RESEARCH PAPER

Changes in Whistle Structure of Two Dolphin Species During Interspecific Associations

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Abstract

Dolphin communicative signals show great plasticity. Dolphins modify signal structure to cope with their environment, in response to stress, and in some species to mimic group members. Hence, whistle structure variations may offer insights to interspecific associations among dolphin species, which although temporal and opportunistic are common. In this study, I test the hypothesis that interspecific interactions influence dolphin whistle structure, particularly during social events. The study took place in the Southern Caribbean coast of Costa Rica, where interspecific associations of the distantly related Guyana and Bottlenose dolphins occur on daily basis. The results indicate that interspecific groups emit whistles that show intermediate whistle structure compared to whistles emitted in intraspecific groups. This pattern is seen during social interactions between species, but not when interspecific groups are traveling. Social events in interspecific groups were of antagonistic nature, where Bottlenose dolphins isolated and harassed one or two Guyana dolphins. Contour data suggest that the most vocal species during these encounters was the Guyana dolphin. Therefore, the observed modifications in whistles structure likely reflect a stress response by the Guyana dolphins. Another alternative explanation includes signal convergence between interacting species. However, to understand the nature of these potential modifications, future studies should combine acoustic tags and directional recording systems to follow the vocalizing animals. Despite the shortcomings of this study, it provides some of the first insights into dolphin interspecific communication, providing evidence of overall signal change during interspecific interactions.

Introduction

Dolphin communicative signals show great plasticity, they are capable of modifying frequency and temporal components, e.g., in response to stress (Esch et al. 2009), to adjust for changes in their environment (e.g., Morisaka et al. 2005; May-Collado & Wartzok 2008), and in some species to imitate group members (Tyack 1986; Janik 2009). However, little is known if and how whistle structure changes during intraspecific interactions in dolphins, which although temporal and opportunistic, are quite common.

Birds, primates, and cetaceans are among the animals that often form temporary inter-specific groups (e.g., Terborgh 1990; Garcia et al. 2000; Herzing & Johnson 1997; Herzing et al. 2003; Psarakos et al. 2003; Stensland et al. 2003; Quérouil et al. 2008). Generally these associations are temporary and opportunistic, but in areas where sympatric species show high levels of site fidelity, these interactions may become less random and socially complex

(Frantzis and Herzing 2002; Quérouil et al. 2008). Several hypotheses have been proposed to explain inter-specific associations and most of them imply advantages of some sort, i.e., reduction of predation risk, increase exploitation of patchy resources, and reproductive benefits (Stensland et al. 2003; Scott & Cattanach 1998). However, for some species these associations may be neutral or not beneficial at all (Quérouil et al. 2008).

In the Wildlife refuge of Gandoca-Manzanillo in Costa Rica, interspecific associations between two distantly related dolphin species, the Guyana (*Sotalia guianensis*) and the Bottlenose dolphins (*Tursiops truncatus*) are far from opportunistic. In this Refuge, both species live in small populations, show medium to high levels of residency, and they significantly overlap in the spatial use of the Refuge (Gamboa-Poveda 2009) facilitating inter-specific associations on daily basis. Previous studies have documented that these association tend to be more common during social activities where Bottlenose dolphins are generally outnumbered but tend to dominate the much smaller Guyana dolphins, which are often chased, pushed around, and sexually harassed (Acevedo-Gutiérrez et al. 2005; Gamboa-Poveda 2009).

Despite the commonality of these interactions, the factors that prompt such associations are largely unknown, mainly because most of the observations are limited to surface behavior. However, because sound is the most important mean of communication among dolphins, it may provide important insights into the nature of such associations. In fact, a handful of acoustic studies in dolphin inter-specific groups indicate high 'whistle' activity (e.g., Herzing et al. 2003; Herzing 2000; Oswald et al. 2008). In addition, whistle activity in inter-specific groups appear to be higher in tropical latitudes than in temperate latitudes possibly because of a combination of factors such as group size, morphological constraints, and behavioral activities (Oswald et al. 2008). Despite the growing knowledge on dolphin inter-specific associations, if and how dolphins change their whistle structure during these associations are largely unknown.

Previous studies have shown that intraspecific groups of Bottlenose and Guyana dolphins contrast greatly in their whistle frequency and duration possibly as a result of a combination of factors such as differences in size and social structure, as well as distant phylogenetic relatedness (May-Collado and Wartzok 2009; May-Collado et al. 2007a,b). However, it is largely unknown if species-specific whistle structure is maintained during interspecific interactions. In particular, one might expect changes in whistle structure during social events when animals are directly interacting with one another.

The goal of this study is to provide insights into dolphins' interspecific communication by comparing frequency and duration components of dolphins' communicative signals (whistles) between intra- and inter-specific groups during social and travel events.

Methods

Study Site

The study took place in Gandoca-Manzanillo Wildlife Refuge (GMWR) on the southern Caribbean coast of Costa Rica (Fig. 1). In GMWR, Guyana dolphin (*S. guianensis*) and Bottlenose dolphin (*T. truncatus*) overlap in home range forming interspecific species groups on daily basis (e.g., Acevedo-Gutiérrez et al. 2005; Gamboa-Poveda & May-Collado 2006; Gamboa-Poveda 2009).

Surveys and recordings were carried out from a 10-m fiberglass boat with two engines (215 hp/ 4-stroke) within the limits of the Refuge (an area of 9.83 km^2 approximately) during 7 d in Jul. 2004, Sep. 2005, Nov. 2005, and Sep. 2006. During the study period, overall ambient noise levels (third octave) were estimated at 2, 6, 10, 14, and 18 kHz as 99.58, 98.18, 98.61, 104.02, and 92.10 dB, respectively (see May-Collado & Wartzok 2008).
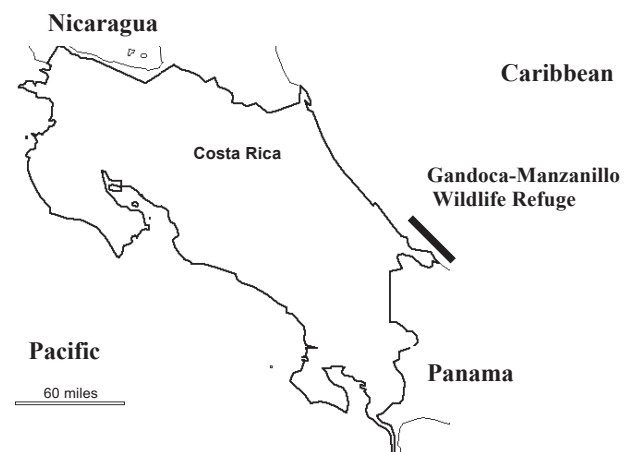
Fig. 1: Map showing the location of the Gandoca-Manzanillo Wildlife Refuge (9°59.972′ N, 82°60.530′ W) in Costa Rica where interspecific are commonly form.

Group Species Composition

Upon sighting, dolphin groups were classified as intraspecific or interspecific groups. Intraspecific groups of Guyana dolphins were easily distinguished from Bottlenose dolphin groups by their dorsal fin shape, body and rostrum size, coloration, and surfacing behavior (Fig. 2a–c). Guyana dolphins have a characteristic triangular dorsal fin, they are small (210 cm), body coloration is light gray on the back and sides, and pink on the belly, the rostrum is relatively long and is the first part of the body to come out of the water when surfacing (Flores 2002; Fig. 2c). In contrast, Bottlenose dolphins have a falcate dorsal-fin, their body is robust and medium sized (up to 380 cm), body coloration is dark gray, rostrum is small, and the demarcation between the melon and the small rostrum is the most evident part of the body when they surface (Wells & Scott 2002, Fig. 2b).

Upon finding a group, recordings and photo-identification data was collected for each group simultaneously. During the study period, about 60% of the photo-identified animals in this study were found in both intraspecific and interspecific groups.

Behavioral Events

For comparison purposes, only groups recorded during social and travel events are included in this study.

Behavioral observations were made from the boat continuously and in synchrony with each recording file as described in the following paragraphs. Because water visibility is generally poor in the study area owing to high sediment input from the Sixaola River, it was not possible to follow the animals underwater. Therefore, behavioral observations are limited to what the animals were doing on the surface. Table 1 provides information on recording effort, group size, total number of groups, and total number whistles analyzed per behavioral context.

Social events were those in which dolphins were engaged in intense and dynamic interactions with each other. Intraspecific groups social behavior consisted of body contact such as rubbing, genital contact, touching, tail slapping, leaps, body rolling, tail walking, spy hoping, chasing, and even performing boat riding with the research or other boats (e.g., Acevedo-Gutiérrez et al. 2005; Edwards & Schnell 2001). In contrast, interspecific groups were dominated by antagonistic behaviors where a few Bottlenose dolphins targeted one or two Guyana dolphins, which were chased, pushed around, forcibly submerged, and sexual harassed. Social group size varied across species. Guyana dolphins group size generally ranged between 10 and 40 individuals, while Bottlenose dolphins groups were much smaller ranging from 4 to 6 individuals. Interspecific group size ranged from 4 to 27 individuals, where bottlenose dolphins were often outnumber (2–11

Fig. 2: Photographs of both studied dolphin species. (a) In the upper left, a bottlenose nose dolphin (*Tursiops truncatus*) is shown, and in the upper right, a Guyana dolphin (*Sotalia guianensis*) is shown. Photographs (b) and (c) show the characteristic rostrum of bottlenose and Guyana dolphins, respectively. (Photographs a and c were captured by Laura J. May-Collado and photograph b was captured by Ingi Agnarsson).

Total recorded time = 1848.7 min	Mixed groups		Guyana dolphins		Bottlenose dolphins		**Table 1:** Summary information of the about the groups recorded and the whistle analysis
Total analyzed time = 620.4 min	Social	Travel	Social	Travel	Social	Travel	
Number of whistles	217	95	148	91	131	97	
Number of groups	5	3	3	4	4	3	
Mean group size	15.1 ± 9.6		17.8 ± 10.7		4.28 ± 0.75		

60% of the dolphins photo-identified in both intra and interspecific groups were the same.

individuals) by the Guyana dolphins (2–16 individuals). Overall, calve presence was rare in Bottlenose dolphin groups and Guyana dolphin calves were not targeted by bottlenose dolphin during any observation in this study.

Traveling events consisted of dolphin groups swimming either slow or fast while maintaining a defined direction, and diving and resurfacing synchronously (e.g., Edwards & Schnell 2001; Acevedo-Gutiérrez et al. 2005; Daura-Jorge et al. 2005). Interspecific groups during traveling activities ranged from 7 to 30 individuals (Bottlenose dolphins: 3–10 individuals; Guyana dolphins: 4–20 individuals), while Guyana dolphins ranged between 10 and 20 individuals and Bottlenose dolphin groups consisted of four individuals.

Dolphin Field Recordings and Whistle Analysis

Dolphin signals were recorded with the research engine off using a broadband system consisting of a RESON hydrophone (-203 dB re $1V/\mu$Pa, 1 Hz to 140 kHz) connected to AVISOFT recorder and Ultra Sound Gate 116 (sampling rate 400–500 kHz 16 bit) that sent the signals to a laptop. The recordings were made continuously in files of two to 3 min at sampling rate ranging between 384 and 500 kHz (see May-Collado & Wartzok 2008; 2009). Dolphin whistles were analyzed manually using the program Raven 1.1 (Cornell Laboratory of Ornithology, Ithaca, New York, USA) with a fast Fournier transformation size of 1024 points, an overlap of 50%, and using a 512–522 sample, Hann window. Only whistles with a clear and 'loud' contour from start to end where included in the analysis.

To reduce over-representation 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 previous studies with similar methods Azevedo & Van Sluys 2005; May-Collado & Wartzok 2008; 2009). Seven standard whistle variables were measured on the fundamental frequency of each: starting frequency (StartF), ending frequency (EndF), minimum frequency (MinF), maximum frequency (MaxF), delta frequency (DeltaF = MaxF—MinF), duration (s), and number of inflection points (e.g., Bazúa-Durán & Au 2002, 2004; Morisaka et al. 2005). Peak frequency (PeakF) was also measured and is defined as the frequency at which maximum power occurs (Bazúa-Durán & Au 2002, 2004; May-Collado & Wartzok 2007, 2008; 2009). The contour for each selected whistle was grouped into one of the following categories upsweep, downsweep, constant, convex, concave, or sine (see Bazúa-Durán & Au 2002).

Data Analysis

Because of the omnidirectional nature of the recording systems, it was not possible to identify the 'vocalizing' individuals within the interspecific groups. Therefore, the analysis is limited to determine differences in whistle structure between intra and interspecific dolphin groups during social and travel events. I used the statistical software PASW Statistics 18.0® (SPSS Institute Inc., Chicago, Illinois, USA) to perform descriptive statistics (mean, standard deviation, and frequency range). The nonparametric Kruskal–Wallis test was used to determine if intra- and inter-specific groups varied in their whistle structure. Because of the multiple comparisons, I used the Bonferroni procedure to adjust the level of significance owing to Type I error to $\alpha = 0.006$, and for the pairwise comparisons, I used a $\alpha = 0.00027$. I also performed a chi-square test to evaluate if there are differences in the distribution of whistle contour of intra- and inter-specific dolphin groups.

I performed a Discriminant Analysis to determine if whistles recorded from interspecific associations have a greater level of overlap than those recorded from intraspecific groups. If modifications toward whistle 'similarity' in whistle acoustic structure is occurring, one should be able to observe a decrease in the overall test power to predict species membership during interspecific association. For this analysis, all whistles frequency and duration variables were Box-Cox

transformed to normalize their distribution (Sokal & Rohlf 1995). The normalize data was used for the Discriminant Analysis to determine the overall correct classification percentage by species within intra and interspecific groups during both behavioral states. I used a sample of 239 whistles from intraspecific groups of Guyana dolphins (May-Collado and Wartzok 2009), 228 whistles from Bottlenose dolphins recorded during social and travel events for the Discriminant Analysis (May-Collado & Wartzok 2008), and 312 whistles recorded from interspecific groups. Because the covariance matrices for the group compositions were significantly different (Box's M = 800.7, df1 = 84, p < 0.0001), I selected a regularized compromise Discriminant method with lambda = 0 and gamma = 0.1. The Kappa Index test was used to assess how well the Discriminant function does vs. chance alone at the statistical significance level of 0.05 (Green & Salkind 2003). The cross-validated method was used to calculate correct classification scores for the Discriminant functions as well as a chi-square test was performed to evaluate the accuracy of the classification at the p-value level of p = 0.05 (Green & Salkind 2003).

Results

Whistles recorded from intraspecific groups of Guyana and Bottlenose dolphins differ significantly in frequency and duration and both differ from interspecific groups (see statistics in Table 2). Interspecific dolphin groups emit whistles with intermediate values for all frequency and temporal variables of those emitted by intraspecific groups of Guyana and Bottlenose dolphins (Fig. 3). When accounting for behavioral context, I find this pattern during social events but not during travel events where whistles emitted by interspecific groups are not different from those emitted by intraspecific groups of Guyana dolphin (see statistics in Table 3, Fig. 3).

The distribution of whistle contour varied between intra and interspecific groups ($\chi^2 = 238.2$, df = 10, p < 0.0001). The most common whistle contour for Guyana dolphin groups (59%) and interspecific groups (54%) were upsweep whistles, while sine whistles were more common for Bottlenose dolphin groups (49.5%). There were no differences in the distribution of whistle contour for the intraspecific groups in relation to behavioral context. However, in the interspecific groups, more upsweep whistles where emitted during social events (73.6%) than when traveling (23.4%) ($\chi^2 = 30.9$, df = 5, p < 0.0001).

Table 2: Summary of the statistics comparing whistle acoustic parameters for Guyana and Bottlenose dolphins in mixed and single species groups

Groups	Stats	MinF	MaxF	DeltaF	StartF	EndF	PeakF	Duration	IP
Guyana dolphin groups n = 239	Mean ± SD	12.54 ± 5.37	21.73 ± 6.17	9.34 ± 5.31	14.01 ± 6.50	20.41 ± 6.43	16.19 ± 5.87	0.20 ± 0.19	0.48 ± 1.19
	Range								
Mixed groups n = 312	Mean ± SD	10.4 ± 5.7	19.8 ± 5.7	9.3 ± 5.1	12.2 ± 6.4	17.9 ± 6.5	14.6 ± 5.8	0.398 ± 0.559	0.8 ± 2.1
Bottlenose dolphin groups n = 228	Mean ± SD	5.57 ± 1.89	16.16 ± 4.10	10.70 ± 3.75	9.00 ± 3.51	10.56 ± 5.13	10.43 ± 3.54	1.03 ± 0.64	3.35 ± 3.88
	Test	269.6	137.2	20.6	94.6	250.8	169.2	289.0	168.6
	df	2	2	2	2	2	2	2	2
	p-Value	<0.00001*	<0.00001*	0.0001*	<0.00001*	<0.00001*	<0.00001*	<0.00001*	<0.00001*
	Pairwise comparisons	S > M* M > T* S > T*	S > M* M > T* S > T*	S > M M < T* S < T*	S > M* M > T* S > T*	S > M* M > T* S > T*	S > M* M > T* S > T*	S < M* M < T* S < T*	S > M M < T* S < T*

*Significant; NS, not significant; S, Guyana dolphins; T, Bottlenose dolphins; M, interspecific groups; IP, inflection points.
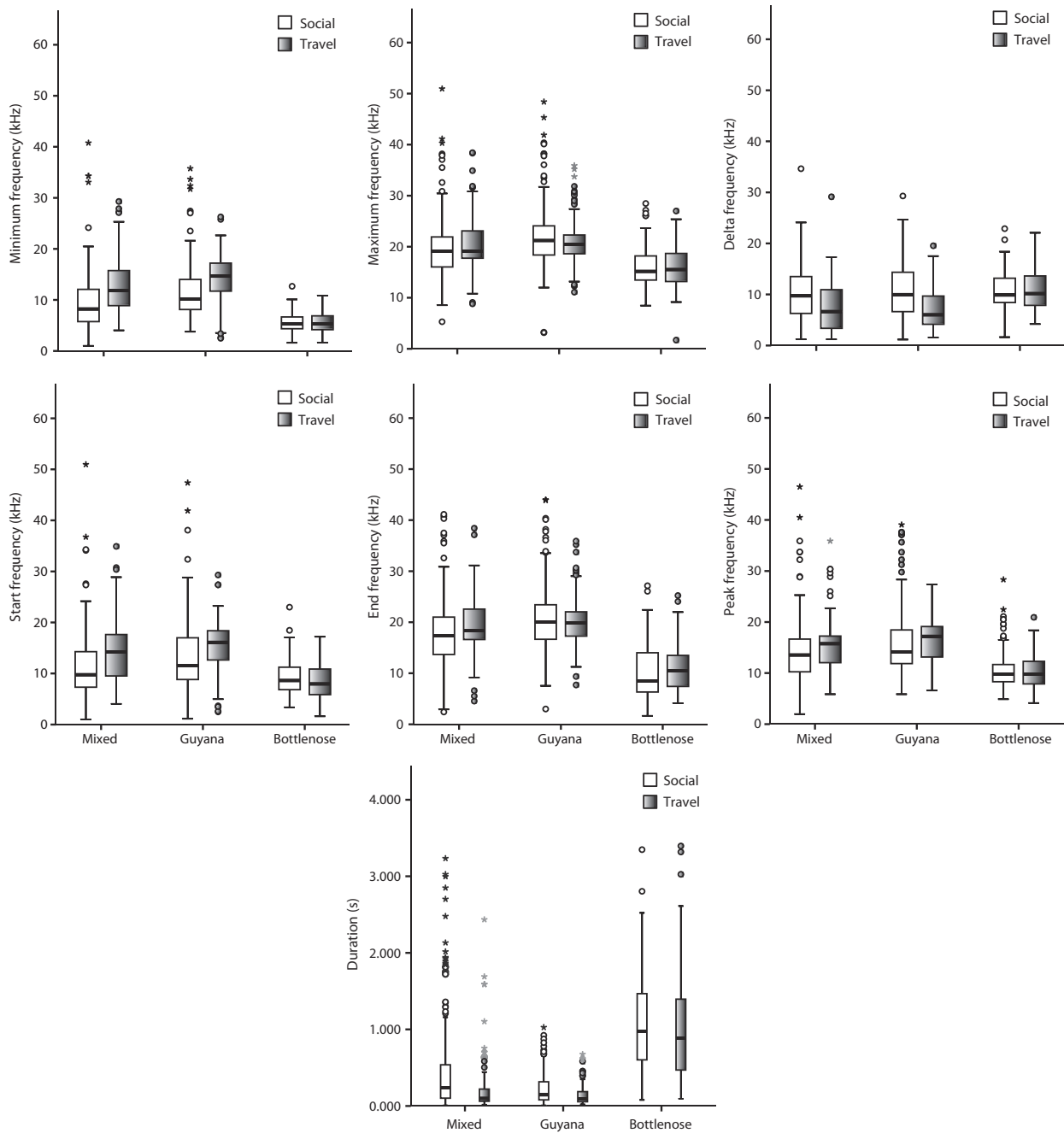
Fig. 3: Whistle variation of intraspecific groups of Guyana and Bottlenose dolphins and interspecific groups based on behavioral context.

While species whistles are clearly distinct when found in intraspecific groups, this is not the case when the species are interacting in interspecific groups (Table 4). The overall predictive power of the Discriminant Analysis to classify whistles was reduced to 58.1% in intraspecific groups during social events (Kappa = 0.35) compared to that of the intraspecific groups (Kappa = 0.80) (Table 4). Intermediate whistle structure values and less powerful discrimination power for interspecific groups suggest that whistle structure might be modified as a result of these interactions.

Discussion

Dolphin communication is one of the most controversial topics in animal behavior from Lilly's work on trying to teach dolphins a human language (Lilly

Table 3: Summary of the statistics comparing whistle acoustic parameters for Guyana and Bottlenose dolphins between intra an interspecific groups in relation to behavioral states

Stats	MinF	MaxF	DeltaF	StartF	EndF	PeakF	Duration	IP
Social (n = 496)								
Test	139.7	89.4	NS	31.2	147.6	81.7	160.3	82.6
df	2	2		2	2	2	2	2
p-Value	<0.0001	<0.0001		<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Pairwise comparisons	S > M*	S > M*	–	S > M	S > M*	S > M	S < M	S < M
	M > T*	M > T*		M > T	M > T*	M > T*	M < T*	M < T*
	S > T*	S > T**		S > T*	S > T*	S > T*	S < T*	S < T*
Travel (n = 283)								
Test	142.7	49.7	42.7	81.3	108.8	97.2	140.1	91.2
df	2	2	2	2	2	2	2	2
p-Value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Pairwise comparisons	S > M	S > M	S > M	S > M	S > M	S > M	S > M	S < M
	M > T*	M > T*	M < T*	M > T*	M > T*	M > T*	M < T*	M < T*
	S > T*	S > T*	S < T*	S > T*	S > T*	S > T*	S < T*	S < T*

*Significant; NS, not significant; S, Guyana dolphins; T, Bottlenose dolphins; M, interspecific groups.

Table 4: Overall correct classification percentages of the Discriminant Analysis for species in intra- and inter-species groups using all whistle parameters as discriminant. The respective results of the prediction power analysis using the Kappa Index and chi-square test statistics are in bold

	Intraspecific groups Guyana vs. Bottlenose dolphins			Interspecific groups Guyana vs. Bottlenose dolphins		
	Overall (n = 467)	Social (n = 279)	Travel (n = 188)	Overall (n = 777)	Social (n = 494)	Travel (n = 283)
Classification %	90.6%	90%	91.5%	57%	58.1%	62.2%
Kappa Index	**0.81**	**0.80**	**0.83**	**0.36**	**0.35**	**0.43**
Chi-square test p-value	p < 0.0001	p < 0.0001	p < 0.0001	p < 0.0001	p < 0.0001	p < 0.0001

Kappa Index ranges from −1 to +1, a value of 1 indicates a perfect prediction and values below 0 indicate poor prediction by chance alone.

1965) to the Caldwell's providing evidence on dolphin emission of individual 'signature whistles' as contact calls (Caldwell & Caldwell 1965, 1979; Caldwell et al. 1990) to Tyack (1986) showing how dolphins can mimic each other's signature whistles to strengthen important associations.

Prior work on dolphin communication provides ample evidence of whistle plasticity in frequency and time domain. Dolphins are known to imitate synthetic sounds (e.g., Richards et al. 1984; Reiss & McCowan 1993) and imitate conspecifics in both captive and wild conditions (e.g., Tyack 1986; Janik 2000; Watwood et al. 2004). In addition, dolphins can modify their whistle acoustic properties to cope with changes in background noise (e.g., Morisaka et al. 2005; May-Collado & Wartzok 2008) and in response to stress (Esch et al. 2009).

In this study, I found evidence for interspecific groups of Guyana and Bottlenose dolphin species emitting whistles with intermediate frequency and duration values compared to whistles emitted by the same species (and possibly the same animals see

Methods) in intraspecific groups. This is particularly evident during social events where species are directly interacting with another. Modification in signal structure was also supported by a decrease in the power of discriminate analysis species classification during species interactions. This indicates that whistle similarity increases during interspecific interactions, while whistles from intraspecific groups are readily discriminated from one another.

Although morphological and phylogenetic constraints in these two species likely enhance their species-specific signal differentiation, there is some overlapping in signal characteristics, particularly in the frequency domain. The observed modifications in signal structure toward intermediate values in whistle parameters may reflect an increment or an emphasis in this overlap. The relatively high site fidelity that both Guyana and Bottlenose dolphins show in the study area (Gamboa-Poveda 2009) may be promoting less random and more complex social interactions between these two species (Quérouil et al. 2008), which in turn might be promoting

signal convergence to some extent (e.g., Haavie et al. 2004; Gorissen et al. 2006).

Signal convergence or signal matching has being documented in passerine birds, where many hypotheses have been proposed to explain the positive and negative effects of such phenomena (Gorissen et al. 2006; Garamszegi et al. 2007). However, little is known about dolphin interspecific communication and much less about the role (if any) that signal matching may play in it.

Another explanation to the observed whistle changes may be related to stress. Acevedo-Gutiérrez et al. (2005) described Guyana and bottlenose dolphin interspecific social interactions in the context of reproduction (formation of hybrids). However, during this study all the interspecific social interactions appeared antagonistic (aggressive), contrasting with the social interactions observed in intraspecific groups that involved more 'playing' (touching, tail slapping, leaps, body rolling, spy hoping, and short-distance chases). Antagonistic events during interspecific associations involved the Bottlenose dolphins separating and harassing one or two Guyana dolphins. These dolphins were then chased, pushed around, forcibly submerged and even sexually harassed, while the rest of Guyana dolphins remained within the vicinity. Depending on the number of Bottlenose dolphins, separation of the much smaller Guyana dolphin could consist of multiple and simultaneous separation events.

During these antagonistic social events, the majority of whistles emitted were upsweep in contour (73.6%), which are also the most common whistle contour emitted by intraspecific groups of Guyana dolphins in this and previous studies (e.g., Erber & Simão 2004). Thus, the observed whistle modifications in interspecific groups might have been largely caused by whistles emitted by the 'isolated' Guyana dolphins. One possibility is that they are attempting either to emit threats 'in the language of the intruder' (Gorissen et al. 2006) or express stress. Watts & Stookey (2001) suggested that vocal response to forced isolation could be a distress reaction that is either context specific or an attempt to communicate with conspecifics, or both. A recent study on bottlenose dolphins provided evidence of stress in their whistle structure during routinely brief capture-release monitoring events in Sarasota Bay. The study showed that isolated females (deprived of their calves) emitted whistles that were higher in frequency and shorter in loop duration (Esch et al. 2009). In contrast, by lowering frequency and increasing whistle duration slightly, Guyana dolphins

may be trying to make certain stress signals to reach their conspecific, which tend to distance themselves from the harassing area. Interestingly, during traveling events, the whistles recorded from Guyana dolphins groups were not significantly different from those recorded in interspecific groups, suggesting again that the most vocal animal during these events was the Guyana dolphin.

Unfortunately the methodology of this study does not allow me to evaluate properly the signal convergence and signal stress hypothesis. Future studies should combine acoustic tags and directional recording system that allow individual identification and follow up of group members before and during interspecific associations. Despite the shortcomings, this study provides some of the first insights into dolphin interspecific communication by providing evidence of overall change in whistle structure during interspecific interactions.

Conclusion

Guyana and Bottlenose dolphins form temporary associations but unlike most reported dolphin interspecific-species associations, these associations occur on a daily basis often with the same individuals involved. Because sound is the most important mean of communication among dolphins, I use it to gain insight into the nature of these interactions. The results from this study indicate that while whistles from intraspecific groups are readily discriminated, there is a change in whistle acoustic structure occurring in interspecific groups. Specifically, interspecific groups showed intermediate values in frequency and temporal parameters. Multiple factors may be promoting these modifications (i.e., signal convergence, signal stress) that cannot be evaluated with the data collected in this study. Despite these, the present study provides evidence that signal modification occurs, thus contributing to our understanding of dolphin communication occurring between distantly related species. Future studies should complement directional passive acoustic technology with acoustic tags in order to evaluate the potential factors promoting interspecific signal modification.

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