

Social familiarity influences whistle acoustic structure in adult female bottlenose dolphins (*Tursiops truncatus*)

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Abstract

The composition and organization of the bottlenose dolphin whistle repertoire are poorly understood and currently under debate. Because recent studies report a sharing of whistle contours between individuals both within the across different social groups and a predominant but not individualized whistle type, we need to examine differences in acoustic structure other than whistle contour to determine whether such acoustic structure can discriminate individuals, social groups, or populations of dolphins as found in other species. In this study, acoustic parameters of the predominant whistle type, shared by all individuals across captive social groups in a recent study, were statistically compared across a subset of the population composed of adult female bottlenose dolphins. The whistles from individuals from similar and different captive social groups and capture locations were compared to determine which parameters, if any, differentiated the whistles by individual, social group, or capture location. Results suggest that social group membership, and particularly specific social companions, have a strong influence on whistle acoustic structure in captive adult female dolphins and that the variables responsible for this difference coincide well with results from field studies on their wild counterparts. These data suggest, on a preliminary basis, that social familiarity influences whistle acoustic structure and may be one mechanism behind 'regional' dialects in dolphins.

Key words: animal communication, acoustics, vocal learning, dialects, dolphins

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Introduction

Quantifying the acoustic structure and variability of vocalizations is important for elucidating the acoustic basis of individual, kin, and social group recognition in different species. A number of past studies have indicated that animal vocalizations contain individual distinctiveness or population differences within specific call types. Several mammalian and avian species as varied as non-human primates (Smith *et al.*, 1982; Macedonia, 1986; Goedecking & Newman, 1987; Maeda & Masataka, 1987; Chapman & Weary, 1990; Hohmann & Vogl, 1991; Butynski *et al.*, 1992; Hauser, 1991, 1992; Jones *et al.*, 1993; Hammerschmidt & Todt, 1995), wolves (Tooze *et al.*, 1990), raccoons (Sieber, 1986), bats (Gelfand & McCracken, 1986; Balcombe, 1990; Balcombe & McCracken, 1992; Scherrer & Wilkinson, 1993), birds (Weary *et al.*, 1990; Bauer & Nagl, 1992) and penguins (Robisson *et al.*, 1993) show systematic acoustic differences in their calls across individuals or populations. Many species exhibit acoustic distinctiveness in various temporal and frequency parameters that likely provides the acoustic basis for individual or kin recognition (Symmes *et al.* (1979); Chapman & Weary (1990); Tooze *et al.* (1990); Bauer & Nagl, 1992; Robisson *et al.*, 1993; Biben & Bernhards, 1994; Rendall *et al.*, 1996; Robertson, 1996). In addition, dialects have been well documented in many avian species (Mundinger, 1982; Adret, 1986; Sorjonen, 1987) and some cetacean species (pilot whales: Taruski, 1976, 1979; killer whales: Ford & Fisher, 1983; Ford, 1991). Recent studies suggest that some primate species exhibit population and social group differences in call structure (chimpanzees: Mitani *et al.*, 1992; Mitani & Brandt, 1994; marmosets: Elowson & Snowdon, 1994) indicating a possible function for social recognition and/or cohesion.

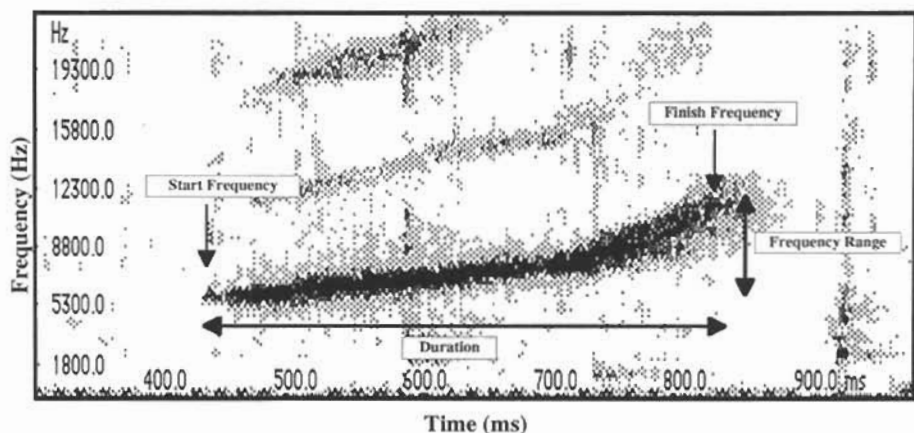


Figure 1. Representative spectrogram of a whistle type 2 whistle indicating four of the 38 acoustic variables analyzed.

The composition and organization of whistle repertoires in bottlenose dolphins (*Tursiops truncatus*) are poorly understood and currently under debate. One model, the 'signature whistle hypothesis', proposes that an individualized whistle contour (relative changes in frequency over time) accounts for 70–95% of a dolphin's whistle repertoire (Caldwell *et al.*, 1990 for review), and has been used to explain much of the acoustic variability observed between individuals. Another model, the 'whistle repertoire model', proposes that dolphins possess a larger and more complex whistle repertoire, share whistle types both within and across social groups, and produce a predominant but not individualized whistle type (Dreher & Evans, 1964; Burdin *et al.*, 1975; Kaznadzei *et al.*, 1976; McCowan & Reiss, 1995a; Ding *et al.*, 1995; Moore & Ridgway, 1995; see McCowan & Reiss, 1997 for a review). In one study, no evidence for a signature whistle, as defined by the signature whistle hypothesis, was found in adults or infants (McCowan & Reiss, 1995a, 1995b); (McCowan & Reiss, 1997). Indeed, the most predominant whistle type for all individuals across social groups was the same whistle type, termed whistle type 2 (McCowan & Reiss, 1995a, 1995b). Past studies have focused on individual (Caldwell *et al.*, 1990 for review), or group differences (Ding *et al.*, 1995) in whistle contour, but because recent studies are now reporting a sharing of whistle contours between individuals both within and across different social groups, we need to examine differences in acoustic structure other than whistle contour, to determine which acoustic features, if any, can discriminate individuals, social groups, or populations of dolphins.

To address this issue, acoustic parameters of the most predominant whistle type, Whistle type 2 (see

Fig. 1), shared by all individuals across captive social groups in a recent study (McCowan & Reiss, 1995a), were compared for a subset of the population comprised of adult female dolphins from similar and different captive social groups and capture locations to determine which acoustic parameters, if any, differentiated the whistles of adult bottlenose dolphins by individual, social group, or capture location. Furthermore, we examined whether captive social group membership or capture location provided a better predictor of whistle acoustic structure in captive bottlenose dolphins.

Methods

Subjects and whistle samples

Five adult females bottlenose dolphins from Marine World Africa USA in Vallejo, California were the subjects of this study. Two pairs of two adult females were from both the same captive social group and capture location. One adult female was from the social group of two of these adult females and the capture location of the other two adult females (see Table 1). This combination of individuals from similar and different social groups and capture locations allowed us to test whether whistles grouped by capture social group membership or capture location. Recordings were made as a part of a larger study of infant whistle development in captive bottlenose dolphins (McCowan & Reiss, 1995a, 1995b). Only whistles positively identified to individuals (total $N=304$) were used in these analyses (see Table 1). The detailed procedure for housing and recording individuals and determining positively identified whistles can be found in McCowan & Reiss (1995a, 1995b).

Table 1. Description of captive social group membership, wild capture location, recording time, and whistle sample for the 5 study subjects

Individual	Social group	Capture location (CL)	Date acquired	No. hours recorded	No. whistles analyzed
Circe	1	Compano Bay, Texas*	6/7/78	55	48
Terry	1	Compano Bay, Texas	1/5/80	55	17
Chelsea	2	Gulfport, Mississippi*	8/23/83	164	89
Sadie	2	Gulfport, Mississippi	8/23/83	58	82
Stormy	2	Compano Bay, Texas	6/7/78	70	68

*Both Compano Bay, Texas and Gulfport, Mississippi sites are located along the coast of the Gulf of Mexico, approximately 1000 miles part.

Whistle acoustic variables

The methods used to quantitatively categorize adult whistle contours have been presented and described in detail in previous publications (McCowan, 1995; McCowan & Reiss, 1995a, 1995b). Whistles categorized as whistle type 2 (total N=304; see Table 1) from the five subjects were used in these analyses to compare individual, social group, and capture location differences in 38 acoustic variables. Acoustic variables were measured or derived from the fundamental frequency of each whistle contour. Table 2 lists the 38 acoustic variables and their definitions used in these analyses (also see Fig. 1). Two of these acoustic variables representing overall spectral shape, the 'jitter' factor (JF) and the frequency variability index (FVI), were adopted from Mitani & Brandt's (1994) analysis of 'pant-hoots' in chimpanzees.

The equations used to calculate COFM (1), JF (2) and FVI (3) are provided below. The coefficient of frequency modulation represents a summary measure of the amount and magnitude of frequency change across each whistle (McCowan & Reiss, 1995b). The 'jitter' factor represents the amount of frequency change across each whistle. The frequency variability index represents the magnitude of frequency change in each whistle.

$$(1) \quad COFM = \frac{\sum_{i=1}^{19} |Y_{i+1} - Y_i|}{10000},$$

where Y_i = the frequency at the i th frequency point.

$$(2) \quad JF = \left(\frac{1}{n-1} \right) \sum_{i=1}^{19} \frac{|Y_i - (Y_{i+1})|}{(\text{average frequency})} \times 100,$$

where Y_i = frequency of the i th value and $n=20$.

$$(3) \quad FVI = (\text{Variance in average frequency}) / (\text{average frequency})^2 \times 1000$$

Statistical analyses

Principal component analysis in BMDP Statistical Software (Dixon *et al.*, 1990) was first conducted to (1) isolate independent and uncorrelated acoustic variables from the original set of 38 acoustic variables and (2) meet the assumption of independence for discriminant analysis and ANOVA. All variables were tested for normality using Shapiro and Wilk's test in BMDP Statistical Software prior to statistical analysis. Because most of our variables required transformation and many remained non-normal after attempting various transformations, we used the factor scores from principal component analysis in all subsequent statistical tests.

Stepwise discriminant analysis in BMDP Statistical Software was conducted on the factor scores from principal component analysis. The data set consisting of 304 whistles, their factor scores and codes for individual identity, captive social group membership, and capture location was subjected to several discriminant analyses by individual, social group, and capture location. In addition, forced discriminant analyses, where all variables were entered into the discriminant function, were conducted for comparison to each stepwise discriminant test. In all analyses, forced functions were less accurate in discriminating groups than the stepwise function (determined by 'jackknife' percent correct classification). Thus all analyses that are presented below represent the original stepwise discriminant analyses. One-way or Nested ANOVA (including Levene's statistic for unequal variances and Brown-Forsythe equality of means statistic) and Bonferroni pairwise comparisons in BMDP Statistical Software were also conducted to determine if individuals, social groups, or capture locations differed significantly in specific and/or sets of spectral and temporal features. Significance was evaluated at a level of $P < 0.05$.

Table 2. List of acoustic variables and their definitions

Acoustic parameter	Description
Coefficient of frequency modulation- McCowan & Reiss (1995b)	Calculated variable that represents the amount and magnitude of frequency modulation across a whistle, computed by summing the absolute values of the difference between sequential frequencies divided by 10 000
Jitter Factor Mitani & Brandt (1994)	Calculated variable that represents a weighted measure of the amount of frequency modulation, by calculating the sum of the absolute value of the difference between two sequential frequencies divided by the mean frequency. The sum result is then divided by the total number of points measured minus 1 and the final value is obtained by multiplying it by 100
Frequency variability index Mitani & Brandt (1994)	Calculated variable that represents the magnitude of frequency modulation across a whistle, computed by dividing the variance in frequency by the square of the average frequency of a whistle and then multiplying the value by 10
Start frequency	Frequency at start of whistle, measured in hertz
Finish frequency	Frequency at end of whistle, measured in hertz
Minimum frequency	Lowest frequency attained by whistle, measured in hertz
Peak frequency	Highest frequency attained by whistle, measured in hertz
Mean frequency	Calculated as average frequency across whistle
Median frequency	Calculated as median frequency across whistle
Frequency range	Calculated as peak frequency minus minimum frequency
Peak frequency-Mean frequency	Calculated as peak frequency minus mean frequency
Peak frequency/Mean frequency	Calculated as peak frequency divided by mean frequency
Mean frequency-Minimum frequency	Calculated as mean frequency minus minimum frequency
Mean frequency/Minimum frequency	Calculated as mean frequency divided by minimum frequency
Variance in frequency	Calculated as the variance in frequency across whistle
Standard deviation in frequency	Calculated as the standard deviation in frequency across whistle
Minimum frequency location	Location of minimum frequency in whistle, given as percentage of duration
Peak frequency location	Location of peak frequency in whistle, given as percentage of duration
Duration	Temporal distance of whistle, measured in msec
Initial slope	Calculated as (Frequency 2-Start Frequency)/(Time 2-Start Time)
Slope 2	Calculated as (Frequency 3-Frequency 2)/(Time 3-Time 2)
Slope 3	Calculated as (Frequency 4-Frequency 3)/(Time 4-Time 3)
Final slope	Calculated as (Frequency 20-Frequency 19)/(Time 20-Time 19)

Results

Components of acoustic variability

Principal component analysis on whistle type 2 whistles of five bottlenose dolphins generated 38 statistically independent components. Eigenvalues of the first 10 components met Kaiser's criterion of 1.00 (Table 3). These 10 components accounted for 81% of the variation in the original data set. Table 3 lists the factor loadings for each of these 10 components. Factor 1 represents measures of spectral shape, as well as frequency range, maximum frequency, and finish frequency of whistle type 2 whistles. The three calculated variables representing subtle variations in spectral shape loaded highly with this factor. Factor 2 represents the mean, median, start, and minimum frequencies of whistles. Factors 3 through 10 each represent highly correlated measures of slope at various points in the whistle (see Table 2 for definitions). In addition, minimum frequency location loaded most highly with Factor

4; maximum frequency location loaded most highly with Factor 7; and duration loaded most highly with Factor 8.

Inter-individual variability

Discriminant analysis of whistles by individual was conducted to determine if an individual's whistles contained potential 'signature information' in acoustic structure. Four separate analyses were conducted to evaluate where differences between individuals might be found: discriminant analysis was conducted by (1) individual excluding information on captive social group membership and capture location, (2) individuals from same captive social group, (3) individuals from same capture location, and (4) individuals from same captive social group and capture location.

Discriminant analysis by individual revealed that individuals could be differentiated by whistle acoustic structure (see Table 4a). Yet, percent correct classification of whistles to individuals was

Table 3. Principal component loadings of acoustic variables, their eigenvalues, and their percent variance explained for whistle type 2 whistles from 5 captive adult female bottlenose dolphins

Acoustic variable	Principal component									
	1	2	3	4	5	6	7	8	9	10
Frequency range	0.98	0.02	-0.02	0.07	-0.01	0.02	0.13	-0.02	0.03	0.05
Standard deviation in frequency	0.98	0.03	0.02	0.03	0.08	0.06	-0.04	-0.07	0.00	0.00
Variance in frequency	0.94	0.05	0.01	-0.04	0.08	0.07	-0.13	-0.11	0.00	-0.02
Frequency variability index	0.92	-0.26	0.01	-0.02	0.04	0.03	-0.04	-0.11	0.04	-0.02
Max frequency-Mean frequency	0.92	-0.04	-0.04	-0.07	-0.07	-0.05	0.29	-0.11	0.09	0.04
Coefficient of frequency modulation	0.89	-0.01	0.21	-0.09	-0.03	0.03	0.04	0.01	0.11	-0.05
Jitter factor	0.84	-0.34	0.11	-0.10	-0.09	-0.05	0.25	-0.02	0.14	-0.01
Maximum frequency	0.83	0.50	-0.02	0.01	-0.02	0.00	0.19	-0.09	0.05	0.05
Max frequency/Mean frequency	0.83	-0.32	-0.04	-0.08	-0.10	-0.09	0.34	-0.09	0.12	0.04
Mean frequency-Min frequency	0.81	0.15	0.02	0.33	0.12	0.17	-0.25	0.19	-0.12	0.06
Finish frequency	0.79	0.51	-0.03	0.02	-0.04	-0.01	0.27	-0.09	0.05	0.08
Mean frequency/Min frequency	0.76	-0.20	0.01	0.33	0.11	0.17	-0.27	0.23	-0.12	0.03
Mean frequency	0.24	0.95	0.01	0.12	0.06	0.08	-0.05	0.00	-0.03	0.04
Median frequency	0.02	0.95	0.03	0.18	0.05	0.13	-0.07	0.09	-0.09	0.05
Minimum frequency	-0.30	0.92	0.00	-0.11	-0.02	-0.03	0.12	-0.13	0.05	0.00
Start frequency	-0.24	0.88	0.01	-0.29	-0.03	-0.07	0.06	-0.13	0.05	-0.17
Slope 10	0.01	0.03	-0.95	0.00	0.02	0.06	-0.01	-0.03	-0.02	0.00
Slope 6	0.00	0.07	-0.84	0.19	0.04	0.17	0.07	-0.05	-0.05	-0.16
Slope 9	0.01	0.00	0.81	0.11	0.06	-0.29	-0.04	-0.14	-0.03	0.08
Slope 11	0.06	0.01	0.80	-0.06	0.29	0.24	0.10	-0.03	0.25	-0.03
Slope 8	0.02	0.08	0.75	-0.01	0.01	0.26	0.04	0.06	0.01	-0.11
Slope 13	0.20	0.05	0.68	-0.05	-0.07	0.05	-0.10	-0.23	-0.49	-0.10
Min frequency location	0.02	0.10	0.13	-0.76	-0.07	-0.18	-0.18	-0.10	0.12	-0.24
Slope 3	0.05	0.08	-0.16	0.66	-0.01	0.01	0.05	-0.10	-0.11	-0.44
Slope 2	-0.01	0.04	0.13	0.65	-0.06	-0.35	-0.21	0.00	0.25	0.19
Slope 12	0.06	0.03	-0.13	-0.05	0.87	0.01	-0.02	-0.10	0.06	0.00
Slope 5	-0.06	0.03	0.38	0.13	0.82	-0.14	0.06	-0.06	-0.02	0.03
Slope 4	0.04	0.08	0.05	0.17	-0.20	0.77	-0.05	-0.03	-0.05	0.17
Slope 17	0.10	-0.07	-0.20	-0.23	-0.11	0.60	0.19	-0.11	0.37	-0.17
Slope 7	0.08	0.09	0.02	-0.09	0.28	0.53	0.06	-0.16	0.00	0.31
Max frequency location	0.19	0.02	-0.09	0.09	0.12	0.09	0.72	0.07	-0.20	0.01
Final slope	0.08	0.08	0.14	-0.03	-0.10	0.03	0.64	-0.08	0.44	-0.03
Duration	0.20	-0.14	-0.11	-0.13	-0.07	-0.24	-0.06	0.75	-0.22	0.05
Slope 15	0.44	0.02	-0.05	-0.16	0.09	0.07	-0.08	-0.55	-0.05	0.07
Slope 16	0.41	-0.02	0.09	-0.07	0.31	-0.07	-0.04	-0.51	0.02	-0.09
Slope 14	0.24	-0.03	0.08	-0.03	0.08	0.05	-0.05	-0.14	0.77	-0.02
Initial slope	0.01	-0.03	0.02	0.13	0.04	0.19	-0.05	0.05	-0.04	0.79
Slope 18	0.23	0.03	-0.05	-0.03	-0.15	-0.07	0.35	-0.41	0.01	0.46
Eigen value	10.28	4.53	4.31	2.66	2.04	1.87	.58	1.29	1.19	1.13
% variance explained	27	12	11	7	5	5	4	3	3	3

significantly different from random classification ($20\%; \chi^2, df=1$) for only three of the five individuals (Table 4a). Variables that accounted for the difference between individuals were Factors 2, 1, 8, and 9

and Fig. 2A shows that individuals within social groups were more similar to each other than to individuals outside of their social group for the two most important factors in this discriminant

Table 4. Discriminant analysis of whistle type 2 whistles by (A) individual, (B) individual from same captive social group, (C) individual from same wild capture location, and (D) individual from the same social group and capture location for 5 captive adult female bottlenose dolphins

(A) Individual

Variables entered: Factor 2 (F entered=17.672); Factor 1 (F entered=11.161); Factor 8 (F entered=9.226); Factor 9 (F entered=4.385)

Individual	N	% CC	Classification matrix ^a				
			Circe	Terry	Chelsea	Sadie	Stormy
Circe	48	79.2*	38	1	5	3	1
Terry	17	5.9	8	1	5	3	0
Chelsea	89	38.2*	9	19	34	8	19
Sadie	82	28	3	13	13	23	30
Stormy	68	32.4*	8	9	9	20	22
Total	304	38.8	66	43	66	57	72

(B) Individuals from same captive social group

Social group 1

Variables entered: Factor 2 (F entered=8.008)

Individual	N	% CC	Classification matrix	
			Circe	Terry
Circe	48	75*	36	12
Terry	17	58.8	7	10
Total	65	70.8	43	22

Social group 2

Variables entered: Factor 8 (F entered=15.925); Factor 10 (F entered=5.429)

Individual	N	% CC	Classification matrix		
			Chelsea	Sadie	Stormy
Chelsea	89	67.4*	60	16	13
Sadie	82	37.8	19	31	32
Stormy	68	33.8	25	20	23
Total	239	47.7	104	67	68

function. ANOVA supported the results of discriminant analysis showing that significant differences were not consistent between all individuals. In an analysis of all ten factors, only Factors 1, 2, and 8 showed significant differences and only between certain individuals. For Factor 1, Circe significantly differed from Chelsea, Sadie and Stormy, and Terry significantly differed from Chelsea and Stormy ($F=10.05$; $df=4, 168$). For Factor 2, only Circe was found to significantly differ from all other individuals ($F=13.39$; $df=4, 71$). For Factor 8, only Chelsea was found to significantly differ from Sadie and Stormy ($F=9.04$; $df=4$).

Both discriminant and ANOVA analyses could not discriminate effectively between individuals when neither social group membership nor capture location were taken into account. We therefore conducted discriminant analysis by individual within each social group and then subsequently by individual within each capture location to evaluate whether individuals from the same social group or capture location could be more clearly differentiated when considered separately.

Discriminant analysis by individual within social group (SG) 1 revealed that Circe was differentiated from Terry and the correct percent classification of

Table 4 (Continued)
(C)

Compano Bay
Variables entered: Factor 2 (F entered=20.551); Factor 1 (F entered=10.764); Factor 8 (F entered=5.635)

Classification matrix

Individual	N	% CC	Circe	Terry	Stormy
Circe	48	77.1*	37	6	5
Terry	17	17.6	7	3	7
Stormy	68	66.2*	6	17	45
Total		63.9	50	26	57

Gulfport, Mississippi
Variables entered: Factor 8 (F entered=25.202); Factor 4 (F entered=11.551); Factor 9 (F entered=5.292)

Classification matrix

Individual	N	% CC	Chelsea	Sadie
Chelsea	89	73*	65	24
Sadie	82	69.5*	26	56
Total		70.8	91	80

(D) Individuals from same social group (SG) and capture location (CL)

Variables entered: Factor 2 (F entered=21.023); Factor 1 (F entered=12.373); Factor 8 (F entered=8.746); Factor 9 (F entered=5.692); Factor 4 (F entered=4.604)

Classification matrix

Individual	SG	CL	N	% CC	Circe	Terry	Chelsea	Sadie
Circe	1	Compano Bay	48	77.1*	37	2	6	3
Terry	1	Compano Bay	17	5.9	8	1	5	3
Chelsea	2	Gulfport, Mississippi	89	47.2*	11	20	42	16
Sadie	2	Gulfport, Mississippi	82	52.4*	1	20	18	43
Stormy	3	Compano Bay	68	0	7	11	16	34
Total			304	52.1	64	54	87	99

[^]All classification matrices are Jackknife classification.

*X² significance at $P < 0.05$.

Italic indicates that category was not used in the classification function.

whistles for Circe were significantly different from random assignment (50%, χ^2 , $df=1$; Table 4b). Terry, however, was not effectively differentiated from Circe and the percent correct classification of her whistles in comparison to random assignment was not significant. The variable that differentiated Circe from Terry in social group 1 was Factor 2 (see Table 4b; Fig. 1B). Discriminant analysis by individual within social group 2 yielded a similar result. Only Chelsea was found to significantly differ in the percent correct classification of her whistles from

random assignment (33.3%; χ^2 , $df=1$; Table 4b). Variables that distinguished Chelsea from Sadie and Stormy in social group 2 were Factors 8 and 10 (Table 4b; Fig. 2C). Interestingly, Sadie's and Stormy's values were almost identical for these factors (Fig. 2C).

Discriminant analysis by individual from the same capture location of Compano Bay, Texas, revealed that both Circe (SG1) and Stormy (SG2) were differentiated effectively from each other and from Terry (SG1). Both Circe and Stormy showed

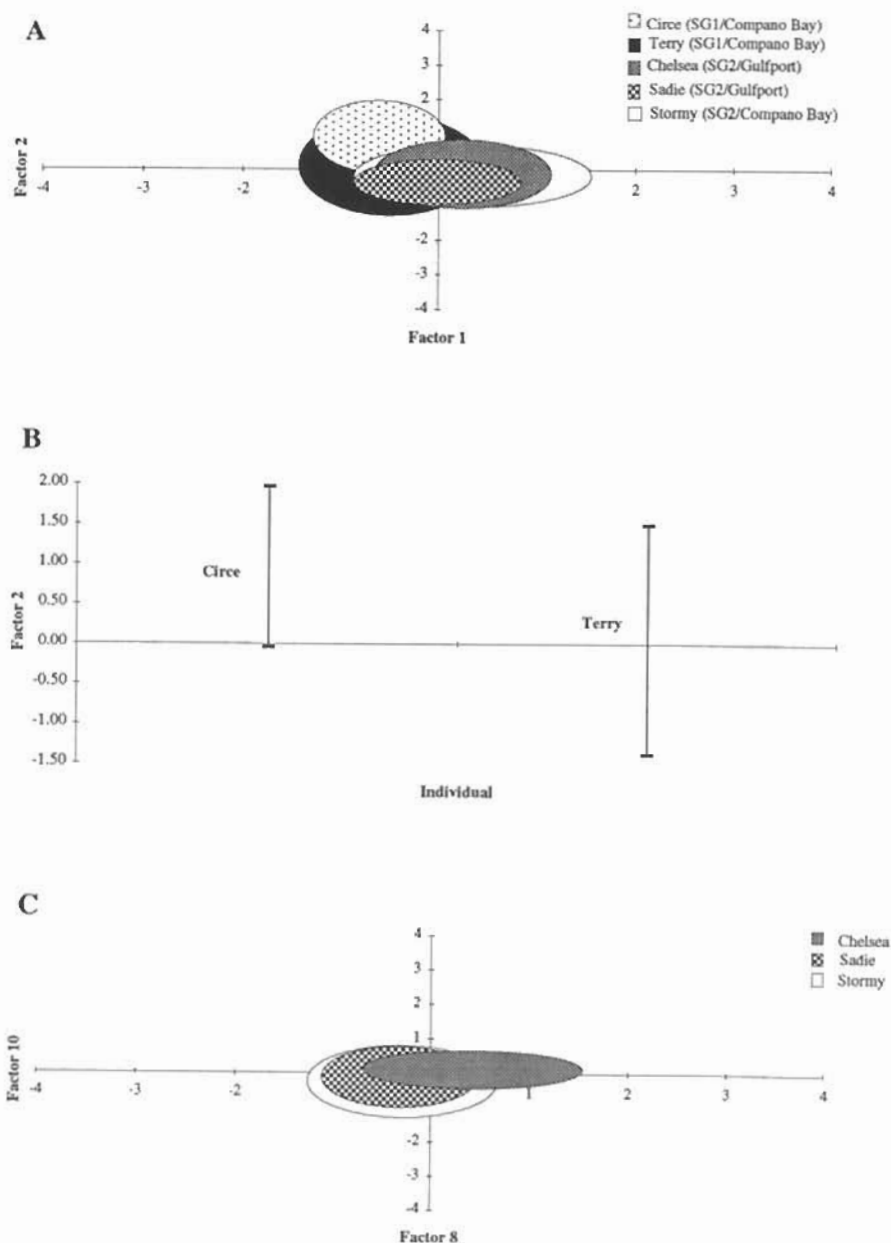


Figure 2. Mean and first standard deviation for the two most important factors from discriminant analysis for (A) individuals discluding information on captive social group membership or capture location, (B) individuals from social group 1, and (C) individuals from social group 2.

correct percent correct classification of their whistles based on capture location that were significantly different from random assignment (33.3%; χ^2 , $df=1$; see Table 4c). Variables that discriminated individuals from Compano Bay were Factors 2, 1 and 8 (see Table 4c; Fig. 2A). As in the

previous analysis by social group, Terry's whistles showed no significant difference from random assignment. It is interesting to note that while Circe and Stormy were acquired contemporaneously, Terry was acquired several years earlier from Compano Bay (see Table 1), although it is also

possible that this lack of significance was due to Terry's low sample size. Discriminant analysis by individual of dolphins from the Gulfport, Mississippi revealed that Chelsea (SG2) and Sadie (SG2) were discriminated effectively from each other. Both individuals showed percent correct classification of their whistles that significantly differed from random assignment (50%; χ^2 , $df=1$; see Table 4c). Variables that accounted for the difference were Factors 8 and 9. Similar to Circe and Stormy, Chelsea and Sadie were acquired contemporaneously in Gulfport, Mississippi.

Finally, we conducted discriminant analysis by individual from only four of the dolphins, 2 pairs each of whom came from both the same social group and capture location (Circe and Terry; Chelsea and Sadie) and excluded the one dolphin (Stormy) who came from one capture location and the other social group. Stormy's whistles were excluded from the discriminant function and classified on the basis of the subset discriminant function. We removed Stormy's whistles from the discriminant function to determine if her whistles would be classified with the whistles from individuals within her social group or with those from individuals of the same capture location.

Analysis revealed that three of the four individuals used in the classification function were effectively discriminated by Factors 2, 8, 9, and 4 (see Table 4d). Circe, Chelsea, and Sadie showed percent correct classification of their whistles that were significantly greater than random assignment (25%; χ^2 , $df=3$; see Table 4d). As in previous analysis, Terry did not show significance in the percent correct classification of her whistles (see above). Interestingly, Stormy's whistles were significantly more often assigned to individuals (and specifically to Sadie) within her social group than to individuals from her capture location (random assignment: 50%; χ^2 , $df=1$).

Social group and capture location differences

The series of discriminant analysis and ANOVA tests by individual revealed that individual differences were more clearly found between individuals from the same capture location than between individuals from the same captive social group. We therefore conducted discriminant analysis by social group and capture location to determine if whistles could be discriminated based upon these population measures of acoustic variability.

Discriminant analysis by social group revealed that whistle acoustic structure is well discriminated by social group. Both social group 1 and social group 2 significantly differed in the percent correct classification of their whistles from random assignment (50%; χ^2 , $df=1$; see Table 5a). Variables responsible for this difference were Factors 2, 1, 7

and 9 (see Fig. 3A). Discriminant analysis by capture location yielded different results. While Gulfport, Mississippi whistles appeared to classify correctly significantly more often than random (50%; χ^2 , $df=1$; see Table 5b), Compano Bay whistles classified more randomly between the two capture sites (see Fig. 3B). Only one variable accounted for the difference, Factor 2 (see Table 5b). However, one individual from social group 2 was also an individual acquired from Compano Bay. Thus results from discriminant analysis by capture location could be confounded by this individual. Therefore, a final discriminant analysis on the same social group and capture location was conducted in which the individual (Stormy) from one capture location (Compano Bay) and the other social group (social group 2) was removed from the discriminant function. We conducted this analysis so that we could (1) determine if classification would improve for capture location and (2) determine if the removed whistles would classify with those from the same social group or from the same capture location.

The percent correct classification of whistles was significantly different from random assignment for both Social group 1/Compano Bay and Social group 2/Gulfport, Mississippi (50%; χ^2 , $df=1$, see Table 5c). Variables entered were Factor 2, 1, 7, and 9 (see Fig. 3C). This result is not surprising because discriminant analysis by social group showed such clear discrimination (see Table 5a). Most revealing, however, was the classification of whistles from Stormy, the individual from social group 2/Compano Bay. Stormy's whistles were significantly more often classified with those from her social group than with those from her capture location (see Fig. 3C).

Discussion

Inter-Individual variability

Only one of our analyses on individual variability indicated that dolphins have 'individual signature information' in their whistle type 2 whistles. Individuals from the same capture location who were acquired contemporaneously differed in their whistle acoustic structure. All other analyses on whistle individuality were inconclusive. Only one or a subset of individuals could be reliably distinguished from the others in these analyses. In addition, when discrimination was found, individuals were discriminated by different factors (e.g., Factor 2 for Circe, Factors 8 and 10 for Chelsea). Thus, discriminated individuals were not differentiated by the same acoustic parameter(s) but different ones.

The lack of conclusive evidence could be due to several reasons. First, our list of acoustic variables was extensive ($N=38$) but not exhaustive. Signature

Table 5. Discriminant analysis of whistle type 2 whistles by (A) social group, (B) capture location, and (C) same social group and capture location for 5 captive adult female bottlenose dolphins

(A) Social group

Variables entered: Factor 2 (F entered=51.382); Factor 1 (F entered=36.333); Factor 9 (F entered =7.576); Factor 7 (F entered=7.329); Factor 10 (F entered=4.677)

Social group	Individuals	N	% CC	Classification matrix [^]	
				1	2
1	Circe, Terry	65	73.8*	48	17
2	Chelsea, Sadie, Stormy	239	84.5*	37	202
Total		304	82.2	85	219

(B) Capture location

Variables entered: Factor 2 (F entered=13.792)

Acq. Location	Individuals	N	% CC	Classification matrix	
				1	2
Compano Bay	Circe, Terry, Stormy	133	49.6	66	67
Gulfport, Mississippi	Chelsea, Sadie	171	67.3*	56	115
Total		304	59.5	122	182

(C) Same social group and capture location

Variables entered: Factor 2 (F entered=44.035); Factor 1 (F entered=31.19); Factor 7 (F entered=10.993); Factor 9 (F entered=8.469)

Social group/ Cap. location	Individuals	N	% CC	Classification matrix	
				1	2
SG1/Compano Bay	Circe, Terry	65	75.4*	49	16
SG2.Gulfport, Mississippi	Chelsea, Sadie	171	82.5*	30	141
<i>SG2. Compano Bay</i>	Stormy	68	0	11	57
Total		304	80.5	90	214

[^]All classification matrices are Jackknife classification.*X² significance at $P < 0.05$.

Italic indicates that category was not used in the classification function.

information may be contained in other acoustic variables such as in the harmonics of whistles. We were unable to measure the whistle harmonics due to technological limitations and thus further study is necessary to determine its importance. This possibility is encouraging though as Bain (1986) has reported signature information in the harmonics of orca vocalizations, and not in the fundamental frequency. Second, bottlenose dolphins are well known for their ability to imitate both artificial and conspecific signals (Richards *et al.*, 1984; Tyack, 1986; Reiss & McCowan, 1993). They have been

reported to match precisely the frequency and duration parameters of artificial signals both spontaneously (Reiss & McCowan, 1993) and on command (Richards *et al.*, 1984). Thus, dolphins may not significantly differ on an individual basis in whistle acoustic structure because they acoustically match certain whistle parameters of specific social companions (see '*Social Group and Capture Location Differences*' below). Nevertheless, because whistle communication is used by dolphins both remotely and within close social interactions (Smolker *et al.*, 1992; McCowan & Reiss, 1997 for

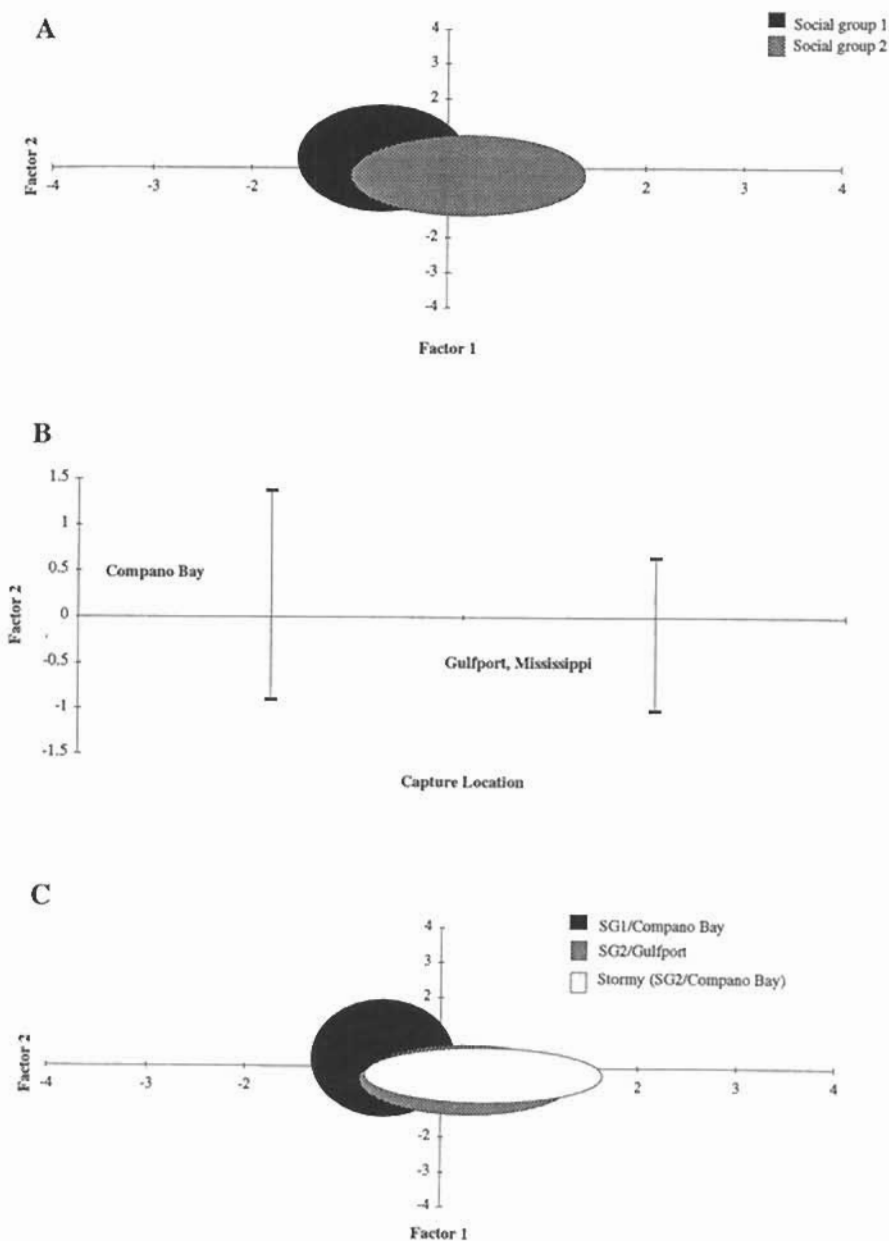


Figure 3. Mean and first standard deviation for the two most important factors from discriminant analysis for (A) social groups, (B) capture locations, and (C) same social groups/capture locations (Stormy's whistles were not included in the discriminant function but rather were classified based upon the subset discriminant function; see text for explanation).

review), it is very likely that they have some acoustic mechanism for individual identity. Again, we need to look more closely at other acoustic variables, such as those within the harmonics of whistles, for an answer.

Social group and capture location differences

Whistle acoustic structure, using our acoustic parameters, was well differentiated by captive social group membership but not capture location. This result is not surprising given the differences we

found in our first discriminant analysis by individual. Individuals within social groups were more acoustically similar to each other than to individuals outside of their social groups even if outsiders were from the same capture location (Fig. 1A). In fact, the key to how acoustic variability functions in dolphin whistles may be found in our final discriminant analysis in which we tested how the whistles of one individual from one capture location and the other social group were classified. In this case, Stormy's whistles were classified with those of her social group (and specifically one individual, Sadie) and not her capture location, suggesting that she produced whistles more similar to those of her social companions than to those of individuals from her capture location in the wild (see Fig. 2C). Thus, whistles of individuals may acoustically differ from individuals from the same capture location because they were subsequently housed in a different captive social environment.

Our results on captive dolphins coincide well with those reported for some wild populations (Ding *et al.*, 1995; Bazua, 1997). Spectral and statistical analysis of three populations among the Texas coast indicated that differences in whistle structure were greater in groups separated by larger distances than in adjacent areas. Notably, the frequency variables of whistles from the three different populations showed low intra-group and high inter-group variability (Ding *et al.*, 1995). Our results on captive dolphins support these findings. Another common result was that inter-group differences were found in the beginning frequency (a parameter that loaded highly with Factor 2; see Table 3) and finish frequency (a parameter that loaded highly with Factor 1; see Table 3) of whistles. Notably, the study populations of this field work inhabit the same general area from which our captive dolphins were acquired (the Gulf of Mexico, see Table 1). These data taken together suggest, on a preliminary basis, that social familiarity influences whistle acoustic structure and may be one mechanism behind 'regional' dialects in dolphins.

Conclusion

These preliminary data suggest that social familiarity influences whistle acoustic structure in adult female bottlenose dolphins. Dolphins may modify the acoustic properties of their whistles to match close social associates and perhaps this apparent acoustic matching functions in social interaction, recognition or cohesion as reported for other animals, such as in male chimpanzees (Mitani *et al.*, 1992; Mitani & Brandt, 1994) and some avian species (Baptista & Morton, 1981; Baptista & Petronovich, 1984). Indeed, this functional explanation coincides well with the

behavioural ecology of bottlenose dolphin populations. Longitudinal field studies have indicated a fission-fusion type social structure, showing social complexity rivaling that found in chimpanzee societies (Würsig, 1978; Connor & Smolker, 1985; Wells *et al.*, 1987; Connor *et al.*, 1992). The fact that bottlenose dolphins are a highly social species coupled with their adaptations for existence in an aquatic habitat suggests that acoustic flexibility plays an important role in the formation and maintenance of social relationships and during social interactions. Alternatively, these social group differences may be related to differences in the acoustic frequency and/or duration of ambient noise in captive environments (Dalheim *et al.*, 1984; Sinnott *et al.*, 1975; Masataka, 1986). For example, Dalheim *et al.* (1984) measured various aspects of ambient noise and bottlenose dolphin vocalizations in a Baja California lagoon and reported that dolphin vocalizations generally occurred at frequencies above or below other biological noise. Extensive observational data on several captive individuals from both similar and different capture locations, including the type and amount of social interactions between individuals, is necessary to conclusively test these alternative hypotheses. Such data on social interactions between individuals sharing or differing in acoustic parameters will help us more definitively determine if dolphins modify their whistle acoustic structure to match close social companions. In addition, perception and categorization experiments are needed to determine if the acoustic differences found between individuals and social groups have perceptual and social significance to the dolphins.

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