know how coda usage patterns vary between groups, social units and individuals, how they vary geographically, how codas are used, and whether clan dialects are functional.

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