

The freshwater dolphin *Inia geoffrensis geoffrensis* produces high frequency whistles

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Because whistles are most commonly associated with social delphinids, they have been largely overlooked, ignored, or presumed absent, in solitary freshwater dolphin species. Whistle production in the freshwater dolphin, the boto (*Inia geoffrensis geoffrensis*), has been controversial. Because of its sympatry with tucuxi dolphins (*Sotalia fluviatilis*), a whistling species, some presume tucuxi whistles might have been erroneously assigned to the boto. Using a broadband recording system, we recorded over 100 whistles from boto dolphins in the Yasuní River, Ecuador, where the tucuxi dolphins are absent. Our results therefore provide conclusive evidence for whistle production in *Inia geoffrensis geoffrensis*. Furthermore, boto whistles are significantly different from tucuxi whistles recorded in nearby rivers. The Ecuadorian boto whistle has a significantly greater frequency range (5.30–48.10 kHz) than previously reported in other populations (Peru and Colombia) that were recorded with more bandwidth limited equipment. In addition, the top frequency and the range are greater than in any other toothed whale species recorded to date. Whistle production was higher during resting activities, alone or in the presence of other animals. The confirmation of whistles in the boto has important implications for the evolution of whistles in Cetacea and their association with sociality. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2404918]

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I. INTRODUCTION

The Amazon River dolphin, or boto, is known to produce a variety of sounds, e.g., echolocation clicks, single intense clicks, jaw snaps, and burst-pulsed sounds (Caldwell and Caldwell 1967, Caldwell *et al.* 1966). Whistles were first reported by Nakasai and Takemura (1975) in Peru and later documented in more detail by Wang *et al.* (1995a, 2001). Whistles have been also reported in the boto from the Orinoco River (Diazgranados and Trujillo 2002). Despite these reports, whistle production in this riverine dolphin has been questioned on the basis that boto distribution overlaps largely with tucuxi dolphins (*Sotalia fluviatilis*), a well documented whistling species. Hence, tucuxi whistles may have been erroneously assigned to the boto (e.g., Podos *et al.* 2002). In fact, it has been suggested that whistles are unique to social delphinids (Herman and Tavolga 1980; Podos *et al.* 2002). Certainly, whistles are best studied in social delphinids, where they are used for various communication purposes such as individual identifiers, coordination of group behavior, and maintenance of group cohesion (e.g., Caldwell and Caldwell 1965; Caldwell *et al.* 1990; Fripp *et al.* 2005; Herzog 2000; Janik 2000; Tyack 1997, 2000; Watwood *et al.* 2004). However, nondelphinid toothed whale species like the Chinese river dolphin *Lipotes vexillifer* (Jing *et al.* 1981;

Xianying *et al.* 1981; Wang *et al.* 1989; Wang *et al.* 2006), the beaked whales of the genus *Berardius* spp (Dawson *et al.* 1998, Rogers and Brown 1999), the narwhal *Monodon monocerus*, and the beluga *Delphinapterus leucas* (e.g., Belikov and Bel'kovich 2001, 2003; Ford and Fisher 1978; Karlsen *et al.* 2002; Shapiro 2006; Sjare and Smith 1986; Watkins *et al.* 1970) are known to produce whistles as well in a variety of contexts.

Here we document whistles and their behavioral context in the boto dolphins of the Yasuní River, Ecuador, and discuss the potential of these signals as communicative signals in this solitary freshwater dolphin.

II. METHODS

A. Study site

The boto is one of the most widely distributed freshwater dolphins. In parts of its distribution it is sympatric with *Sotalia fluviatilis* (da Silva 2002). The boto inhabits principal tributaries of the Amazon River as well as small rivers and lakes across its distribution (da Silva 2002). Since one of the main criticisms of previous work on boto whistles is the presence of *S. fluviatilis* in the area of recordings, it was important for our study to be conducted in areas where only botos were found. We selected the Yasuní River, a tributary of the Napo River, a narrow river that inundates the adjacent forest and lagoons, during the high-water season (Fig. 1). During the low-water season the river becomes narrower and

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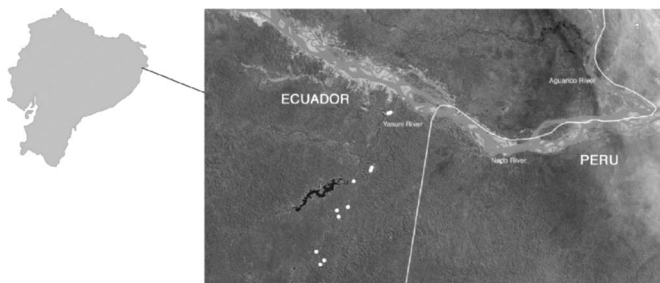


FIG. 1. Map showing the location of the Yasuni River and groups of botos (white dots) recorded during this study.

the lagoons dry out (Galacatos *et al.* 2004), not the type of habitat in which *S. fluviatilis* is known to occur (da Silva 2002).

Overall *S. fluviatilis* is believed to have low population densities in Ecuador (Dekinger 2001, Zapata-Rios and Utreras 2004). While relatively common in the Putumayo and Morona Rivers, local biologists (Zapata-Rios and Utreras 2004, Victor Utreras pers. com. 2006), park rangers, and inhabitants of the area confirm that *S. fluviatilis* is rare in the Yasuní, Napo, and Aguarico rivers, and absent in the Yasuní during the low-water season. Our study took place in the Yasuní River during the low-water season when boto were confined to deeper areas of this narrow river.

We recorded boto dolphins from 14 to 19 August 2005 between 6 a.m. to 6 p.m. In order to decrease chances of encountering (and accidentally recording) *S. fluviatilis* we recorded botos at least 1.5 km away from the point of intersection with the Napo River where the chances to see *S. fluviatilis* may be higher (Zapata-Rios and Utreras 2004). As expected, we observed only botos in the Yasuní River and are thus confident that all the whistles presented in this study correspond exclusively to the boto. To verify this, we compare and contrast boto whistles with 20 whistles recorded from six individuals of *S. fluviatilis* and 13 whistles from one group that contained both species at the intersection between the Napo and the Aguarico rivers, about 14 km downstream from the intersection between Yasuní and the Napo rivers. The 20 whistles recorded from single animals were very similar in contour, time, and frequency parameters to other *S. fluviatilis* populations (e.g., Podos *et al.* 2002, Azevedo and Van Sluys 2005, Wang *et al.* 1995a, 2001). These single animals were recorded near the boat and botos were not present in the area. The other 13 whistles were identical to these in all acoustic parameters therefore they were assigned to *S. fluviatilis*.

B. Whistle definition

To understand the evolutionary history of whistles and the factors that may have influenced their evolution we must first understand their distribution among cetaceans. To do so it is important not to *a priori* bias whistle definition, e.g., by defining them in the context of a behavior that may have much more limited distribution than the sounds themselves. Rather, it seems less presumptuous to define sounds in terms of acoustic parameters. Whistles are tonal sounds produced

by toothed whales. These sounds have a specific acoustic structure that consists of narrowband and frequency modulated sounds (Richardson *et al.* 1995). Whistles may be complex in contour (e.g., sine, convex, concave, upsweep, downsweep) or simply constant in frequency, e.g., *Lagenorhynchus albirostris* (Rasmussen and Miller 2002), *Sotalia guianensis* (Azevedo and Van Sluys 2005) and *Stenella longirostris* (Barzúa-Durán and Au 2002). Often whistle fundamental frequency is below 20 kHz (Richardson *et al.* 1995), but not limited to this range, e.g., Oswald *et al.* (2004) found that *Delphinus delphis*, *Stenella attenuata*, *S. coeruleoalba*, and *S. longirostris* produced whistles with frequencies up to 24 kHz, in *Lagenorhynchus albirostris* whistle fundamental frequency can go up to 35 kHz (Rasmussen and Miller 2002) and up to 41 kHz in *Tursiops truncatus* (Boisseau 2005). Whistles may be continuous or consist of series of breaks and segments (Richardson *et al.* 1995) and contain or not harmonics (Au 2000). Some dolphin species like *S. longirostris* (Lammers and Au 2003) and *L. albirostris* (Rasmussen *et al.* 2006) produce whistles with high order harmonics. Finally, whistles vary greatly in duration. For instance, *Sousa chinensis* whistles can range from 0.01 to 1.3 s (Van Parijs and Corkeron 2001) and in *Tursiops truncatus* from 0.05 to 3.2 s (Wang *et al.* 1995b).

C. Recordings and behavioral observations

Dolphin signals were recorded using a broadband system consisting of a RESON hydrophone (−203 dB re 1 V/μPa, 1 Hz–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. Recordings were made continuously. For accompanying behavioral observations, recording sessions were segmented into 3 min intervals. Behavioral observations were made in every other 3 min interval and the predominant behavior during that interval was recorded. Because the river was narrow and relatively shallow, animals were in sight for the observers most of the time. When animals were not in sight during a 3 min scanning period, the behavior was noted as unknown. Only 3 min periods with acoustic and behavioral information were used for the analyses. Five behavioral categories were defined: (1) Feeding/Foraging, when animals were actively searching, pursuing, and/or consuming prey were assigned to this category, (2) Social activities, when dolphins interacted among themselves, e.g., body contact, tail slapping, and animals following the boat or other animals, (3) Traveling, when dolphins were swimming either slowly or fast while maintaining a defined direction, (4) Resting was defined as in Dekinger (2001) were animals showed nondirectional swimming and surfaced regularly at a slow speed or when surfacing occurred in the same area without any abrupt or fast movement, (5) Unknown behavior, was assigned when the animals were not in sight and thus the behavior activity could not be determined.

Group size, group composition, photo-ID, and geographical position data were also collected. Recordings were obtained from 14 to 19 August 2005, giving a total of 214 files recorded (~9 h and 45 min of recorded time). We ana-

TABLE I. Descriptive statistics of boto whistles with comparison to previously published data (in bold values for all 121 whistles and in parenthesis values for 70 whistles with frequency values below 25 kHz for comparison purposes).

	<i>Min F</i> (kHz)	<i>Max F</i> (kHz)	<i>Start F</i> (kHz)	<i>End F</i> (kHz)	<i>Delta F</i> (kHz)	<i>Peak F</i> (kHz)	<i>Duration</i> (s)
This Study							
<i>Mean</i>	14.54 (12.59)	24.71 (19.26)	23.30 (18.49)	15.48 (13.10)	10.18 (6.71)	18.62 (15.36)	0.009 (0.010)
<i>SD</i>	4.32 (3.96)	8.37 (4.0)	8.53 (4.10)	5.70 (4.35)	7.02 (2.47)	6.61 (4.52)	0.011 (0.014)
<i>Range</i>	5.30–26.44 (5.30–21.37)	10.88–48.10 (10.88–24.89)	9.77–48.10 (9.77–24.89)	5.30–42.99 (5.30–24.62)	2.94–34.39 (2.99–16.52)	3.22–48.83 (6.35–22.95)	0.002–0.080 (0.002–0.080)
<i>CV%</i>	29.7 (31.5)	33.9 (20.8)	36.1 (22.1)	38.60 (33.3)	68.9 (36.9)	35.50 (29.5)	128.2 (134.2)
Wang <i>et al.</i> (1995a, 2001) ^a							
<i>Mean</i>	2.54	2.97	2.61	2.86	1.14
<i>SD</i>	0.76	0.84	0.75	0.77	1.01
<i>Range</i>	0.220–4.22	0.5–5.16	0.220–4.22	0.360–4.86	0.16–4.42
<i>CV%</i>	29.88	28.11	28.55	27.01	91.10
Diazgranados and Trujillo (2002)							
<i>Mean</i>
<i>SD</i>
<i>Range</i>	3	13
<i>CV%</i>

^aRecording system with maximum frequency limited to 25 kHz.

lyzed all good quality whistles using the program Raven 1.1 (Cornell Laboratory of Ornithology, New York) with a fast Fourier transform size of 1024 points, an overlap of 50%, and using a 512–522 sample Hann window.

Eight parameters were measured for each whistle: starting frequency (SF), ending frequency (EF), minimum frequency (MinF), maximum frequency (MaxF), delta frequency (DF=MaxF—MinF), peak frequency (PF, measured in the whistle contour where intensity was the highest), duration (s), number of inflection points and contour type. Contour type was categorized as by Azevedo and Simão (2002).

We used SYSTAT® statistical software for descriptive and nonparametric statistics. After testing for normality using the K-S Lilliefors, Skewness, and Kurtosis tests, nonparametric tests were selected to analyze the data. The Kruskal-Wallis test was used to determine if whistle acoustic parameters varied across behavioral states and groups (sightings) and Chi-square one sample test for Goodness of Fit to determine if whistle production rate (No. whistles/min/individual) varied across behaviors. The Kolmogorov-Smirnov test for two independent samples was used to determine if the medians of the acoustical parameters differed between the two species. A multivariate discriminant function analysis was used to classify whistles within and between species. The Jackknife method was used to calculate the percent of correct classification for each species.

III. RESULTS

A total of 121 high quality tonal sounds fitted the definition of “whistles” (see above) until now only described in delphinids and a few other toothed whales. However, these whistles were not produced in bouts as in many delphinid species. They were produced singly and spaced in time. The overall whistle production was 0.015 whistles/min/individual.

Whistle fundamental frequency ranged from 5.30 up to 48.10 kHz and was short in duration (0.002–0.080 s) (Table I, Fig. 2). About half (48%; $n=58$) of the whistles had maximum frequency values above 24 kHz. This demarcation point was chosen because most dolphin whistles reportedly do not go beyond 24 kHz (with the exceptions mentioned earlier) and this is often the upper limit of recording equipment used in many earlier studies. Similarly 42.1% ($n=51$) of beginning frequency, 13.2% ($n=16$) of peak frequency, 5.78% ($n=7$) of end frequency, and 1.65% ($n=2$) of minimum frequency measurements were above 24 kHz.

In terms of whistle contours 95.8% ($n=116$) of the whistles were descending in frequency. Examples of whistle contours produced by botos are shown in Fig. 2 in conjunction with tucuxi whistles for comparison purposes. Only five of all selected whistles had harmonics. The highest frequency harmonic reached 43.5 kHz.

The whistles were recorded during three behavioral categories: slow traveling, feeding, and resting. Although more whistles were produced during travel activities when accounting for time and number of individuals, whistle production was significantly higher during resting activities with 0.24 whistles/min/per individual ($\chi^2=0.50$, $df=1$, $p<0.05$) compared to traveling (0.03) and feeding (0.03). There were no significant differences in the acoustic parameters of whistles across behaviors at p -value 0.05 level (Table II).

Whistles did vary significantly in their acoustic structure across sighted groups (only groups with more than five whistles were compared) for all whistles parameters except delta frequency (Kruskal-Wallis test, $df=8$, $n=121$: MinF $\chi^2=20.31$, $p=0.026$; MaxF $\chi^2=25.46$, $p=0.005$; SF $\chi^2=23.31$, $p=0.010$; EF $\chi^2=23.86$, $p=0.008$; PF $\chi^2=23.28$, $p=0.010$; Duration $\chi^2=25.46$, $p=0.005$, DF $p>0.05$, Table III). Whistle acoustic parameters did not vary significantly when comparing whistles of groups consisting of adults with groups of adults with calves ($p>0.05$).

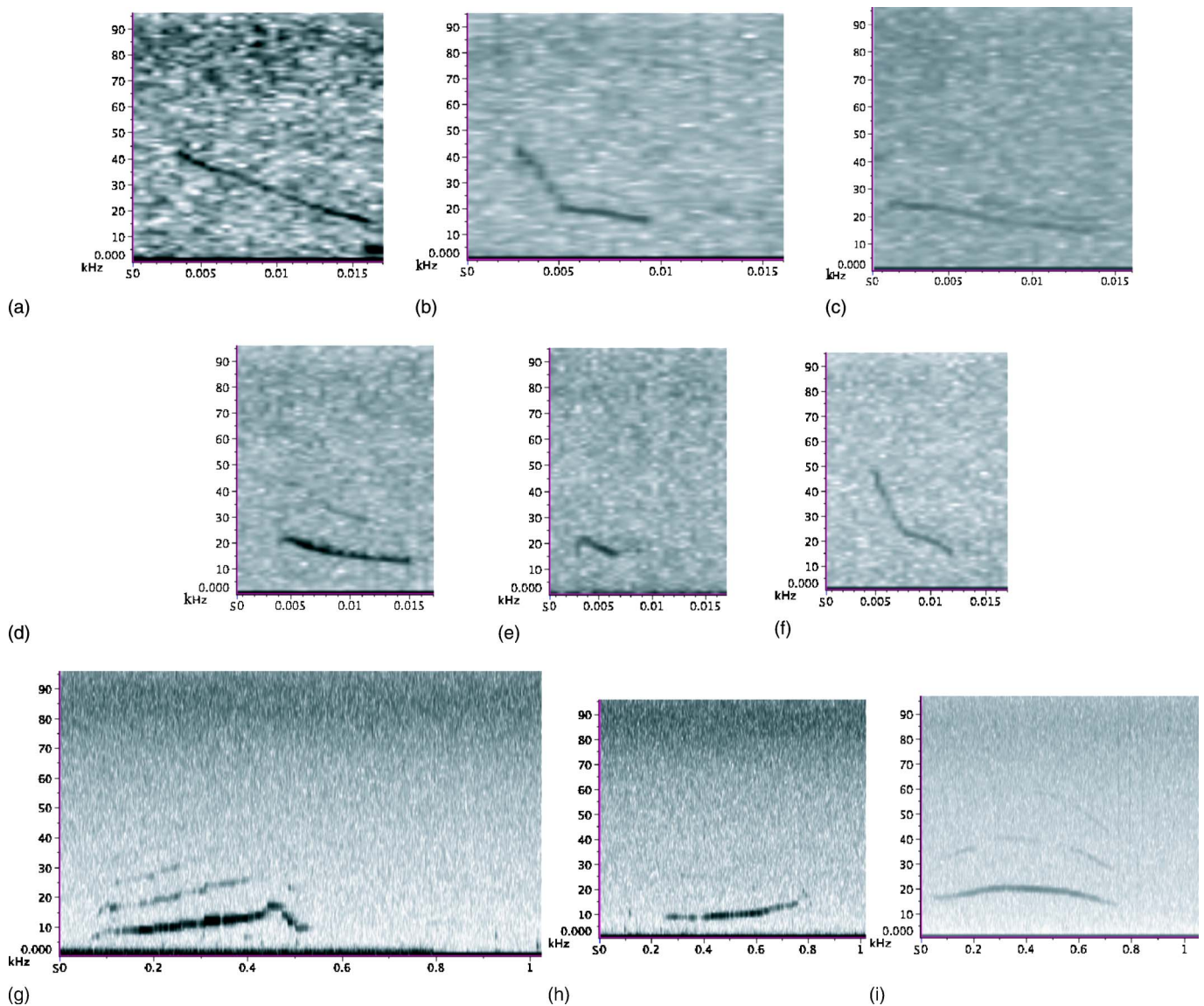


FIG. 2. Examples of whistles (y axis=frequency in kHz, x axis=time in seconds) recorded from *Inia geoffrensis geoffrensis* in the Yasuni River, Ecuador (a)–(f). Examples of whistles recorded from *Sotalia fluviatilis* in the Napo and Aguarico River are given for comparison purposes (h)–(i).

When comparing boto and tucuxi whistles we found significant differences in all whistle parameters medians (MinF Kolmogorov–Smirnov (KS)=0.543, $p < 0.001$; MaxF KS =0.537, $p < 0.001$; DF KS=0.190, $p < 0.001$, SF KS=0.683, $p < 0.001$; EF KS=0.298, $p < 0.001$; PF KS=0.336, $p < 0.001$; Duration KS=0.901, $p < 0.001$). The boto whistles were higher in frequency for all frequency parameters and much shorter in duration than the whistles produced by tucuxis recorded from the Napo and Aguarico rivers (Fig. 3). Tucuxis produced two classes of whistles that can be described as (1) whistles with maximum frequencies below 20 kHz and minimum frequencies below 10 kHz, and (2) whistles with maximum frequencies below 25 kHz and minimum frequencies above 10 kHz (see Fig. 4). Both categories of whistles overlap with boto whistles. Despite this overlap in frequency, the discriminant function analysis correctly classified (based on all acoustical parameters) all boto whistles (100%). Only 15% of the tucuxi whistles were incorrectly classified.

IV. DISCUSSION

Our results confirm previous findings that botos indeed whistle (Wang *et al.* 1995a, 2001, Diazgranados and Trujillo 2002) and suggest that boto whistles are frequency modulated with one of the widest frequency ranges ever reported in a toothed-whale species. Interestingly, the acoustic structure of these whistles is not only distinct from those of the sympatric *S. fluviatilis* but also appears quite distinct from other acoustically known boto populations in Colombia (*Inia geoffrensis humboldtiana*) (Diazgranados and Trujillo 2002) and Perú (*Inia geoffrensis geoffrensis*) (Wang *et al.* 1995a, 2001). However, the comparison between these studies is difficult due to differences in recording equipment as discussed below.

A. Between and within species variation

Boto whistles differ from tucuxi whistles in all their acoustical parameters. As shown in Fig. 4, botos produced

TABLE II. Descriptive statistics for each behavioral class for a total of 121 whistles recorded in relation to their behavioral context (there were not significant differences for any of these parameters across behaviors).

Parameters	Feeding (n=32)	Resting (n=21)	Slow Traveling (n=68)
Min F (kHz)			
(mean±SD)	14.48±4.95	14.59±4.66	14.56±4.39
Range	6.56–21.22	6.26–23.10	5.30–26.44
CV%	28.0	32.0	30.2
Max F (kHz)			
(mean±SD)	25.25±9.28	22.84±6.97	25.03±8.36
Range	11.83–43.68	12.76–41.72	10.88–48.06
CV%	36.8	30.5	33.4
Delta F (kHz)			
(mean±SD)	10.84±7.84	8.25±6.48	10.47±6.77
Range	3.82–28.24	2.99–30.35	2.94–34.40
CV%	72.3	78.6	64.7
Start F (kHz)			
(mean±SD)	22.79±9.06	22.15±7.14	24.43±8.68
Range	11.83–43.68	12.76–41.72	9.77–48.06
CV%	39.7	32.2	35.5
End F (kHz)			
(mean±SD)	16.85±7.85	15.62±5.21	14.80±4.50
Range	7.06–42.98	6.26–26.85	5.30–27.34
CV%	46.6	33.3	30.4
Peak F (kHz)			
(mean±SD)	17.95±4.95	16.15±5.80	18.49±5.75
Range	7.81–27.34	3.22–26.86	6.35–33.69
CV%	27.6	35.9	31.1
Duration (s)			
(mean±SD)	0.006±0.007	0.008±0.008	0.010±0.014
Range	0.002–0.039	0.002–0.039	0.002–0.080
CV%	111.5	103.4	129.4

higher frequency whistles. These whistles are more limited in their contour diversity (95.8% of the whistles were down-sweep) than tucuxi whistles (and those of most other dolphins). Several factors have been proposed to explain interspecific whistle variation including: morphological constraints (Wang *et al.* 1995a, Matthews *et al.* 1999), environment (Wang *et al.* 1995a), sociality (Podos *et al.* 2002), zoogeographical relationships (Steiner 1981), and phylogenetic relationships (Steiner 1981, Wang *et al.* 1995a).

Body size is the most important morphological factor believed to influence signal frequency in animals (Marquet and Taper 1998). Overall, the larger the animal the lower frequency sounds it tends to produce. This is because body size and the size of sound producing organs are often correlated (Fletcher 1992). Some authors (e.g., Wang *et al.* 1995a, Podos *et al.* 2002) have proposed a similar relationship between body size and maximum frequency. However, in the case of cetaceans a recent study showed that when accounting for phylogeny the proposed relationship between body size and maximum frequency disappears (May-Collado *et al.* in press). Thus the fact that botos (~2.6 m, 160 kg) can produce much higher frequency whistles than the smaller tucuxis (~1.52 m, 40 kg) is not counter to any general rule.

It is unlikely that whistle variation is explained by differences in habitat acoustic structure since both species live in very similar environmental conditions. Another proposed factor to explain interspecific whistle variation is zooge-

graphical relations. Steiner (1981) suggested “the degree of differences in the whistle vocalizations among (five dolphin) species closely followed predictions based on classic allopatric/sympatric relations among species.” This idea is congruent with the “species recognition hypothesis” (see Sætre *et al.* 1997) that states that animal vocal acoustic structure has evolved “to” reduce hybridization. Unfortunately, there is very little quantitative information of the extent to which botos and tucuxis are allopatric and sympatric at both spatial and temporal scales to test this idea.

Botos and tucuxis are not closely related (e.g., Hamilton *et al.* 2001, May-Collado and Agnarsson 2006) which could largely explain their differences in whistle structure. However, there is recent evidence that social structure (or at least some components of sociality) could also explain part of this variation. For instance, differences in whistle contour and frequency and time parameters of the distantly related spinner and bottlenose dolphins (e.g., Hamilton *et al.* 2001, LeDuc *et al.* 1999, May-Collado and Agnarsson 2006) have been largely explained in terms of “group fluidity” (a component of sociality) (Barzúa-Durán 2004). Botos and tucuxis are not only more distantly related but also differ even more radically in their social structure. While botos appear to be solitary (Best and da Silva 1993) or at least live in small nonstructured groups (where the strongest social bond appears to be limited to mother and calf) (e.g., Aliaga-Rossel 2002; McGuire and Winemiller 1998), *Sotalia spp.* lives in

TABLE III. Whistle acoustic structure described for each recorded single animal and group.

Groups	Min F (kHz)	Max F (kHz)	Delta F (kHz)	Start F (kHz)	End F (kHz)	Peak F (kHz)	Duration (s)	No. of whistles	No. individuals present	Group composition
G1 Mean±SD	17.20±2.48	30.23±8.28	13.04±7.62	29.63±9.27	17.80±2.60	23.43±4.56	0.006±0.007	6	1	Adult ^a
Range	13.90–20.04	19.71–38.60	3.62–23.27	16.10–38.60	13.9–20.04	17.58–27.34	0.002–0.019			
C.V.%	14.4	27.4	58.4	31.3	14.6	20.0	111.8			
G2 Mean±SD	14.44±4.18	23.68±8.93	9.24±7.56	23.44±9.13	14.53±4.01	17.32±4.69	0.005±0.003	23	3	Adults
Range	7.18–24.90	11.83–43.68	3.82–28.02	11.83–43.68	7.44–21.22	7.81–24.90	0.002–0.017			
C.V.%	27.1	37.7	81.8	38.9	27.6	27.1	76.0			
G3 Mean±SD	16.08±5.03	26.95±7.82	10.87±7.72	26.37±8.22	16.19±5.11	19.03±6.6.30	0.009±0.015	33	4	3 Adults 1 calf ^b
Range	5.30–26.44	12.58–48.10	2.94–34.39	9.77–48.07	5.30–27.34	3.22–27.83	0.002–0.080			
C.V.%	31.1	29	71.0	31.2	31.6	33.1	156.9			
G4 Mean±SD	14.60±3.22	24.36±6.40	9.77±4.47	24.36±6.40	14.60±3.22	18.80±4.85	0.004±0.002	8	3	2 Adults 1 Juvenile ^c
Range	7.43–17.68	12.07–33.14	4.64–18.14	12.07–33.14	7.43–17.68	9.76–24.41	0.002–0.007			
C.V.%	22.1	26.3	45.7	26.3	22.1	25.8	43.1			
G5 Mean±SD	14.53±3.72	24.39±9.84	9.84±7.89	23.80±10.17	14.66±3.76	17.94±6.35	0.008±0.009	12	3	2 Adults 1 Juvenile
Range	7.85–18.31	10.88–41.44	2.99–25.02	10.84–41.44	7.85–18.31	8.79–33.69	0.002–0.030			
C.V.%	25.6	40.4	80.2	42.7	25.7	35.4	116.2			
G6 Mean±SD	8.92±3.48	16.20±4.07	7.28±1.07	16.03±4.15	8.92±3.48	11.28±3.52	0.026±0.014	9	1	Adult
Range	6.53–17.80	14.13–27.01	6.02–9.21	13.67–27.01	6.53–17.80	7.81–19.53	0.002–0.046			
C.V.%	39.0	25.1	14.8	25.9	39.0	31.2	54.4			
G7 Mean±SD	13.84±4.10	27.89±9.81	14.05±8.09	19.17±6.48	22.56±13.40	18.30±5.35	0.012±0.012	7	2	1 Adult 1 calf
Range	7.06–18.87	13.98–42.99	6.93–28.24	13.98–29.92	7.06–42.99	10.90–21.41	0.002–0.039			
C.V.%	29.6	35.2	57.6	33.8	59.4	29.3	105.3			
G8 Mean±SD	13.83±2.11	21.83±2.36	8.0±2.44	20.51±2.87	14.93±2.22	18.42±2.58	0.010±0.011	7	2	Adults
Range	11.71–16.66	17.11–24.39	4.01–10.98	16.11–23.44	12.7–18.55	14.65–22.95	0.003–0.033			
C.V.%	15.3	10.8	30.6	14	14.9	14	111.9			
G9 Mean±SD	13.98±3.17	26.63±8.06	9.65±7.76	22.63±8.31	15.25±4.51	17.14±4.39	0.007±0.003	13	2	1 Adult 1 calf
Range	9.12–19.60	17.11–41.72	3.45–30.35	16.11–41.72	9.12–26.85	11.23–26.86	0.002–0.012			
C.V.%	22.7	34.1	80.4	36.7	29.6	25.6	45.3			
G10 Median±SD	17.27	34.10	17.98	27.85	23.51	23.9320.51–	0.006	2	2	1 Adult 1 calf
Range	15.53–19.01	28.02–40.18	14.78–21.17	15.53–40.18	19.01–28.02	27.34	0.004–0.008			
C.V.%	14.2	25.2	25.2	62.6	27.1	20.2	47.1			
G11 Mean±SD	12.51	17.66	5.15	16.11	17.66	12.51	0.008	1	1	Adult
Range			
C.V.%			

^aAdult is defined as full sized individuals.

^bCalf is defined as an individual that is less than half the adult's size.

^cJuvenile defined as an individual larger than a calf but not as big as an adult.

structured social groups (Monteiro-Filho 2000). Additionally, May-Collado *et al.* (submitted B) found that whistle complexity—a concept based on whistle mean number of inflection points—may be influenced by group size and social structure (two components of sociality). More specifically, they found that simple whistles (mean number of inflection points equal or below one) were particularly concentrated in “solitary” species while the phylogenetic distribution of complex whistles and social species largely overlap.

Although boto dolphins from the Yasuní River produced whistles with frequency parameters that appear to be far above (5.30–48.10 kHz) the values reported by Wang *et al.* (1995a, 2001) in botos from the Marañon and Tigre Rivers in Peru (0.22–5.16 kHz) and by Diazgranados and Trujillo (2002) in the Orinoco River (3–13 kHz) (Table I) comparisons cannot be done at this point. This is due in part to differences in the recording systems maximum frequency limitations (up to 25 kHz), to the lack of information on several standard acoustic parameters (Diazgranados and

Trujillo (2002), and the uncertainty regarding the assignment of the low frequency whistles to boto dolphins (Wang *et al.* 1995a, 2001). Therefore, until we have full frequency range recordings from other botos populations, comparisons are difficult and speculative.

We limit this part of the discussion to the observed differences among “groups” (note that several of the groups consisted of only one individual) where with the exception for delta frequency, whistle acoustic parameters vary significantly across groups (Table III). In most delphinids within species variation is primarily in duration and modulation (e.g., Wang *et al.* 1995b, Morisaka *et al.* 2005a, 2005b, Barzúa-Dúran and Au 2002, 2004) rather than in frequency as observed in this boto population (also see Azevedo and Van Sluys 2005, Rossi-Santos and Podos 2006 for *Sotalia guianensis*). In part, this variation has been explained as product of adaptation to local ecological conditions (e.g., ambient noise, see Morisaka *et al.* 2005b). It is unlikely that the among group whistle differences observed in this boto population are explained by contrasting habitat acoustic

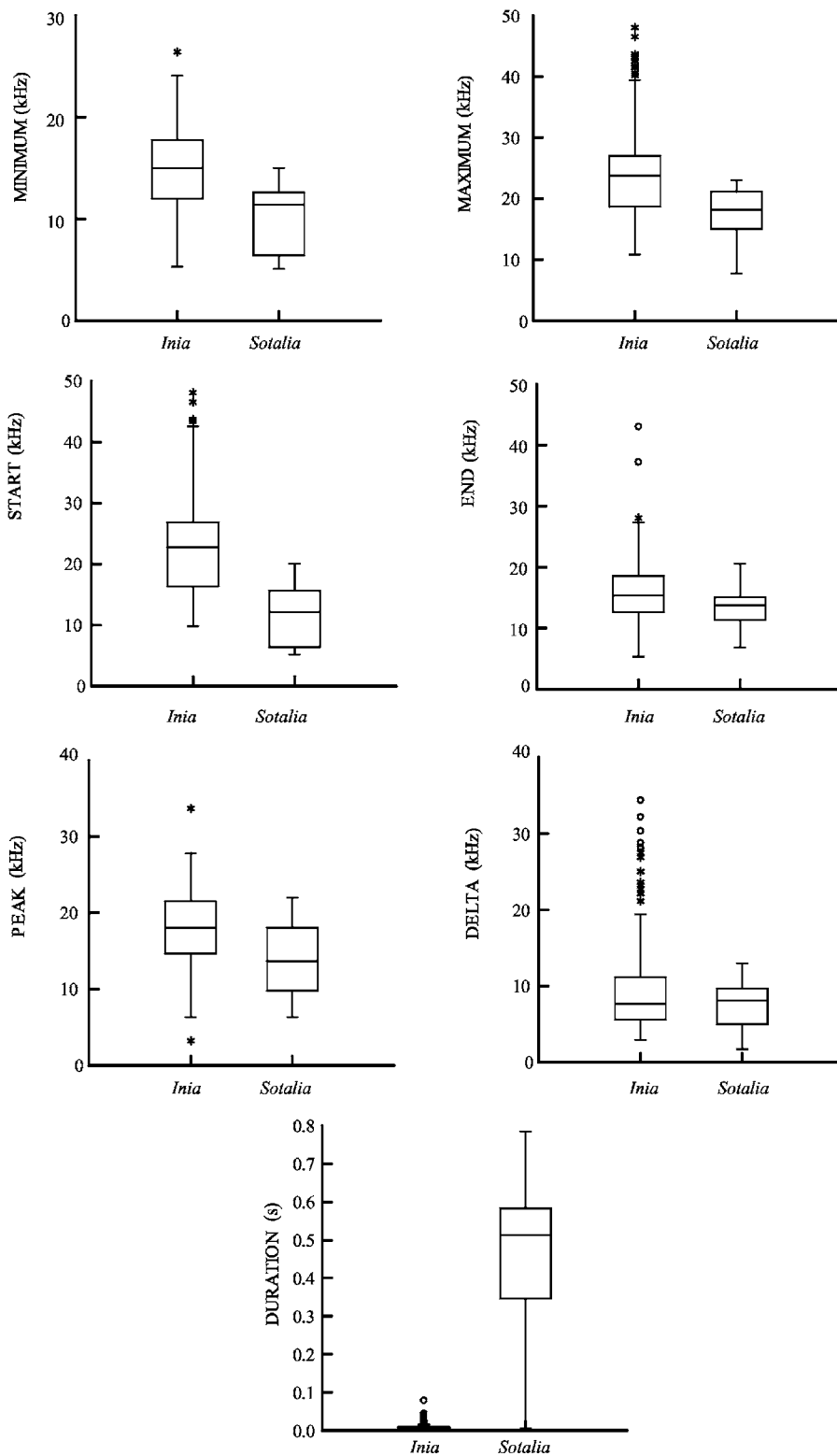


FIG. 3. Distribution of whistle acoustic parameters as a function of dolphin species where * and ° represent outside and far outside values of the 50% central tendency (*Inia*=121 whistles, *Sotalia*=33 whistles).

characteristics alone, since recorded single animals and groups were in the same environment. Furthermore, age composition and behavioral states appear not to influence whistle variation either. However, our sample size is too small and geographically restricted to conclude age and behavior does not have some influence on boto dolphin whistles acoustic structure. In addition to these two factors, others such as genes, gender, and overall inter-individual variation, merit further study.

B. Behavior and communication

Diazgranados and Trujillo (2002) reported that boto whistles were produced within groups that engaged in social and feeding activities. Half of the whistles produced by the botos in this study occurred during traveling activities, but when accounting for time of the encounter and number of individuals present, whistle production was higher during resting activities. In addition, whistles were produced by both solitary and grouped animals.

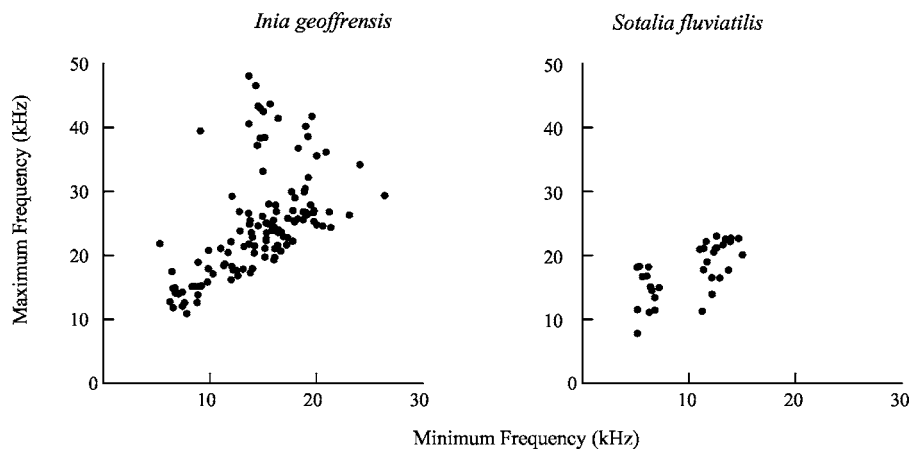


FIG. 4. Plot of maximum versus minimum frequency of all recorded whistles for each species (*Inia*=121 and *Sotalia*=33 whistles).

The closest neighbor maximum distance was found at approximately 0.15–1.5 km, suggesting these animals might be still in acoustic contact. Because of the behavioral context at which most whistles were emitted and the low whistle production, it is possible that whistles in boto dolphins may be used to keep distance between animals, rather than promote social interactions or cohesion among individuals as it occurs in delphinids (e.g., Jones and Sayigh 2002). Assuming cylindrical spreading loss and freshwater absorption at the mean maximum frequency, the boto whistles could propagate as far as 3.3 km before falling below the ambient noise although the actual range will be less depending on channel depth, bottom type, and vegetation (Quitana-Rizzo *et al.* 2006). Wang *et al.* (2006) assuming spherical spreading losses estimated that *Lipotes vexillifer* low frequency whistles (with dominant frequency 5.7 kHz) could propagate in a very calm environment up to 6.6 km, but possibly only 22–220 m considering the noisy conditions of the Yangtze River. The Yasuní River is a very calm environment; unlike the Yangtze River, it is protected and boat traffic is limited to park rangers and scientists.

During the period of this study botos produced whistles randomly and not in bouts as many delphinids species. Based on our data it appears that boto dolphins in Yasuní whistle rarely. Our sample size is too small not only to clearly associate these sounds with the same social contexts as in delphinids but also to determine how frequently botos and other riverine dolphin species generally whistle. Nevertheless, confirming the presence of whistles in botos and other freshwater toothed whales helps illuminate the evolutionary history of whistles, and their relation to sociality—a factor proposed to have shaped the complexity of toothed whale whistles (May-Collado *et al.* submitted B).

V. CONCLUSIONS

This study confirms whistles in the solitary freshwater dolphin *Inia geoffrensis geoffrensis*. The frequency range of boto whistles we document is among the greatest ever reported in a cetacean species. The acoustic structure of these whistles in Ecuadorian botos differs from that of the sympatric *Sotalia fluviatilis* and apparently from conspecific populations from Perú and Colombia. Differences in the acoustic structure of boto and tucuxi whistles may be in large prod-

uct of their distant phylogenetic relationships and their different social structure. Although our study suggests remarkable whistle variation between populations, this may be largely a product of limited recording systems used by previous studies. Finally, although the use of whistles for communication purposes has been largely attributed to social dolphin species, it is possible that botos (even solitary animals) use them to communicate but in the context of keeping distances among animals rather than to promote group cohesion. We propose this based on two observations (1) whistles were produced when the animals were engaged in resting activities, and (2) based on the fact that solitary animals were potentially within acoustic range of each other (estimated maximum of 3.3 km). Finally, better understanding of whistle production in solitary freshwater species will further understanding of the evolutionary history of whistles and their proposed association with sociality.

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