

Guyana dolphins (*Sotalia guianensis*) from Costa Rica emit whistles that vary with surface behaviors

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Abstract: Guyana dolphins show remarkable intraspecific whistle variation. This variation has been largely explained in terms of distance among populations; however, other factors such as behavior may also be important. A broadband recording system recorded the whistles of Guyana dolphins under three behavioral states. A discriminant analysis found that during social and travel events, dolphins emit whistles with high delta and minimum frequency, respectively. Whistle duration was also important in discriminating behaviors. This study indicates that behavior is an important factor contributing to whistle variation of Guyana dolphins. Understanding how dolphin whistles vary with behavioral context will advance our understanding of dolphin communication and enable appropriate comparative studies.

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1. Introduction

The whistles of Guyana dolphins (*Sotalia guianensis*) show great whistle variation among populations, with some populations emitting whistles with frequencies up to 23.99 kHz (Azevedo and Van Sluys, 2005) and others up to 48.4 kHz (May-Collado and Wartzok, 2009). This remarkable variation between populations has been largely explained in terms of distance among populations (Azevedo and Van Sluys, 2005; Rossi-Santos and Podos, 2006; May-Collado and Wartzok, 2009). However, there are other factors such as behavior that can also promote significant intra-population variation and thus may significantly contribute to the overall species whistle variation.

Dolphin whistle contour diversity and emission rate have been previously associated with behavioral context (e.g., Jacobs *et al.*, 1993; Jones and Sayigh, 2002; Acevedo-Gutiérrez and Stienessen, 2004; dos Santos *et al.*, 2005; Nowacek, 2005; Quick and Janik, 2008; Hawkins and Gartside, 2010). For example, some bottlenose dolphin populations tend to increase the number of whistles when feeding (Hawkins and Gartside, 2010) while others show a higher whistle emission rate during social events (Quick and Janik, 2008). In some species whistle contour diversity is also associated with behavioral contexts, while in others like the Indo-Pacific bottlenose dolphins certain whistle types are associated to specific behaviors (Hawkins and Gartside, 2010).

Our understanding of how behavior influences whistle emission rate and whistle diversity in dolphins is growing (e.g., Jacobs *et al.*, 1993; Jones and Sayigh, 2002; Acevedo-Gutiérrez and Stienessen (2004); dos Santos *et al.*, 2005; Erber and Simão, 2004; Quick and Janik, 2008; Hawkins, 2010; Hawkins and Gartside, 2010; Henderson *et al.*, 2012; Hernandez *et al.*, 2010; Díaz López, 2011; Panova *et al.*, 2012). However,

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it remains largely unknown how dolphin whistle acoustic structure (frequency and duration) is associated with surface behaviors (e.g., [Pivari and Rosso, 2005](#); [Hawkins and Gartside, 2010](#); [Hernandez et al., 2010](#); [Díaz López, 2011](#)) and how this lack of information may hinder comparisons among populations. In this study, I evaluate the potential association between surface behavioral states and whistle acoustic variables of the Guyana dolphins.

2. Materials and methods

Guyana dolphin sounds were recorded during seven days in July 2004, September and November 2005, and September 2006 off the Gandoca-Manzanillo Wildlife Refuge in the southern Caribbean coast of Costa Rica (see details in [May-Collado and Wartzok, 2009](#)). We recorded dolphin signals using a broadband system consisting of a RESON (Goleta, CA) hydrophone (-203 dB re 1 V/ μ Pa, 1 Hz to 140 kHz) connected to AVISOFT (Berlin, Germany) recorder and Ultra Sound Gate (Berlin, Germany) 116 (sampling rate 400–500 kHz 16 bit) that sent the signals to a laptop. All recording sessions were made with the engine off. Recordings were made continuously and saved into files of two to three minutes at sampling rate ranging from 384 to 500 kHz. To reduce overrepresentation of the most “vocal” dolphins, the maximum number of whistles to be analyzed per group was set to four times the number of individuals present in the group (see [May-Collado and Wartzok, 2008, 2009](#)). A total of 405 high quality whistles (those with a complete clear contour) were manually selected and analyzed using the program Raven 1.1 (Cornell Laboratory of Ornithology, Ithaca, NY) with a fast Fourier transform size of 1024 points, an overlap of 50%, and using a 512–522 sample Hann window. The following standard whistle parameters ([Erber and Simão, 2004](#); [Azevedo and Van Sluys, 2005](#); [Pivari and Rosso, 2005](#); [May-Collado and Wartzok, 2009](#)) were measured: starting frequency, ending frequency, minimum frequency (MinF), maximum frequency (MaxF), frequency at $[1/4]$, $[1/2]$, and $[3/4]$, delta frequency ($\Delta F = \text{MaxF} - \text{MinF}$), peak frequency (measured in the whistle contour where intensity was the highest), duration (s), number of inflection points, and number of harmonics.

Due to poor water visibility, behavioral observations were limited to what the animals were doing near the surface (see [May-Collado, 2010](#)). The predominant surface behavior was noted when the animals were being acoustically recorded using scan-group-sampling, every two to three minutes. However, it is important to note that during a scanning interval some individuals might have been underwater executing different behaviors from those at the surface, biasing the correspondence between behavior and acoustic recordings. All recording sessions included in this study were in the presence of a single small group (2 to 20 individuals). When another group was suspected to be in the vicinity of the recording session (approximately 200 m radius), the recordings were excluded from the analysis. Because recordings were made with the engine noise off, dolphins tended to move away from the boat depending on their behavior, thus distance of the focal group during a recording session varied considerably within and between groups.

The behavioral categories with sample sizes sufficient for statistical analysis were foraging, socializing, and traveling. Foraging was defined as movement in a multi-directional fashion, short and non-synchronized dives, presence of birds, fish scraps on surface, fish near the surface, and animals consuming prey ([Edwards and Schnell, 2001](#); [Acevedo-Gutiérrez et al., 2005](#); [Daura-Jorge et al., 2005](#)). Social events include periods of active interactions with other group members, including body contact such as rubbing, genital contact, touching, tail slapping, leaps, body rolling, tail walking, chasing, and even performing boat riding with the research or other boats ([Edwards and Schnell, 2001](#); [Acevedo-Gutiérrez et al., 2005](#); [May-Collado, 2010](#)). Finally, travel behavior was defined as dolphins swimming either slow or fast while maintaining a defined direction, and diving and resurfacing synchronously ([Edwards and Schnell, 2001](#); [Acevedo-Gutiérrez et al., 2005](#); [Daura-Jorge et al., 2005](#); [May-Collado, 2010](#)).

The statistical software JMP[®] 9 [SAS Institute Inc. (Cary, NC)] was used for statistical analyses. Descriptive statistics were performed to provide mean, standard

deviation, frequency range, and coefficient of variation values for each whistle. The Kruskal–Wallis test was used to test which acoustic variables vary with behavior. Because of the multiple comparisons, I used the Bonferroni procedure to adjust the level of significance owing to type I error to $\alpha = 0.0045$, and for the pairwise comparisons, I used $\alpha = 0.01$. Then, I used a discriminant function analysis to determine which acoustic variables are more likely to predict behavioral states. For this analysis, all acoustic variables were Box-Cox transformed to normalize their distribution (Sokal and Rohlf, 1995). The Box's M indicated the covariance matrices were significantly different (Box's $M = 1146.9.2$, $df = 110$, $p < 0.0001$). Prior probabilities were proportional to whistle occurrence. I used the Wilk's lambda and chi-square tests to evaluate the strength of the discriminant analysis. The Kappa index test was used to assess how well the discriminant function does vs change alone at the statistical significant level of 0.05 (Green and Salkind, 2003). The cross-validated method was used to calculate correct classification scores of whistles (using the leave-one-out option) for the discriminant functions as well as a chi-square test performed to evaluate the accuracy of the classification at the p -value level of $p = 0.05$ (Green and Salkind, 2003).

3. Results

About half of the dolphins' whistle variables varied significantly with behavior. Whistles were significantly shorter ($\chi^2 = 14.5$, $df = 2$, $p = 0.0007$), and minimum frequency ($\chi^2 = 28.9$, $df = 2$, $p < 0.0001$) and start frequency ($\chi^2 = 14.2$, $df = 2$, $p = 0.0008$) were significantly higher when dolphins were traveling (Table 1). Delta frequency ($\chi^2 = 31.0$, $df = 2$, $p < 0.0001$) and number of harmonics ($\chi^2 = 26.6$, $df = 2$, $p < 0.0001$) were significantly higher during social events, and ending frequency was significantly lower during foraging events ($\chi^2 = 14.3$, $df = 2$, $p = 0.0008$; Table 1). Additionally, whistle duration increased with modulation only during foraging and socializing activities ($x = 5.4$, $df = 1$, $p = 0.02$).

There were significant differences among behavioral contexts across all whistle predictors [$\Lambda = 0.764$, $\chi^2(24, N = 405) = 106.8$, $p < 0.01$] even after removing the effects associated with the first discriminant function [$\Lambda = 0.916$, $\chi^2(11, N = 405) = 34.7$, $p < 0.01$]. The first discriminant function had an eigenvalue of 0.20 and a canonical correlation of 0.41, indicating that 17% of the variability of the scores for the first discriminant function is accounted for by differences among the three behaviors. The second discriminant function had an eigenvalue of 0.09 and a canonical correlation of 0.29, indicating that only 8% of the variability of the scores of the second discriminant function was accounted for by behavior. Based on the standardized canonical discriminant function coefficients and the functions at group centroids during social events, whistle delta frequency had the highest mean scores, and for traveling whistle minimum frequency had the highest mean scores. After cross-validation 56.0% (Kappa = 0.33, $p < 0.01$) of the whistles were correctly classified into their behavioral contexts.

4. Discussion

In this study, I found that the Guyana dolphins modify various parameters of their whistle structure depending on their surface behavior. Despite this variation, social and travel behaviors can be predicted primarily based on whistle delta and minimum frequency, respectively. Similar results have been found in bottlenose dolphins where minimum frequency was one of the best predictors of behavioral states (Hernandez *et al.*, 2010). Furthermore, high frequency whistles seem to be an innate ability of Guyana dolphins (e.g., Azevedo and Van Sluys, 2005; May-Collado, 2010; May-Collado and Wartzok, 2009). We know very little of Guyana dolphin social structure and the role that high frequency whistles may have in their society. However, this natural tendency of emitting high frequency whistles (delta, minimum, and start frequencies) suggests that Guyana dolphins have evolved shorter range-communication strategies than other delphinids.

Table 1. Descriptive statistics for all acoustic variables measured for twelve groups of Guyana dolphins from the Wildlife Refuge of Gandoca-Manzanillo, Costa Rica (2004–2006). From top to bottom values indicate mean±standard deviation, range, and coefficient of variation.

	Foraging (n = 166)	Social (n = 148)	Traveling (n = 91)
MinF	11.7 ± 4.8	11.6 ± 5.5	14.0 ± 4.8
	1.4–37.8	3.8–35.7	2.5–26.3
	41.2%	47%	34.3%
MaxF	20.4 ± 5.2	22.1 ± 6.7	21.1 ± 5.2
	6.5–39.7	3.0–48.4	1.1–35.9
	25.5%	30.3%	24.48%
DeltaF	8.4 ± 5.0	10.7 ± 5.4	7.1 ± 4.3
	0.9–24.4	1.2–29.3	1.6–19.5
	59.7%	50.6%	60.2%
StartF	13.3 ± 5.6	13.3 ± 7.0	15.1 ± 5.3
	1.4–36.3	1.1–47.3	2.5–29.3
	42.8%	52.8%	35.2%
EndF	18.2 ± 6.0	20.6 ± 7.0	20.1 ± 5.5
	1.5–39.4	3.0–44.0	7.7–35.8
	33.3%	33.9%	27.2%
PeakF	16.0 ± 5.3	16.0 ± 6.6	16.6 ± 4.3
	1.8–38.4	5.8–39.1	6.6–27.3
	33.3%	41.7%	26.0%
1/4f	15.1 ± 5.1	15.2 ± 6.1	16.8 ± 4.5
	1.1–36.3	7.8–39.1	6.6–30.0
	34.0%	40.2%	28.4%
1/2f	16.6 ± 5.0	16.3 ± 6.0	17.0 ± 4.8
	1.1–37.2	7.3–37.5	7.7–32.2
	29.7%	37.0%	28.8%
3/4f	17.1 ± 5.0	18.1 ± 6.0	17.8 ± 4.8
	5.4–37.8	9.3–39.1	8.6–33.0
	29.3%	33.2%	27.6%
Duration (s)	0.207 ± 0.179	0.234 ± 0.215	0.150 ± 0.146
	0.027–1.05	0.007–1.027	0.02–0.675
	86.7%	92.1%	98.0%
Inflection points	0.42 ± 0.81	0.64 ± 1.41	0.21 ± 0.57
	0–4	0–8	0–4
	194.0%	218.6%	260.9%
Number of harmonics	0.81 ± 1.23	1.30 ± 1.48	0.60 ± 1.40
	0–7	0–7	0–10
	151.0%	114.0%	235.6%

Whistle duration has been previously shown to be an important parameter to discriminate among populations in this dolphin species (e.g., [Azevedo and Van Sluys, 2005](#); [Rossi-Santos and Podos, 2006](#); [May-Collado and Wartzok, 2009](#)) and similar findings have been reported in spinner dolphins ([Bazúa-Durán and Au, 2004](#); [Camargo et al., 2006](#)), Indo-Pacific bottlenose dolphins ([Morisaka et al. 2005a](#)), Atlantic spotted dolphins ([Azevedo et al., 2010](#)), and bottlenose dolphins (e.g., [Wang et al., 1995](#); [May-Collado and Wartzok, 2008](#); [Díaz López, 2011](#)). In this study, whistle duration varied with behavior; traveling groups of Guyana dolphins emitted shorter duration whistles than groups involved in socialization and foraging. [Steiner \(1981\)](#) suggested that duration might be a good indicator of individual differentiation. Additionally, a positive association between whistle modulation and duration has been supported previously

(May-Collado *et al.*, 2007) highlighting the importance of both whistle variables in dolphin communication. Guyana dolphins' whistle duration was positively associated with whistle modulation (measured as the number of inflection points) only during foraging and social activities, behaviors that generally involve direct interactions between group members. Based on these results, I hypothesize that Guyana dolphin short whistles during travel activities might carry specific individual information that enhance group cohesion, e.g., announcing their presence and/or spatial location when moving in a directional fashion, while longer and more modulated whistles in active behaviors such as foraging and social may enhance exchange of additional information such as "emotional" state information of the individuals involved during the interaction.

Dolphins' whistle variation has been largely explained in terms of degree of isolation (e.g., Wang *et al.*, 1995; Azevedo and Van Sluys, 2005; Rossi-Santos and Podos, 2006) and fluctuations in their habitat acoustic structure (e.g., Erbe, 2002; Foote *et al.*, 2004; Morisaka *et al.* 2005b; May-Collado and Wartzok, 2008). More recent studies are showing the significant contribution of behavior in dolphin whistle variation (Hawkins, 2010; Hernandez and Gartside, 2010; Díaz López, 2011). Here, I show evidence that Guyana dolphins emit whistles with characteristics that vary depending on behaviors and are consistent with close range-communication. Relatively small sample size, lack of information on group composition, and the difficulty of matching acoustic recordings with behavior may have reduced the explanatory power of the analysis presented (Díaz López, 2011; Gridley *et al.*, 2012). Nevertheless, even when the power of the classification is not as high as in other studies (e.g., Hernandez *et al.*, 2010), this study provides preliminary evidence that Guyana dolphins can modify their whistle acoustic structure depending on the behavioral state. Whistles play an important role in dolphin societies. Consequently, identifying those factors that significantly contribute to whistle variation is fundamental in understanding how these animals communicate and adapt to their habitat.

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