Behav Ecol Sociobiol (1981) 9:241–246

Behavioral Ecology and Sociobiology

Species-Specific Differences in Pure Tonal Whistle Vocalizations of Five Western North Atlantic Dolphin Species

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Received January 20, 1981 / Accepted August 25, 1981

Summary. Pure tonal 'whistle' vocalizations from five species of dolphins found in the western North Atlantic had consistent, species-specific characteristics. The degree of differences between species, as based on the results of multivariate discriminant analysis (Fig. 2), correlated with the taxonomic and zoogeographic relations of the five dolphin species. Congeneric species had more similar vocalizations than species of different genera. Differences between sympatric species were greater than differences between allopatric species. Of the six whistle parameters measured, maximum frequency had the lowest coefficient of variation for all five species, and duration and number of inflection points had the highest coefficients of variation for all five species.

Introduction

Species-specific communicative signals are widespread throughout the animal kingdom (Wilson 1975). The ability of an individual to recognize its conspecifics is necessary in a myriad of circumstances. One would expect to find species-specific communication systems in the many species of dolphins, family Delphinidae, with their often complex social structures and rich vocal repertoires. Surprisingly, although many researchers have suggested and assumed the existence of such species-specific systems (Watkins 1980), they have never been quantitatively demonstrated. Therefore, I have tested whether or not species-specific characteristics were present in one type of vocalization, the pure tonal 'whistle', emitted by five species of dolphins which inhabit the western North Atlantic.

The modern study of cetacean acoustics began in 1949 with the first underwater electronic recording of beluga whale (*Delphinapterus leucas*) vocalizations (Schevill and Lawrence 1949). Since that time, researchers have demonstrated that most dolphin species have two primary types of vocalizations: 1) brief, broad band sounds which are characterized by the simultaneous emission of energy at many frequencies; and 2) pure tonal sounds commonly called 'whistles' (Caldwell and Caldwell 1977; Busnel and Fish 1980). The broad band sounds are used for echolocation and, apparently, also communication. Laboratory studies have documented the remarkable precision and acuity of dolphin echolocation systems (Evans 1973; Au et al 1974, 1978). It is commonly assumed that the pure tonal sounds are used only for communication; however, very little is known about how the whistles are used for communication, for example, whether meaning varies with context, if any syntactical arrangements are important, or if species-specificity is present. Early studies attempted to ascertain the contextual meaning of specific dolphin vocalizations (Lilly and Miller 1961a, 1961b; Lang and Smith 1965), but the conclusions were highly speculative and are as yet unconfirmed. It has been suggested that individual signature whistles may be present in several species of dolphins (Caldwell and Caldwell 1965, 1968; Taruski 1976; Steiner 1980).

I have examined the question of species-specific characteristics of dolphin whistle vocalizations using multivariate discriminant analysis. Whistle vocalizations were recorded and quantiatively characterized by six different variables. Linear discriminant analysis was used to estimate variability within each species' whistle vocalization repertoire and then to identify differences among the five species.

Materials and Methods

I studied the whistle vocalizations of five species of dolphins: *Tursiops truncatus* (Montagu), bottlenosed dolphin; *Globicephala melaena* (Traill), long-finned pilot whale; *Lagenorhynchus acutus*

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0340-5443/81/0009/0241/$01.20

Table 1. Date, location and number of whistles measured from all recordings used in multivariate analysis

Recordings	Date	Location	No. of whistles
Tursiops truncatus			
Recording 1	Aug 1964	40°00 N 70°00 W	36
Recording 2	Dec 1966	34°04 N 76°04 W	383
Recording 3	Aug 1968	39°59 N 69°16 W	238
Recording 4	Oct 1968	33°33 N 77°45 W	50
Recording 5	Feb 1969	18°00 N 67°56 N	130
Recording 6	Jan 1971	17°52 N 67°20 W	21
			858
Lagenorhynchus acutus			
Recording 1	Aug 1967	43°45 N 59°49 W	1119
Recording 2	Apr 1977	42°05 N 70°12 W	572
			1691
Globicephala melaena			
Recording 1	Aug 1969	43°55 N 59°00 W	649
Recording 2	Aug 1971	44°45 N 59°53 W	880
			1529
Stenella plagiodon			
Recording 1	Dec 1966	30°15 N 80°30 W	375
Recording 2	Dec 1967	35°16 N 76°30 W	192
			567
Stenella longirostris			
Recording 1	Feb 1973	18°40 N 64°41 W	2088

(Gray), Atlantic white-sided dolphin; *Stenella plagiodon* (Cope), Atlantic spotted dolphin; *Stenella longirostris* (Gray), spinner dolphin.

Recordings were made of dolphin herds engaged in a variety of conditions and behavioral circumstances at sea: apparent feeding, riding a ship's bow wave, milling, and swimming rapidly as part of a school. The recordings were made from 1964–1977[1] in locations ranging from Nova Scotia to the Caribbean (Table 1). Various combinations of recording equipment were used: AN/BQR-3a directional hydrophone, California Mfg. Corp. R-130 hydrophone, Clevite CH-1 hydrophone, AN/UNQ-7a sonar recorder, Precision Instrument PI-200 recorder, Uher 4400 Report Stereo recorder, and Ithaco 267A amplifier. Overall frequency response curves varied, but all systems were sufficient to over 20 kHz (±5 dB).

For analysis, I selected recordings with suitable signal/noise levels and positive animal identifications. At least two separate recordings were analyzed for four of the five species, but only one recording of *S. longirostris* was suitable. Original recordings were re-recorded at 1/16 original speed, and then played into a Saicor 53B spectrum analyzer and Honeywell 1856 Visicorder to produce continuous spectral energy versus time graphs (spectrograms). The analyzer was set to a scanning range of 0–2 kHz for *T. truncatus, L. acutus, S. plagiodon,* and *S. longirostris.* A range of 0–1 kHz was used for *G. melaena.* Thus, the true frequency bands analyzed were 0–32 kHz, and 0–16 kHz, respectively.

I inspected the spectrograms while simultaneously listening to the original recordings, marking with pencil all clear, unambiguous whistles not excessively obscured by overlapping whistles. All whistles were measured using a Tektronix 4006 minicomputer and graphics board. Six variables were measured and quantified from each whistle: 1) beginning frequency, 2) final frequency, 3) maximum frequency, 4) minimum frequency, 5) duration in seconds, and 6) number of inflection points (defined as a change in slope of the spectrographic contour from negative to positive or vice versa).

I used computer programs for multivariate discriminant analysis to compare overall whistle structures within and between species. The programs provided a stepwise analysis procedure, a jackknife percent correct classification table, a Mahalanobis D^2 statistic, a canonical correlation matrix, and a MANOVA approximate F-test for comparing mean vectors (Dixon 1975; Barr et al. 1976). The percent correct classification score is a measure of the difference between the groups being measured as indicated by how many individual whistles are distinctive enough to be correctly assigned, by the discriminant functions, to their proper recording or species. The absolute value of the percent correct classification in a given analysis must be considered relative to the percent correct classification expected by chance alone, for example, 50% for two species, 33% for three species, 20% for five species. The Mahalanobis D^2 statistic is a sample size-independent measure of the differences between overall whistle forms as determined by the distance between mean vectors in multivariate space; the greater the D^2 statistic, the greater the differences. Canonical correlation is another multivariate measure of the differences in overall whistle forms. When the first two canonical variates of each species are plotted on an X–Y coordinate system, the relative distances between values on the graph are proportional to the relative differences between species.

The F-statistic is a MANOVA test of the equality of mean vectors. However, since the absolute F-value is sample size-dependent, it's use as a comparative measure of the results from different tests is precluded. Therefore, when I examined whether the relative difference between Species A and B was greater or less than the relative difference between Species C and D, I used sample size-independent measures: percent correct classification, Mahalanobis D^2, and canonical correlation.

The analyses included a series of within-species comparisons, and a series of between-species comparisons. Within-species whistle variability was estimated for each respective species by comparing recordings of the same species made at different locations and time. There was only one recording of *S. longirostris* and, thus, it was not included in this procedure. To estimate differences between species, I combined all recordings within each of the five species into five respective species' samples and ran all possible pairwise species comparisons, a total of 10 analyses. Finally, I ran a simultaneous five-way comparison of all species using the entire sample of whistles, and randomly selected smaller sample sizes.

Results

The characteristics of the generalized whistle forms for the five dolphin species are listed in Table 2. The mean values of the six parameters varied widely among the five species, but in all species, maximum frequency had the lowest coefficient of variation, and duration and number of inflection points had the

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[1] All recordings from 1964–1973 were made by Mr. Paul Perkins, Dr. Charles Fish, and Dr. Howard Winn. All recordings are stored at the Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island, USA

Table 2. Means, standard deviations, and coefficients of variation for six variables from whistle vocalizations of five dolphin species

	Maximum frequency (Hz)	Minimum frequency (Hz)	Beginning frequency (Hz)	Final frequency (Hz)	Duration (s)	No. of inflection points
T. truncatus						
Mean	16,235	7,332	11,264	10,225	1.30	2.86
Stan. Dev.	2,688	1,658	3,986	3,646	0.63	2.45
C.V. (%)	17	23	35	36	48	86
S. longirostris						
Mean	14,317	8,764	9,759	13,168	0.43	0.55
Stan. Dev.	2,763	2,616	3,506	3,100	0.33	0.97
C.V. (%)	19	30	36	24	76	174
S. plagiodon						
Mean	13,302	6,532	8,779	11,862	0.46	1.33
Stan. Dev.	3,441	2,158	3,393	3,906	0.30	1.49
C.V. (%)	26	33	39	33	65	111
L. acutus						
Mean	12,140	8,210	11,506	9,625	0.50	0.92
Stan. Dev.	2,723	2,318	2,900	2,729	0.27	1.05
C.V. (%)	22	28	24	28	54	113
G. melaena						
Mean	4,716	2,821	3,695	3,498	0.71	1.01
Stan. Dev.	1,937	1,188	1,683	1,883	0.69	1.29
C.V. (%)	41	42	46	54	97	127

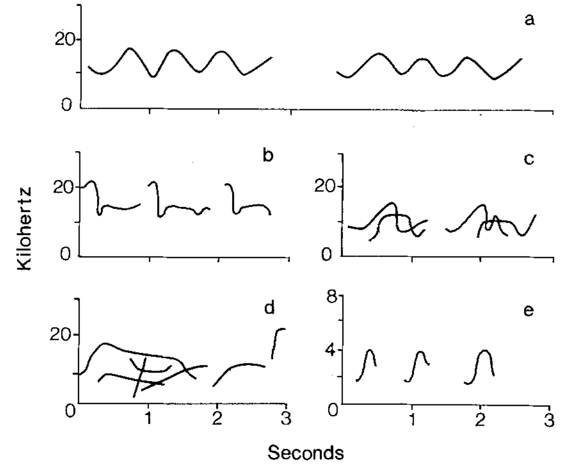

Fig. 1 a–e. Representative whistles from each of five dolphin species. **a** *Tursiops truncatus*; **b** *Lagenorhynchus acutus*; **c** *Stenella plagiodon*; **d** *Stenella longirostris*; **e** *Globicephala melaena*

Table 3. Results of discriminant analyses comparing recordings of whistles within four of five dolphin species

Species comparisons[a]	D^2	Correct classification (%)
T. truncatus		
Recording 2 vs 3	1.2	57[b]
Recording 2 vs 5	1.8	
Recording 3 vs 5	2.0	
S. plagiodon		
Recording 1 vs 2	0.5	61
G. melaena		
Recording 1 vs 2	0.7	68[c]
L. acutus		
Recording 1 vs 2	2.7	80[c]

[a] All MANOVA approximate F-tests were significant at $\alpha=0.001$ level

[b] Three-way comparison of Recordings 2 vs 3 vs 5. Chance percent correct classification level of 33%

[c] Chance correct classification level of 50%

greatest coefficients of variation. Examples of whistles from all five species are shown Fig. 1.

Estimates of the variability of whistles within each species are listed in Table 3. Percent correct classification scores comparing recordings from within *S. plagiodon* (61%), *G. melaena* (68%), and *T. truncatus* (57%) were only slightly greater than scores expected by chance classification. Recordings of *L. acutus* had a percent correct classification score of 80%; this was higher than the other species. The Mahalanobis

Table 4. Results of discriminant analyses of all paired species comparisons and five-way comparison of whistles of five species of dophins

Species comparisons[a]	D^2	Correct classification (%)
G. melaena vs *T. truncatus*	20.0	99[b]
G. melaena vs *S. longirostris*	16.2	98
G. melaena vs. *S. plagiodon*	12.4	95
G. melaena vs. *L. acutus*	10.3	96
T. truncatus vs *L. acutus*	7.6	91
T. truncatus vs *S. longirostris*	7.1	89
T. truncatus vs *S. plagiodon*	6.2	86
L. acutus vs *S. plagiodon*	3.1	90
L. acutus vs *S. longirostris*	2.8	80
S. longirostris vs *S. plagiodon*	1.8	78
Simultaneous five-way comparison		
300 whistles from each species		71[c]
500 whistles from each species		71
All whistles included		69

[a] All MANOVA approximate F-tests were significant at $\alpha = 0.001$ level

[b] Chance percent correct classification level of 50%

[c] Chance percent correct classification level of 20%

D^2 statistics were all 2.7 or lower. Again, *L. acutus* had the highest D^2 statistic, indicating the greater variability within its whistle form.

The results of discriminant analyses comparing the different species to one another are shown in Table 4. Comparisons of *G. melaena* with the other four species resulted in D^2 statistics of 10.3–20.0, and percent correct classification scores of 95%–99%. These values for D^2 and percent correct classification were all greater than any within-species values. The whistle form of *T. truncatus* was also very different from the other four species. The D^2 statistics derived from paired species comparisons involving *T. truncatus* ranged from 6.2–20.0, and percent correct classification scores ranged from 86%–99%. Again, these values were all greater than any within-species comparisons.

Analyses comparing *L. acutus, S. longirostris,* and *S. plagiodon* with each other had less dramatic results. The calculated D^2 statistics of 1.8–3.1 were not significantly greater than the highest D^2 statistic derived from within-species comparisons (2.7). The percent correct classification score of *L. acutus* versus *S. plagiodon* was 90%. This was relatively high, but the other two percent correct classification scores involving the three species, 78% and 80%, were the lowest of any paired species comparison. *Stenella longirostris* versus *S. plagiodon* had both the lowest D^2 statistic (1.8) and the lowest percent correct classification score (78%).

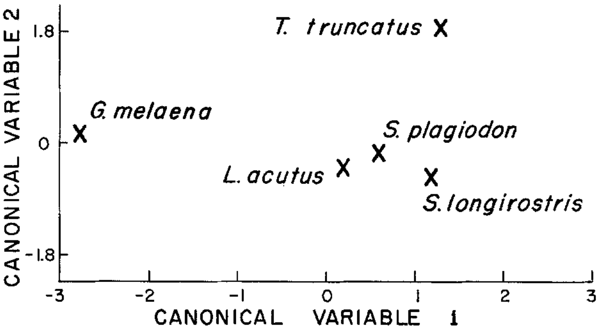

Fig. 2. Plot of the first two canonical variates as computed for whistle forms for each of five species of dolphins. The canonical correlation was computed using six variables measured on each of 6733 whistle vocalizations. X = intersection of first two variates for each species, respectively

Results of final analyses comparing all five species simultaneously are shown in Table 4. The percent correct classification score of 70% was remarkably consistent, even as the total sample size increased almost five-fold (1,500–6,733). This percent correct classification of 70% was very high when compared to a chance classification score of only 20% for a five-way comparison. Canonical correlation confirmed the relative degree of differences between species (Fig. 2). *Tursiops truncatus* and *G. melaena* were widely separated from *S. longirostris, S. plagiodon,* and *L. acutus.*

Thus, it was clear that the discriminant analysis easily discriminated *G. melaena* and *T. truncatus* whistles from whistles of any of the other three species in the study. However, the analysis did not discriminate between whistles of *L. acutus, S. longirostris* and *S. plagiodon* as well as it discriminated the whistles of the first two species.

Discussion

The results of the discriminant analyses have evolutionary and ecological implications. The relative degree of differences in whistle vocalizations among the five species correlated with taxonomic relations of the five species. *Globicephala melaena* is taxonomically more distinct than the other four species. The morphological structure of *G. melaena* is different enough that some reviewers have placed it in its own family, Globicephalidae (Nishiwaki 1972). Likewise, the whistles of *G. melaena* clearly were the most distinctive of the five species studied. Conversely, the two species that are congeners, *S. longirostris* and *S. plagiodon*, had the most similar whistles.

The degree of differences in the whistle vocalizations among the five species closely followed predictions based on classic allopatric/sympatric relations among the species. *Globicephala melaena* and *T. truncatus* are the only two species in this study that have wide enough ranges in the western North Atlantic to be sympatric with all other species included in this study. Both species are found at least as far north as Nova Scotia. *Globicephala melaena* is reported as far south as 36° N latitude where it overlaps with *G. macrorhynchus,* while *T. truncatus* is distributed south to the Caribbean (Katona et al. 1977). Furthermore, *G. melaena* and *T. truncatus* frequently occur in mixed schools in the North Atlantic (CETAP 1979). If dolphin species utilize whistles for species-specific communication, these two species need to have highly characteristic whistles because of the large number of possible sympatric species. The results supported this prediction. Both *G. melaena* and *T. truncatus* were easily distinguished from the other species, and from one another.

In contrast, there is virtually no geographic overlap between *L. acutus* and the two *Stenella* species. *Lagenorhynchus acutus* is primarily a northern species rarely seen south of 40° N latitude on the east coast of N. America, while *S. plagiodon* and *S. longirostris* are primarily southern species. The great majority of sightings of *Stenella* spp. are south of 39° N (Katona et al. 1977). There is presumably no ecological need for great differences in their vocalizations. Again, the results supported this prediction. The differences between *L. acutus* and the two *Stenella* spp., as indicated by the D^2 statistics and the canonical correlations, were substantially less than the differences seen in other paired species comparisons, and only slightly greater than within-species variability.

Stenella longirostris and *S. plagiodon* are both found south of 39° N, although it is not known to what degree they are sympatric. In the caribbean, *S. longirostris* is sympatric with a form of spotted dolphin, *S. frontalis* (Perrin 1975a). There is also a sighting of dolphins tentatively identified as *S. longirostris,* in deep waters offshore from N. Carolina (CETAP 1979), well within the range of *S. plagiodon.* In the Pacific, *S. longirostris* and *S. attenuata* (Pacific spotted dolphin) are found in extensive mixed schools (Perrin 1975b). This has not been observed in the Atlantic. Assuming some degree of sympatry in the Atlantic, one might expect to find greater species-specific differences between *S. longirostris* and *S. plagiodon.* However, my analyses indicated that their vocalizations were more similar to each other than any of the other species studied. Considering that these two species are congeners, and might be expected to have similar ancestral whistle patterns, one may have to look at more detailed whistle structures to find species-specific differences between *S. longirostris* and *S. plagiodon.* It is also possible that species of such close phylogenetic origin have species-specific cues in other types of vocalizations, for example, the wide variety of pulsed sounds emitted by dolphins.

The similar values of the coefficients of variation from all five species suggests that selective pressures have produced divergent species' whistle forms. Maximum frequency had the lowest coefficient of variation in all five species. However, the mean values of the maximum frequencies were significantly different (Steiner 1980). Thus, maximum frequency fits the dual criteria for a species-specific characteristic: low intra-species variability and high inter-species variability. This correlation of low intra-species variability with species-specific acoustic parameters has been previously demonstrated for birds (Hutchinson et al. 1968; Emlen 1972; Wunderle 1979). Whistle duration and number of inflection points were the most variable parameters for all five species, suggesting that these two variables may have been important for individual differentiation. This latter suggestion was emphasized by evidence that individual signature whistles appeared to be present for all five species (Steiner 1980).

These correlations, derived from a study of opportunistic field recordings, all suggest that the differences among the whistles of the five species have biological significance to the animals. However, it must be clearly understood that the final and definitive proof of species-specific communication systems in dolphins is dependent on controlled experiments in which individual dolphins are shown to not only differentiate between the whistles of different species, but to also make proper intra-specific and inter-specific behavioral responses. The results presented here support the importance of acoustic cues in species differentiation in dolphins. The exact communicative functions of the pure tonal whistles are still unknown, and present a challenge for future research.

Acknowledgements. I gratefully thank Dr. Howard Winn for his guidance, financial and logistical support, and encouragement throughout this project. Dr. J. Heltshe and Dr. H.P. Jeffries provided advice on the statistical treatments and manuscript. Field work was supported by the Office of Naval Research, Contract No. N00014-76-C-0226 to H.E. Winn. The author was supported by the Leopold Schepp Foundation of New York City. The minicomputer was provided by the Department of Ocean Engineering, University of Rhode Island; computer time was provided by the Academic Computer Center, University of Rhode Island. The work reported herein was part of a dissertation submitted as partial fulfillment of the requirements for the Ph. D. degree in the Department of Oceanography, University of Rhode Island.

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