

Individually distinctive acoustic features in sperm whale codas

Ricardo Antunes^{a,*}, Tyler Schulz^{b,1}, Shane Gero^{b,1}, Hal Whitehead^{b,1},
Jonathan Gordon^a, Luke Rendell^a

^aSea Mammal Research Unit, University of St Andrews

^bDepartment of Biology, Dalhousie University

ARTICLE INFO

Article history:

Received 18 March 2010

Initial acceptance 6 July 2010

Final acceptance 22 December 2010

Available online 4 February 2011

MS. number: 10-00186

Keywords:

coda

individual variation

Physeter macrocephalus

sperm whale

vocal behaviour

Social animals may develop behavioural strategies that are based on individualized relationships among members. In these cases, there might be selection pressures for the development of identity signals and mechanisms that allow discrimination and recognition of particular individuals. Female sperm whales, *Physeter macrocephalus*, live in long-term, stable social units. Differential interactions among unit members suggest the need for an individual discrimination system. Sperm whales produce stereotyped series of click sounds called codas, which are thought to be used for communication. Although codas were initially proposed as individual signatures, later studies did not support this hypothesis. Using linear discriminant functions and Mantel tests, we tested variation within coda types as a means for individual identification, using recordings where codas were assigned to individual whales. While most coda types showed no indication of individual-specific information, individual differences that were robust to variation among recording days were found in the 5 Regular coda type. Differences in individual-specific information between coda types suggest that different coda types may have distinct functions.

© 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Securing the benefits of group living often requires mechanisms for group cohesion. These require the exchange of information through some form of communication. In long-term social groups, animals may develop behavioural strategies that are based on individualized relationships among members, such as dominance hierarchies and roles within groups (Wilson 1975). In these cases, one would expect selection pressures favouring the development of identity signals and mechanisms that allow discrimination and recognition of particular individuals. Long-term associations among animals also provide the prior experience of particular individuals required for the development of individual-level signal recognition, based on learned familiarization (Bradbury & Vehrencamp 1998; Tibbetts & Dale 2007).

Individual discrimination is possible when signal parameters have individually unique attributes, or when the signal parameters' variability is greater between than within individuals, and these differences persist over time (Beecher 1982, 1989). For example, white-winged vampire bats, *Diaemus youngi*, show individual variation in the structure of social calls, which the bats can discriminate (Carter et al. 2008).

When behavioural responses to signals have different consequences depending on the signaller, the ability to discriminate between group members can also be advantageous. For example, receivers can reduce the costs of responding to alarm calls by varying responses depending on their spatial relationship and on the reliability of the signaller(s) (Robinson 1981; Ydenberg & Dill 1986; Cheney & Seyfarth 1988; Bachman 1993; Kildaw 1995). Animals can also keep track of hierarchical relationships within groups by eavesdropping on signals from interactions of other individuals (Bergman et al. 2003).

The sperm whale, *Physeter macrocephalus*, is a social cetacean species. Females and immature animals of both sexes live in social units whose composition is largely stable over decades (Whitehead & Weilgart 2000). These units contain approximately 12 animals in the Eastern Pacific and North Atlantic, but are smaller in other areas, such as the Caribbean Sea (Christal et al. 1998; Coakes & Whitehead 2004; Gero et al. 2008; Antunes 2009; Jaquet & Gendron 2009). Units are distributed throughout subtropical and tropical waters and are generally matrilineal (Rice 1989; Mesnick 2001).

Individuals within social units have preferred associates among members (Gero et al. 2008), indicating differences in the way an individual interacts with other members of its unit. These preferred associations among unit members suggest the possibility of an individual discrimination system.

Sperm whales produce broadband clicks (0–20 kHz) characterized by a series of usually evenly spaced pulses of decaying amplitude (Backus & Schevill 1966; Watkins & Schevill 1977; Møhl

* Correspondence: R. Antunes, Sea Mammal Research Unit, University of St Andrews, Scottish Oceans Institute, Gatty Marine Lab, St Andrews, Fife KY16 8LB, U.K.

E-mail address: rna@st-andrews.ac.uk (R. Antunes).

¹ T. Schulz, S. Gero and H. Whitehead are at the Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada.

et al. 2003; Madsen et al. 2002a), whose interpulse interval (IPI) has been shown to be correlated with the whales' size (Gordon 1991; Rhinelanders & Dawson 2004). These clicks function in communication, orientation and finding prey (Jaquet et al. 2001; Whitehead 2003; Madsen et al. 2002a, b; Miller et al. 2004a, b; Schulz et al. 2008, 2011).

Sperm whales produce stereotyped patterns of these clicks, termed codas, which are thought to have a communicative function (Watkins & Schevill 1977; Weilgart & Whitehead 1993; Schulz et al. 2008, 2011). The communicative function initially proposed for codas was one of individual signatures (Watkins & Schevill 1977; Watkins et al. 1985). Later studies, which classified codas into distinct types, showed evidence of coda type sharing among individuals, challenging the initial hypothesis (Moore et al. 1993; Weilgart & Whitehead 1993; Rendell & Whitehead 2003b). Sperm whale groups in the South Pacific Ocean have subsequently been shown to have distinct coda dialects, which are stable for periods of at least 6 years (Weilgart & Whitehead 1997; Rendell & Whitehead 2003b, 2005). Schulz et al. (2011) found that most adult animals within a social unit shared the most common coda types, with the exception of the mother–calf pair whose repertoires were different from those of other unit members and each other. Apart from the mother–calf differences, the repertoire similarities of other members did not support the hypothesis of individually distinctive coda type repertoires. This sharing of coda repertoires suggests that they allow group membership recognition, at either the unit or clan levels. This hypothesis is further supported by the fact that social units seem to form groups preferentially with other units of their own clan (Rendell & Whitehead 2003b).

However, codas are not perfectly stereotyped. Within particular coda types that can be identified statistically, there is often considerable variation in the timing patterns. Even though there is no indication that this variability is functional, it is possible that it is specific to individuals. Thus, individuals within groups might be recognizable by the structure of particular coda types rather than by the range of coda types they produce. With this in mind, we hypothesized that variation in particular coda types could potentially carry information about individual identity and therefore codas could contain both group- and individual-level information. In this study, we tested the hypothesis that variation within coda types allows statistical discrimination of individual unit members, potentially allowing for individual identity to be communicated between members in a social unit by means of variation in the patterning of the clicks.

METHODS

We used a data set consisting of recordings of codas from a single social unit collected on the lee coast of the island of Dominica (Schulz et al. 2011). This unit, termed the 'Group of Seven', consisted of five adult females (identification codes no. 5130, no. 5563, no. 5722, no. 5561, no. 5560), one juvenile male (no. 5727) and one male calf (no. 5703; see Gero et al. 2008). These five females have been sighted together for over a decade (Gero et al. 2008). This unit was followed for a total of 41 days from 16 January to 26 March 2005. It was seen on every day (100%) of our 30 days at sea. Despite other animals in the area being readily observed, no other whales, apart from the members of this unit, were observed on days on which recordings used in this analysis were made. As a result, we have a very high confidence that all the vocalizations reported here were made by these seven animals. This unusual residency pattern is rare among sperm whale units and provided us with a unique opportunity to study codas at the individual level. The whales were tracked visually and acoustically using a directional hydrophone (Whitehead & Gordon 1986). During daylight hours the animals were approached while on the surface, usually between foraging dives, and digital photographs of their flukes were taken for individual identification purposes (Arnborn 1987) using a Canon D10 digital SLR camera and a Canon EF 300 mm lens.

Fifteen coda recordings of this unit were made using a towed hydrophone array (consisting of two Benthos AQ-4 elements coupled to Magrec 30 dB preamplifiers with 500 Hz high-pass filter, located 3 m apart in an oil-filled tube, with a 100 m tow cable) while the research vessel's engine was off. Signals were recorded using a Foxtex VF-160 multitrack recorder (48 kHz sampling rate, linear 16-bit resolution, recorded to hard disk). Coda recordings were made opportunistically whenever animals produced them. In this case, coda production occurred in only two contexts: when clusters of two to seven individuals were lying motionless at the surface prior to initiating a foraging dive or in the interval between the initiation of a foraging dive and the first production of echolocation clicks (Schulz et al. 2011). Additionally, recordings of regular echolocation clicks were made whenever solitary individuals fluked at the beginning of a foraging dive.

The recordings were analysed using Rainbow Click, an automatic click detection program (Gillespie 1997) which was used to mark the clicks belonging to the same coda, as well as the series of regular clicks from solitary whales. Typically a series of regular clicks from a diving whale could be distinguished when it first started vocalizing.

Table 1
Coda type repertoire of the 'Group of Seven' social unit, classified using k-means clustering

Coda type	Whale ID numbers							Σ
	no. 5130	no. 5560	no. 5561	no. 5563	no. 5703 _C	no. 5722 _M	no. 5727	
4Reg	2	3	3	0	1	1	0	10
1+3	11	0	3	1	0	34	0	49
2+1+1+1	0	3	0	6	4	0	0	13
1+1+3	21	36	22	18	0	0	7	104
5Reg	0	38	33	4	0	0	8	83
5+1	0	0	0	0	12	0	0	12
6Reg	1	0	0	0	1	1	1	4
7Reg	1	6	0	0	0	0	0	7
6+1	0	0	0	1	5	0	0	6
6+1+1	0	1	0	0	1	0	0	2
1+1+6	0	3	1	0	0	0	0	4
8Reg	0	6	0	1	1	0	0	8
1+1+7	0	1	0	0	0	0	0	1
9Reg	0	5	0	1	3	0	0	9
9+1	0	1	0	0	2	0	0	3
Σ	36	103	62	32	30	36	16	315

Numbers in the classification table correspond to the frequency with which an individual produced each coda type. Bold frequencies correspond to the codas used in the analysis. Subscript C indicates a calf and M indicates its mother.

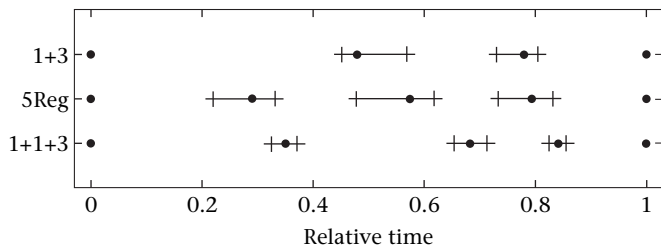


Figure 1. Relative time patterns for the three coda types used in discriminant analysis. Black circles represent the mean location of clicks. Error bars represent 95% percentile variation across all codas for all individuals.

These could be recognized, tracked and labelled through the early part of the recording based on their loudness, relative bearing and spectral characteristics.

The waveforms of the selected clicks were exported and analysed using a custom-written MatLab (Mathworks Inc., Natick MA, U.S.A.) program used to estimate the IPI (time lag between consecutive pulses within a click) modal class of each coda, and each regular click series (Schultz et al. 2011). The IPIs of both coda clicks and regular clicks were compared among individual whales. The clicks of each of the 'Group of Seven' whales had sufficiently distinct IPI among themselves to allow for individual discrimination. Codas were assigned to individuals based on the clicks' IPIs as described by Schulz et al. (2008). Codas with 4–10 clicks were classified into types based on the number and temporal patterns of their clicks using k-means (Duda et al. 2001) classification of interclick interval (ICIs; the time lag between consecutive clicks in a coda) vectors standardized by coda duration, as described in Rendell & Whitehead (2003a, b), using a custom-written computer program in MatLab. The coda types obtained were named following the nomenclature used by Weilgart & Whitehead (1993).

The coda types for which at least five codas had been recorded from each individual were selected for subsequent analysis. Individual discrimination was tested by calculating linear discriminant functions using three sets of variables: Standardized ICIs, Absolute ICIs and the envelope Amplitude of each coda click relative to the loudest in the codas. Relative ICIs were calculated by standardizing the Absolute ICI values by their sum, that is, the total duration of the coda. Because the sum of Relative ICIs equals unity, one of the values is redundant, and so for this data set the last Standardized ICI was not included in the analysis. The Amplitude of each click in a coda was calculated as the ratio between the peak of the click's envelope and the largest envelope peak of all clicks in the coda.

To test whether individuals could be discriminated by their codas, we carried out a linear discriminant analysis for each coda

type. The classification error rates were calculated using a jackknife procedure. In this procedure, one coda at a time was removed from the data set, and the remaining codas were used to calculate linear discriminant functions, which were then used to classify the coda that was left out of the analysis. The proportion of the removed codas that were wrongly classified was calculated as the individual discrimination error rate. The classification error rates were also compared with those obtained by random assignment of codas to individuals. This was done by sampling from the initial set of individuals being compared and randomly assigning codas to individuals, thus keeping the proportion of codas for each individual. This random assignment procedure was repeated for 1000 iterations for each coda type. In each iteration, the proportion of codas incorrectly classified (random assignment error rate) was calculated using the jackknife procedure described above. The proportion of random assignment iterations whose error rates were lower than the observed discriminant function error is a measure of the probability that the calculated classification error rate could have been obtained by chance. The discriminant analysis and error rate calculations were performed using custom-written MatLab code which used the 'Discriminant Analysis Toolbox' by Kieft (1999) after the methods in Ripley (1996).

Because differences observed between individuals could also have been the result of differences in the whales' vocal output between days, we evaluated the combined effects of day of recording and individual using a partial Mantel test (Smouse et al. 1986). This was performed for each coda type. The test was performed using a matrix of pairwise coda similarities (calculated as in Rendell & Whitehead 2003a; basal similarity = 0.001, Euclidean norm) as a response matrix. Two binary pairwise matrices of the same size as the response matrix were used as explanatory variables. The first matrix was built with elements equal to unity for the cases when the pairs of codas were from the same individual, and zero otherwise. A second matrix was similarly built with unity for pairs of codas recorded on the same day. The partial correlation between the response matrix and 'same individual' taking 'same day' into account was then calculated. The value obtained was compared to a distribution of the same parameter calculated by randomizing the identities in the binary matrices, for 1000 iterations.

The present study was entirely observational in nature. Fieldwork conducted in national waters took place under appropriate licence from the national government of the Commonwealth of Dominica. Field protocols were approved by the Dalhousie University Committee on Laboratory Animals (<http://animaletics.dal.ca/>) and were designed to minimize disturbance by approaching whales slowly from behind whenever possible and using minimum required engine power for manoeuvring. No vessel under power approached whales to within 30 m, although occasionally whales would approach drifting vessels of their own accord.

Table 2
Distribution of codas assigned to individuals by date of recording in 2005

Coda type	Whale ID numbers	Recording dates										
		23 Jan	26 Jan	1 Feb	2 Feb	3 Feb	7 Feb	15 Feb	17 Feb	27 Feb	2 Mar	9 Mar
1+3	no. 5130	—	—	3	—	—	7	1	—	—	—	—
	no. 5722	—	—	2	—	—	—	7	—	7	—	18
1+1+3	no. 5130	—	—	16	5	—	—	—	—	—	—	—
	no. 5560	8	—	17	—	9	—	—	—	—	—	—
	no. 5561	9	—	—	2	11	—	—	—	—	—	—
	no. 5563	18	—	—	—	—	—	—	—	—	—	—
	no. 5727	6	—	—	—	1	—	—	—	—	—	—
5Reg	no. 5560	10	—	1	—	7	—	—	8	—	4	—
	no. 5561	12	—	—	—	8	—	—	7	—	—	6
	no. 5727	—	8	—	—	—	—	—	—	—	—	—

Coda types were classified using k-means.

Table 3

Whale classification error rates for coda types 1+3, 1+1+3 and 5Reg, and for variable sets Absolute ICIs, Relative ICIs and Amplitude

Coda type	Whale ID numbers	Absolute ICIs	Relative ICIs	Amplitudes
1+3	5130+5722	0.333 (0.783)	0.267 (0.648)	0.200 (0.218)
1+1+3	5130+5560+5561 +5563+5727	0.625 (0.116)	0.673 (0.356)	0.692 (0.374)
5Reg	5560+5561+5727	0.127 (<0.001)	0.278 (<0.001)	0.468 (0.154)

The probability of obtaining a better classification error rate than by random assignment of identification to individuals (1000 iterations) is shown in parentheses.

RESULTS

The analysis of the coda recordings from the 'Group of Seven' resulted in a total of 315 codas, assigned to 15 types using k-means clustering (Table 1). The calf (individual no. 5703) was left out of the analysis altogether owing to its low representation for some coda types, and because it was the only whale to make a certain coda type. Only coda types 1+3 (16% of the total group repertoire) with four clicks and 1+1+3 (33%) and 5Reg (26%) with five clicks (Fig. 1) had at least two individuals represented by at least five codas and could therefore be used for discriminant analysis (Table 1).

Most of the individual whale repertoires used for discriminant analysis included codas recorded on at least 2 different days for each coda type, with the exception of individual no. 5727 with only 1 recording day for both coda types represented, and individual no. 5563 for coda type 1+1+3 (Table 2).

For two of the three coda types and variable sets included in the analysis, all discriminant function analyses resulted in a number of canonical discriminant functions equal to the number of individual whales being compared minus one. This permits the discrimination between all individuals being compared. In the case of the variable set Relative ICIs for coda type 1+1+3, it was only possible to calculate three canonical discriminant functions, the same as the number of variables in the analysis.

Only two individuals (no. 5130 and no. 5722) were represented with at least five codas of type 1+3, therefore allowing for discrimination only between them (Table 1). The observed classification error rates were lowest for variable set Amplitude, but in all cases higher than or equal to 0.2. The classification error rates for this coda type fell well within the range of those obtained by random classification for all variable sets. This indicates that the classification of codas of type 1+3 to individual whales did not perform better than random assignment of codas to individuals (Table 3).

The distribution of canonical discriminant values for individual no. 5130 completely overlapped those for no. 5722 in all data sets (Fig. 2), indicating a poor discrimination between individuals.

Coda type 1+1+3 was represented with enough codas per individual to allow discriminant analysis for five adult whales (no. 5130, no. 5560, no. 5561, no. 5563 and no. 5727). Classification error rate values for this coda type were lowest for variable set Absolute ICIs, but they fell well within the range of those obtained by random classification for all variable sets. This indicates that the classification of codas of type 1+1+3 to individual whales did not perform better than random assignment of codas to individuals (Table 3). Canonical discriminant function values for all individuals exhibited considerable overlap, and a clear separation pattern was not found for any variable set (Fig. 3). This indicates that separation of individuals using linear discriminants is not possible for coda type 1+1+3.

Only individuals no. 5160, no. 5561 and no. 5727 were represented with more than five codas of type 5Reg. Classification error rates for each variable set in type 5Reg was lowest in variable set

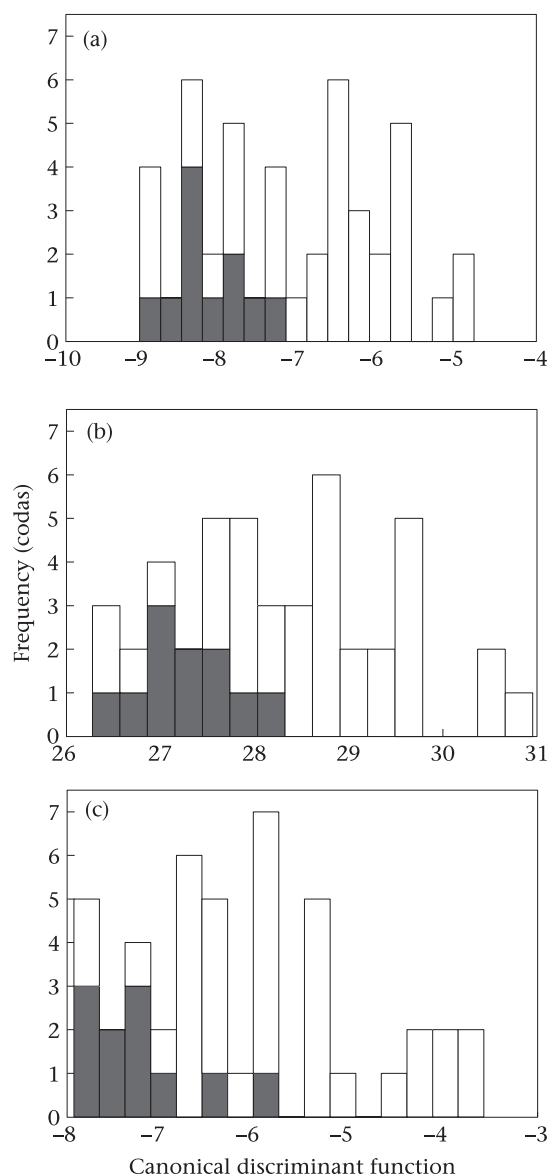


Figure 2. Histograms of canonical discriminant function values for comparisons between individuals no. 5130 (dark bars) and no. 5722 (white bars) for coda type 1+3 and variable sets (a) Absolute ICIs, (b) Relative ICIs and (c) Amplitudes.

Absolute ICIs and highest for variable set Amplitude (Table 3). Classification error rates for variable sets Absolute ICIs and Relative ICIs were outside the range of those obtained by random assignment of individuals to codas (Table 3). In variable sets Relative ICIs and Amplitude the canonical discriminant function values for coda type 5Reg did not show a clear separation between the different individuals (Fig. 4). However, data set Absolute ICIs showed an obvious separation of individuals using linear discriminants.

The pairwise similarity for 5Reg codas showed higher values for comparisons within individuals than between individuals, both within and between days. The same pattern was not apparent for coda types 1+3 and 1+1+3, where similarities were identical regardless of individual identity and day of recording (Fig. 5).

The partial Mantel tests resulted in significant correlation coefficients between coda similarity and being made by the same individual of 0.37 ($P < 0.001$), 0.11 ($P < 0.001$) and 0.55 ($P < 0.001$)

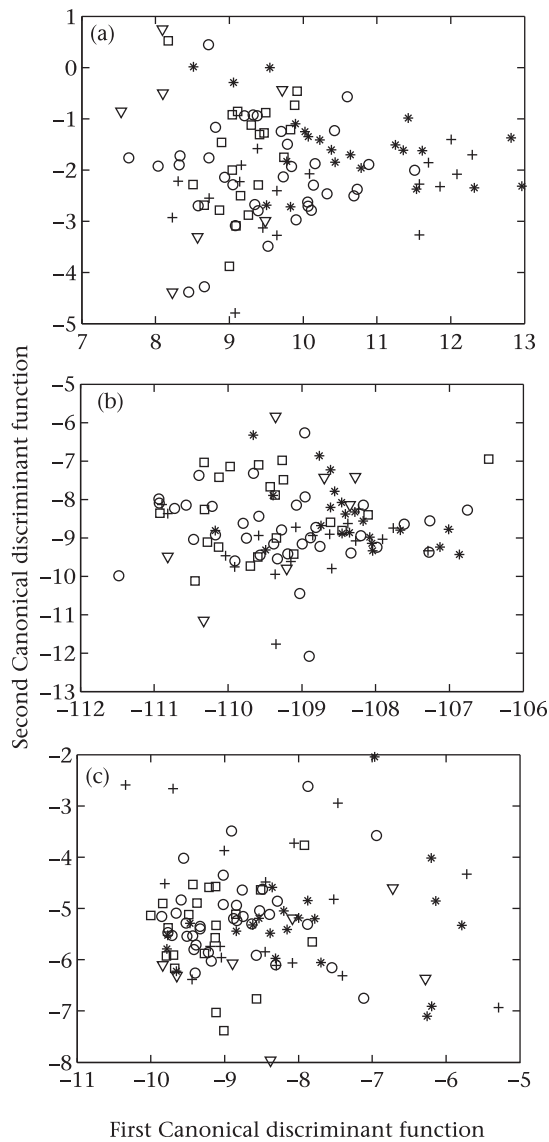


Figure 3. First two canonical discriminant functions for comparison among individuals no. 5130 (□), no. 5560 (○), no. 5561 (*), no. 5563 (+) and no. 5727 (▽) for coda type 1+1+3 and variable sets (a) Absolute ICLs, (b) Relative ICLs and (c) Amplitudes.

for coda types 1+3, 1+1+3 and 5Reg, respectively. The low positive correlation value for coda type 1+1+3 indicates a relatively weaker effect of individual in the similarity of codas. The highest value for coda type 5Reg indicates that the effect of individual identity is stronger even taking into account variation among days. Coda type 1+3 exhibited an intermediate correlation value.

DISCUSSION

Our results show that there is some individual variation in coda production across all the coda types for which we had sufficient data. However, this variation differs across coda types. For the 1+3 and 1+1+3 coda types it does not translate into a reliable discrimination between individuals. In contrast, for 5Reg codas individual variation among the three individuals tested is much more marked, but only when considering Absolute ICLs, as indicated by the discriminant function plots and the classification error rates. It seems plausible that individuals could tell each other apart in this unit based on this coda type.

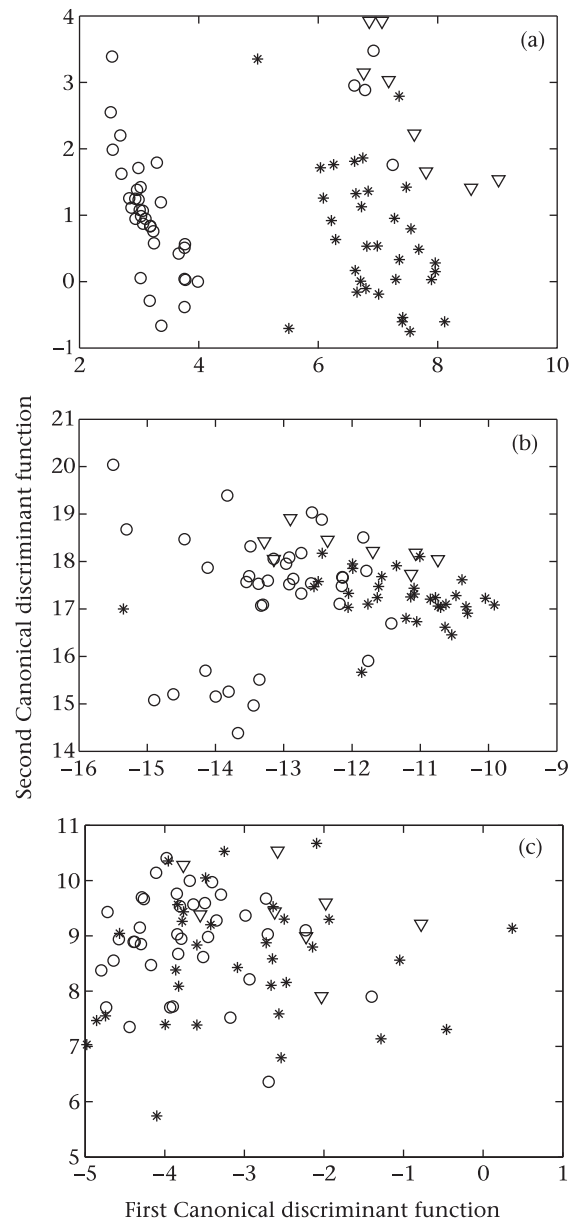


Figure 4. First two canonical discriminant functions for comparison among individuals no. 5560 (○), no. 5561 (*) and no. 5727 (▽) for coda type 5Reg and variable sets (a) Absolute ICLs, (b) Relative ICLs and (c) Amplitudes.

However, there are important caveats pertaining to our results. Our data derive from a single social group, and in part from a subset of individuals in that group, and so cannot tell us whether this kind of individual specificity is a general feature of the 5Reg coda type. Also, we cannot evaluate whether the ability to discriminate individuals from ICLs extends to all group members. Data from other social units are critically needed to examine how 5Reg codas vary between individuals more generally. Furthermore, recordings were generally made in a restricted range of behavioural contexts.

The differences in individual specificity between coda types that we have found suggest different functionality of those types. In the case of the social unit studied here, coda type 5Reg, consisting of five regularly spaced clicks, seems to carry more information with respect to individual identity than the other types, and appears to be stereotyped to this end. In contrast, individual specificity in the

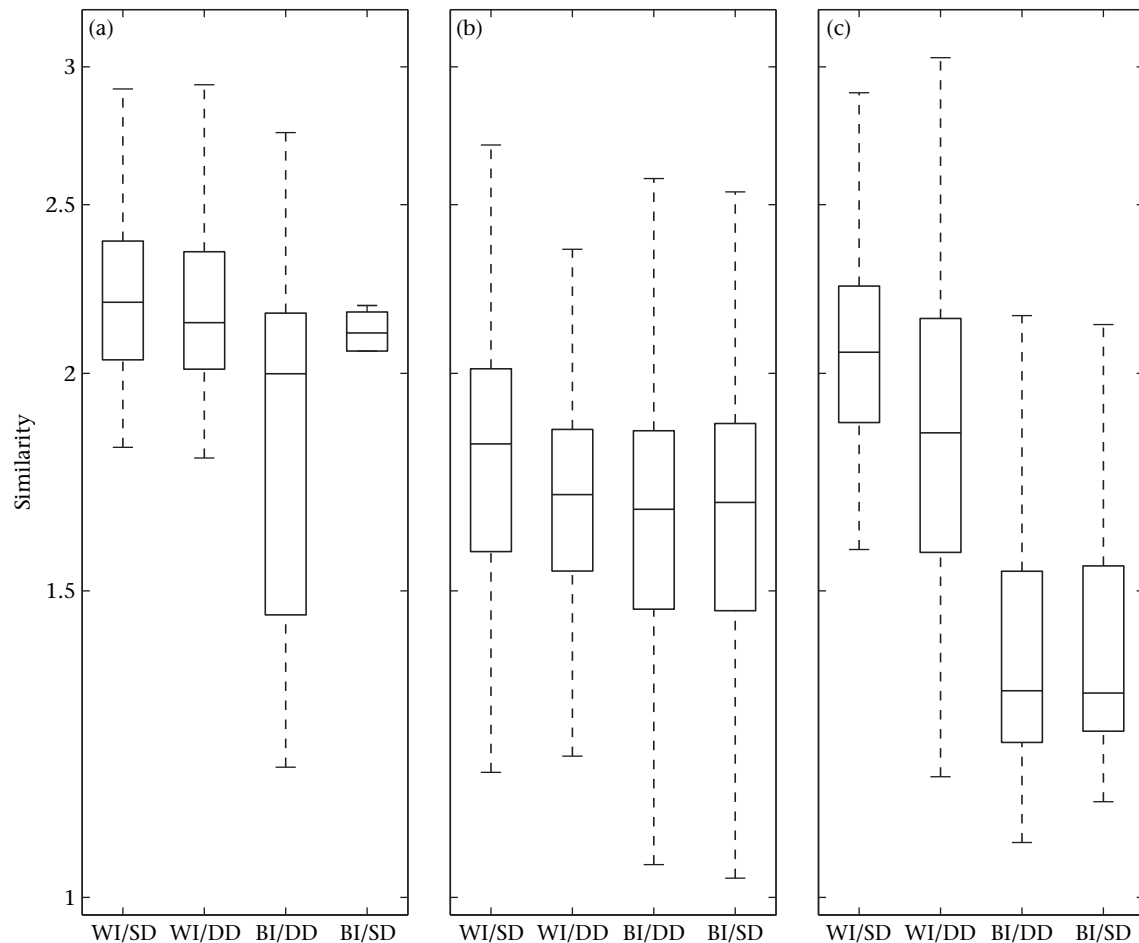


Figure 5. Box plots of coda similarity values within individuals on the same day (WI/SD); within individuals on different days (WI/DD); between individuals on different days (BI/DD); and between individuals on the same day (BI/SD) for coda types (a) 1+3, (b) 1+1+3 and (c) 5Reg. The box plots show the median (horizontal line), the upper and lower quartiles (the box) and the range (dotted vertical lines).

other coda types is not as strong and, although still statistically detectable, is more consistent with a stochastic idiosyncrasy. The 5Reg coda type is noteworthy because it is ubiquitous across geographical areas in which sperm whale coda repertoires have been studied (Caribbean: Moore et al. 1993; Pacific Ocean: Weilgart & Whitehead 1993, 1997), although it seems less common in the Mediterranean (absent in Pavan et al. 2000 but reported in Frantzis & Alexiadou 2008). It has also been highlighted as being more likely to occur at the start of coda exchanges than other coda types (Weilgart & Whitehead 1993). Our results suggest that 5Reg codas could be used for encoding individual identity, which would also help explain both its ubiquity and its frequent occurrence at the start of exchanges. These results appear *prima facie* contradictory to those of Moore et al. (1993) who found that codas assumed to have been produced by the same individuals were no more similar to each other than to those assumed to be produced by different individuals. Their analysis, however, would not have been able to distinguish the individual-specific variation we report here, for two reasons. First, their analysis did not stratify by coda type, instead combining all types in a single test, and second, their data were collected from at least 15 different social units, meaning that variation in coda production between social units (which is large; Rendell & Whitehead 2003b) would probably have made the relatively subtle variations we report undetectable.

The fact that the individual variation within coda types can be used to distinguish individuals suggests hierarchical mapping may be

a feature of coda variation. Hierarchical mapping is typical in bird-song, where a mean pattern of vocalizations indicates species identity, and deviations from this indicate individual identity (Becker 1982; Falls 1982). Hierarchical mapping has also been found to code for individual and sex in electrical fish (*Pollimyrus isidori*: Crawford 1992; *Brienomyrus* sp.: Friedman & Hopkins 1996). In codas, individual information seems to be encoded in variations in timing around the coda type's stereotyped rhythm. For the social unit studied here, the 5Reg type, defined by five (fairly) equally spaced clicks in relative timing, provides the mean pattern from which idiosyncratic variations in absolute time depart. Such a coding scheme would be constrained by the amount of within-type variability possible that would still allow the coda to be recognized as a 5Reg type.

Our results suggest that the common practice of standardizing intervals in these kinds of analyses (e.g. Moore et al. 1993; Weilgart & Whitehead 1997; Rendell & Whitehead 2003a) might actually be discarding important information. The present study also shows the need for further work on the contextual use of codas. If indeed coda types have different functionalities, these could be reflected in contextual use. Male sperm whales in the Mediterranean have been shown to use different coda types depending on behavioural context (Frantzis & Alexiadou 2008); however, no individual-specific variation has been reported. Longer-term study of the individual repertoires of units of sperm whales such as the 'Group of Seven' would increase the sample

size, allowing for a greater control of context and motivational variables and more precise conclusions on the presence of individual information and its variation between coda types. Also, further research targeting the individual repertoires of other social units from the same and other geographical areas with different coda type repertoires will allow the verification of the hypothesis of differential functionality of coda types in transmitting individuality.

In conclusion, we have demonstrated that it is possible to discriminate between individual sperm whales in the social unit we studied based on Absolute ICI variability for one coda type only. This supports the initial hypothesis that individual-specific variation within coda types could allow distinction between group members. However, the discrimination performance was not the same for all coda types, which suggests differential functionality between coda types. The present study also suggests that codas are hierarchically coded signals in which individuality information is encoded in finer variations in timing around the stereotyped rhythm of a given coda type. We suggest that studies of animal communication will benefit from considering the possibility of subtle information coding at different hierarchical levels that may otherwise be overlooked.

Acknowledgments

We thank Phil Hammond, Peter Slater and Peter McGregor and three anonymous referees for providing useful comments on the manuscript. Research in Dominica was carried out under a scientific research permit (SCR 013/05-02) provided by the Ministry of Agriculture and Environment of Dominica. We thank all of Balaena's crew members who participated in data collection and Andrew Amour and the staff at the Anchorage Hotel and Dive Center for their support while in Dominica. We are grateful to the International Fund for Animal Welfare and in particular Doug Gillespie for allowing us to use the Rainbow Click software. R.A. was supported by the Fundação para a Ciência e Tecnologia (FCT) through studentship SFRH/BD/16427/2004. T.S. and S.G. were supported by NSERC graduate scholarships and T.S. by an Izaak Walton Killam Memorial Scholarship. L.R. was supported by a United Kingdom Natural Environmental Research Council (NERC) postdoctoral fellowship (NER/I/S/2002/00632). Work was supported by grants to H.W. from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Whale and Dolphin Conservation Society.

References

- Antunes, R. 2009. Variation in sperm whale (*Physeter macrocephalus*) coda vocalizations and social structure in the North Atlantic Ocean. Ph.D. thesis, University of St Andrews.
- Arnham, T. 1987. Individual identification of sperm whales. *Reports of the International Whaling Commission*, **37**, 201–204.
- Bachman, G. C. 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Animal Behaviour*, **39**, 960–966.
- Backus, R. & Schevill, W. E. 1966. *Physeter* clicks. In: *Whales, Dolphins, and Porpoises* (Ed. by K. S. Norris), pp. 510–528. Berkeley, California: University of California Press.
- Becker, P. H. 1982. The coding of species-specific characteristics in bird sounds. In: *Acoustic Communication in Birds. Vol. 1* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 213–252. New York: Academic Press.
- Beecher, M. D. 1982. Signature systems and kin recognition. *American Zoologist*, **22**, 477–490.
- Beecher, M. D. 1989. Signalling systems for individual recognition: an information theory approach. *Animal Behaviour*, **38**, 248–252.
- Bergman, T. J., Beehner, J. C., Cheney, D. L. & Seyfarth, R. M. 2003. Hierarchical classification by rank and kinship in baboons. *Science*, **302**, 1234–1236.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Carter, G. G., Skowronski, M. D., Faure, P. A. & Fenton, B. 2008. Antiphonal calling allows individual discrimination in white-winged vampire bats. *Animal Behaviour*, **76**, 1343–1355.
- Cheney, D. L. & Seyfarth, R. M. 1988. Assessment of meaning and the detection of unreliable signals by vervet monkeys. *Animal Behaviour*, **36**, 477–486.
- Christal, J., Whitehead, H. & Lettevall, E. 1998. Sperm whale social units: variation and change. *Canadian Journal of Zoology*, **76**, 1431–1440.
- Coakes, A. & Whitehead, H. 2004. Social structure and mating system of sperm whales off northern Chile. *Canadian Journal of Zoology*, **82**, 1360–1369.
- Crawford, J. 1992. Individual and sex specificity in the electric organ discharges of breeding mormyrid fish (*Pollimyrus isidori*). *Journal of Experimental Biology*, **164**, 79–102.
- Duda, R. O., Hart, P. E. & Stork, D. G. 2001. *Pattern Classification*. Chichester: J. Wiley.
- Falls, J. B. 1982. Individual recognition by sounds in birds. In: *Acoustic Communication in Birds. Vol. 2* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 237–278. New York: Academic Press.
- Frantzis, A. & Alexiadou, P. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. *Canadian Journal of Zoology*, **86**, 62–75.
- Friedman, M. & Hopkins, C. D. 1996. Tracking individual mormyrid electric fish in the field using electric organ discharge waveforms. *Animal Behaviour*, **51**, 391–407.
- Gero, S., Hengelhaupt, D. & Whitehead, H. 2008. Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behavioral Ecology and Sociobiology*, **63**, 143–151.
- Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the RSV *Aurora Australis*. *Reports of the International Whaling Commission*, **47**, 897–907.
- Gordon, J. C. D. 1991. Evaluation of a method for determining the length of sperm whales (*Physeter macrocephalus*) from their vocalizations. *Journal of Zoology*, **224**, 301–314.
- Jaquet, N. & Gendron, D. 2009. The social organization of sperm whales in the Gulf of California and comparisons with other populations. *Journal of the Marine Biological Association of the United Kingdom*, **89**, 975–983.
- Jaquet, N., Dawson, S. & Douglas, L. 2001. Vocal behavior of male sperm whales: why do they click? *Journal of the Acoustical Society of America*, **109**, 2254–2259.
- Kieft, M. 1999. Discriminant Analysis Toolbox version 0.3. <http://www.mathworks.com/matlabcentral/fileexchange/loadFile.do?objectId=189> Downloaded 12 April 2008.
- Kildaw, S. D. 1995. The effect of group size manipulations on the foraging behavior of black-tailed prairie dogs. *Behavioral Ecology*, **6**, 353–358.
- Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I. & Møhl, B. 2002a. Sperm whale sound production studied with ultrasonic time/depth-recording tags. *Journal of Experimental Biology*, **205**, 1899–1906.
- Madsen, P. T., Wahlberg, M. & Møhl, B. 2002b. Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behavioral Ecology and Sociobiology*, **53**, 31–41.
- Mesnick, S. L. 2001. Genetic relatedness in sperm whales: evidence and cultural implications. *Behavioral and Brain Sciences*, **24**, 346–347.
- Miller, P. J. O., Johnson, M. P., Tyack, P. & Terray, E. A. 2004a. Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *Journal of Experimental Biology*, **207**, 1953–1967.
- Miller, P. J. O., Johnson, M. P. & Tyack, P. 2004b. Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proceedings of the Royal Society B*, **271**, 2239–2247.
- Moore, K. E., Watkins, W. A. & Tyack, P. L. 1993. Pattern similarity in shared codas from sperm whales (*Physeter catodon*). *Marine Mammal Science*, **9**, 1–9.
- Møhl, B., Wahlberg, M., Madsen, P. T., Anders Heerfordt, A. & Lund, A. 2003. The monopolised nature of sperm whale clicks. *Journal of the Acoustical Society of America*, **114**, 1143–1154.
- Pavan, G., Hayward, T. J., Borsani, J. F. & Priano, M. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985–1996. *Journal of the Acoustical Society of America*, **107**, 3487–3495.
- Rendell, L. & Whitehead, H. 2003a. Comparing repertoires of sperm whales, a multiple methods approach. *Bioacoustics*, **14**, 61–81.
- Rendell, L. & Whitehead, H. 2003b. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society B*, **270**, 225–232.
- Rendell, L. & Whitehead, H. 2005. Spatial and temporal variation in sperm whale coda vocalizations: stable usage and local dialects. *Animal Behaviour*, **70**, 191–198.
- Rhineland, M. Q. & Dawson, S. M. 2004. Measuring sperm whales from their clicks: stability of interpulse intervals and validation that they indicate whale length. *Journal of the Acoustical Society of America*, **115**, 1826–1831.
- Rice, D. W. 1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758. In: *Handbook of Marine Mammals. Vol. 4* (Ed. by S. H. Ridgway & R. Harrison), pp. 177–233. London: Academic Press.
- Ripley, B. D. 1996. *Pattern Recognition and Neural Networks*. Cambridge: Cambridge University Press.
- Robinson, S. R. 1981. Alarm communication in Belding's ground squirrels. *Zeitschrift für Tierpsychologie*, **56**, 150–168.
- Schulz, T., Whitehead, H., Gero, S. & Rendell, L. 2008. Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. *Animal Behaviour*, **76**, 1977–1988.

- Schulz, T., Whitehead, H., Gero, S. & Rendell, L. 2011. Individual vocal production in a sperm whale (*Physeter macrocephalus*) social unit. *Marine Mammal Science*, **27**, 149–166.
- Smouse, P. E., Long, J. C. & Sokal, R. R. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology*, **35**, 627–632.
- Tibbetts, E. A. & Dale, J. 2007. Individual recognition: it is good to be different. *Trends in Ecology & Evolution*, **22**, 529–537.
- Watkins, W. A. & Schevill, W. E. 1977. Sperm whale codas. *Journal of the Acoustical Society of America*, **62**, 1486–1490.
- Watkins, W. A., Moore, K. E. & Tyack, P. 1985. Sperm whale acoustic behaviors in the Southeast Caribbean. *Cetology*, **49**, 1–15.
- Weilgart, L. & Whitehead, H. 1993. Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Canadian Journal of Zoology*, **71**, 744–752.
- Weilgart, L. & Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire on South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, **40**, 227–285.
- Whitehead, H. 2003. *Sperm Whales: Social Evolution in the Ocean*. Chicago: University of Chicago Press.
- Whitehead, H. & Gordon, J. 1986. Methods of obtaining data for assessing and modelling sperm whale populations which do not depend on catches. *Reports of the International Whaling Commission (Special Issue)*, **8**, 149–166.
- Whitehead, H. & Weilgart, L. 2000. The sperm whale, social females and roving males. In: *Cetacean Societies: Field Studies of Whales and Dolphins* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 154–172. Chicago: University of Chicago Press.
- Wilson, E. O. 1975. *Sociobiology*. Cambridge, Massachusetts: The Belknap Press of Harvard University Press.
- Ydenberg, R. C. & Dill, L. M. 1986. The economics of fleeing from predators. *Advances in the Study of Behavior*, **16**, 229–249.