

Gender, Age, and Identity in the Isolation Calls of Antillean Manatees (*Trichechus manatus manatus*)

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Abstract

Empirical evidence of individual vocal recognition has been reported for the Amazonian manatee (*Trichechus inunguis*) and the West Indian manatee (*T. manatus*). Underwater vocalizations of 15 Antillean manatees (*T. m. manatus*) were recorded to verify if this subspecies also conveys individual information through their calls. The isolation calls selected for analysis were digitized to measure eight different variables. Individual vocal patterns were analyzed within two age classes (calves and others) and between sexes. Discriminant function analysis for each age class grouped vocalizations by individual, based on variables related to the fundamental frequency and call duration. Female calls were longer in duration and presented a higher fundamental frequency but lower peak frequency values than males. Calves had significantly higher values for all eight acoustic variables measured with respect to frequency and time. Higher values for all frequency parameters in calf calls and the inverse relationship between total body length and peak frequency suggests that younger, smaller animals emit higher frequency sounds. Furthermore, higher values obtained for the fundamental frequency range of calves and the inverse relationship of this variable with total body length suggest that the fundamental frequency becomes more defined as the animal ages. Vocal learning and genetic inheritance are discussed based on the analyses of vocal patterns among related individuals. In addition to facilitating individual recognition as a possible factor in Antillean manatee social interactions, vocal identity provides a potential means of estimating the size and structure of sirenian populations.

Key Words: Sirenia, manatee, *Trichechus manatus manatus*, calls, sounds, vocalization, gender differences, age differences, vocal identity, communication

Introduction

The West Indian manatee was split into two subspecies: (1) the Florida manatee (*Trichechus manatus latirostris*) and (2) the Antillean manatee (*T. m. manatus*) (Domning & Hayek, 1986). This division has since been questioned by evidence from mitochondrial DNA haplotypes shared between the Florida manatee population and populations from the Greater Antilles, which are considered to be part of the Antillean manatee subspecies (Garcia-Rodriguez et al., 1998). More recently, Catanhede et al. (2005) and Vianna et al. (2006) proposed that *T. manatus*, the West Indian manatee, is a paraphyletic species.

These taxa and other sirenian species may present identity information in their calls. Vocal signature information and individual recognition has already been documented in Amazonian manatees (*T. inunguis*) (Sousa-Lima et al., 2002). Additional evidence stems from individual vocal differences in dugongs (*Dugong dugon*) (Anderson & Barclay, 1995) and individual vocal recognition between a mother and calf pair of Florida manatees that had been physically separated (Reynolds, 1981). Florida manatee vocalizations function to assist mothers and calves in locating and maintaining contact with each other (Hartman, 1979) and also may have the potential for conveying identity information.

Animal communication signals are often accompanied by information about the sender such as motivation, sex, age, or identity (Halliday & Slater, 1983). Such information presumably benefits both parties (sender and receiver), and the acquisition

of these benefits is the function of the exchange (Bradbury & Vehrencamp, 1998). Therefore, if a signal that conveys information about gender, age, or identity of an individual is mutually beneficial, and no other means of recognition is reliable, selection should act to enable individuals to discriminate among such attributes. Selective forces to identify and locate specific individuals, particularly offspring, are typically strongest in colonial species because the probability of misdirecting parental care increases when many offspring are present (e.g., in bats, *Nycticeius humeralis*; Scherrer & Wilkinson, 1993).

Despite the relatively recent large-scale reductions in numbers throughout their range (Lima, 1997), Antillean manatees were once abundant, and groups of over 300 individuals were observed along the Brazilian coast (Whitehead, 1978). Florida manatees were thought to breed year-round with a slight birth peak in spring (Hartman, 1979), but more recently Rathbun et al. (1995) reported that Florida manatees have a more pronounced calving peak between April and May. In Brazil, the Antillean manatee calving season occurs between October and March (Lima, 1997; Paludo & Langguth, 2002). Manatees have low reproductive rates and high maternal investment—that is, long gestation, high birth weights, single offspring (twins are rare), and extended maternal care (O'Shea & Reep, 1990; Rathbun et al., 1995; da Silva et al., 2000, in press). Therefore, it is reasonable to assume that there is selective pressure on mothers to nurse their own calves, rather than other calves implying that there is an adaptive advantage to individual recognition ability.

Recognizing and maintaining contact with specific individuals may be more challenging when the animals are often physically separated and adequate visual contact is not possible. The existence of individual information and/or the capacity for individual recognition has been reported in sounds produced by other marine mammals in which mothers and offspring are often separated and reunited such as in pinnipeds (Insley et al., 2003). Manatees typically inhabit turbid waters (Moore, 1951). In Brazil, Antillean manatees are observed in feeding aggregations around river mouths (Paludo & Langguth, 2002), and their tendency to wander while foraging causes unintentional separations between mothers and calves, thus favoring the location and recognition of individual calves through sound rather than visually (Hartman, 1979; Reynolds, 1981; Sousa-Lima et al., 2002).

In addition to individual identity, social recognition (i.e., age, gender, and reproductive status) might be a possible function of sirenian calls. Although mature male dugongs develop tusks, there is no apparent sexual dimorphism in manatees. The

role of vision and olfaction in the reproduction of fully aquatic mammals, such as sirenians, is limited by the environment and should only be effective at short ranges. The aquatic environment favors the dispersal of mates in space and an increased reliance on acoustical cues for mate location (Anderson, 2002), recognition, and choice.

The recognition process begins with the emission of unique and stereotyped signals by the sender. Herein we predict that the underwater isolation calls of Antillean manatees will show variations that can be attributed to individual, stereotyped differences as well as gender and age information.

Materials and Methods

Underwater sounds from eight male and six female Antillean manatees were recorded at the facilities of the Centro Mamíferos Aquáticos/IBAMA (CMA), a governmental research center located on Itamaracá Island in the northeastern state of Pernambuco, Brazil. Additionally, one rehabilitated and reintroduced female was recorded in an estuarine lagoon located on the southern coast of Maceió City, state of Alagoas, Brazil. Identification information for the animals recorded in this study is given in Table 1. The study animals were mostly newborn, stranded calves that had been rescued and taken to CMA. Individuals younger than 3 y old were considered calves based on the estimated inter-birth interval of 3 to 5 y (da Silva et al., in press) and on direct evidence from the Amazonian species in which weaning takes place after 2 y of age (da Silva et al., 2000).

There were two large pools at CMA (10.1 m in diameter, 4.15 m in depth, and capacity for 400,000 l of water each) connected by a smaller pool (4.45 × 4.1 × 1.2 m and capacity for 20,000 l) where adults and a few calves were maintained. Most calves were kept in another smaller pool (8.0 × 5.0 × 1.5 m and capacity for 96,000 l). Two other small pools were used for isolating calves: a round one (3.0 × 0.8 m) and a rectangular one (4.0 × 2.0 × 0.9 m) with 7.8 and 8.0 m³ of water capacity, respectively.

Two age classes (calves and others) were considered in the analysis because distinguishing adults from subadults based on size is too arbitrary (Hartman, 1979). Individual adults and subadults were isolated in one of the main pools, while calves were transferred on a stretcher to the smaller pools, which were completely isolated during recordings. Individuals were isolated for 25 min to ensure that the sample of recordings from all individuals was taken in a similar context. Animals could not be kept in isolation any longer for ethical reasons, thus limiting the number of

Table 1. Identification of the Antillean manatees recorded in Brazil

Individual	Sex*	Age class♦	Origin (location/state)¶	Body length (cm)	Calls analyzed
Tibau	M	C	Tibau do Norte/RN	159	10
Xiquito	M	C	CMA – Xica’s calf	167	10
Sheila	F	C	CMA – Sereia’s calf	178	10
Boi Voador	M	C	São Luis/MA	182	10
Carla	F	C	CMA – Sereia’s calf	180	10
Araqueto	M	C	Aracati/CE	190	10
Guaju	M	C	Sagi/RN	199	10
Guape	M	C	Coqueirinho/PB	208	10
Poque	M	O	Oiapoque/AP	215	10
Lua	F	O	Morro Branco/CE	240	10
Marbela	F	O	Pipa/RN	252	10
Xuxa	F	O	Morro Branco/CE	266	10
Xica	F	O	Goiana/PE	271	8
Netuno	M	O	Sagi/RN	285	10
Sereia	F	O	Barro Preto/CE	280	5

* M = male; F = female

♦ C = calf; O = other (subadult or adult)

¶ CE: Ceará; MA: Maranhão; CMA: Centro Mamíferos Aquáticos; RN: Rio Grande do Norte; PB: Paraíba; AP: Amapá

suitable vocalizations acquired for analysis. A canoe was used to transport the necessary equipment and to approach the reintroduced animal which was recorded in the wild (Lua; see Table 1) for 3 h at a distance of 5 m. This reintroduced animal was recorded when it was by itself; therefore, no recordings of calls emitted in a social context in the wild were obtained. Captive animals were recorded in two different social contexts, however: (1) in isolation (25 min per individual) and (2) during conspecific interactions (approximately 5 h of recordings in each pool).

Recordings were made using a Sony Walkman Pro (WM-D6C; flat audio frequency response 40 to 15,000 Hz \pm 3 dB) and an omnidirectional hydrophone (Cetacean Research Technology Model 50Ca) with a sensitivity of -161 dB re: 1 μ Pa and a frequency range response of 0.01 to 310.0 kHz. Analyzed calls were chosen based on a high signal-to-noise ratio and on their occurrence in a similar behavioral state (swimming). Analog recordings were digitized at a sample rate of 44,100 Hz; sample size 16 bits. A maximum of 10 sounds per individual were randomly selected; some individuals did not vocalize enough to use a larger sample size (see Table 1). Each sound was analyzed using *Canary 1.2.1* software (Charif et al., 1995), with a filter bandwidth of 699.40 Hz and a frame length of 256 points. The duration and frequency were measured from the most intense harmonic that was clearly visible along the length of the signal. We then divided the frequency measurements by the appropriate factor (number of the harmonic) to yield the value of the fundamental frequency.

We measured eight acoustic variables from the recordings and six of them (listed in Table 2) were used to perform two discriminant function analyses (DFA), one for each age class, to test for differences in individual vocal patterns. The variables “fundamental frequency range” and “harmonic with most energy” were excluded from the DFA because they did not conform to the test’s assumptions (they were linear combinations of other variables). In both DFAs, sounds from each individual were treated as a group (Manly, 1994).

Two separate nested multi-way analyses of variance (MANOVA), using all eight measured variables (Table 3), were performed to test for differences in the vocal pattern between sexes and between age classes. In each analysis, the individual vocalizations were nested by sex and age classes. This procedure removes the effect of the differences between individuals from the main factors (sex and age classes).

The mean values of the variables from each individual were incorporated into a linear regression to examine the correlation between total body length and each of the eight vocal variables (Sokal & Rohlf, 1995).

Results

Vocal Repertoire

Two sound types, clicks and vocalizations, were identified for this species (Figures 1 & 2). The broadband click sounds had dominant frequencies between 1.0 to 4.0 kHz, with energy as high as 20.0 kHz. This sound type was recorded in all contexts observed,

Table 2. Factor loading of each variable on the two canonical functions of the discriminant function analysis; the variables with highest loading are highlighted.

Variable	Calves		Others	
	Function 1	Function 2	Function 1	Function 2
Signal duration	0.0075	-0.8661	-0.0869	0.8966
Number of harmonics	-0.4471	-0.0805	0.3174	0.3723
Mean fundamental frequency	0.8028	-0.2034	-0.9065	-0.2567
Maximum fundamental frequency	0.4104	-0.0256	-0.4659	0.0494
Minimum fundamental frequency	0.4503	0.0914	-0.3859	-0.1586
Peak frequency	-0.0684	0.0847	0.0223	0.2856
Statistics				
Cumulative probability	0.766	0.937	0.865	0.934
Wilk's λ	0.001	0.03	0.005	0.118
X ²	495.3	252.8	288.9	118.6
df	42	30	36	25
<i>p</i>	<0.001	<0.001	<0.001	<0.001

sometimes, but not always, in association with the vocalizations (e.g., Figure 1: O & Figure 2).

In addition to the clicks, the vocalization repertoire was a continuum, ranging from relatively simple sounds with a clear harmonic structure to more complex sounds with a noisy, harsh quality that is comprised either by a combination of harmonic and nonharmonic (e.g., noisy, nonlinear, chaotic) frequency components or by broad frequency bands (e.g., Figure 1: M). Nonharmonic, chaotic components occurred in the beginning, at the end, or throughout the entire signal, although this asynchrony in the frequency bands is mainly observed at the beginning and end of the signal (Figure 1: H, N, O, Q & R). All individuals emitted nonharmonic and harmonic calls and, due to the relative ease of taking measurements from the sounds with clear harmonics, those were the ones explored further in this study.

The vocalizations had only one component with a mean duration of 353 ± 78 ms, ranging from 180 to 480 ms, with both amplitude and frequency modulation. The mean frequency variation (maximum-minimum fundamental frequency) was 0.97 ± 0.50 kHz. The majority of vocalizations recorded began with ascending frequency modulation and ended with descending frequency modulation, although some individuals varied in that respect and can have different modulation features in their calls (Figure 1: N-U). The mean fundamental frequency of these vocalizations was 2.45 ± 0.50 kHz, with peak frequencies ranging from 3.7 to 5.7 kHz. In many cases, several harmonics were more intense than the fundamental (Figure 1).

Individual Stereotypy

Each individual had a single type of clear harmonic isolation call with some degree of variation.

Intraindividual variation is illustrated in the spectrograms (Figure 1) and also in the spread of the symbols representing each individual in the plot of the first two discriminant functions or axes (Figure 3). Calves and noncalves are plotted separately in Figure 3 to enable better visualization of the data ordination due to considerable overlap, mainly in the second axis. The ordination of the six variables separates individuals even though there is great intraindividual variation and overlap between the vocal patterns of some individuals. The first two discriminant functions explained more than 93% of the common variance in the calls for both age classes. Table 2 shows that, for both age classes, the first discriminant function is highly correlated with the mean fundamental frequency and the second highly correlated with signal duration. Note that some overlapping individuals, such as Carla and Sheila (Figure 3a), are twin sisters. Figure 1 (N-Q & R-U) also illustrates the similarities among the calls of these two individuals. In the DFA with all individuals (not presented here due to difficulty in visualization in 2D), another case of overlap between the vocal patterns of kin arose: between a mother and calf pair, Xiquito (Figure 3a) and Xica (Figure 3b).

Age and Sex Discrimination

There were significant differences in the acoustic parameters of vocalizations between sexes and age classes (Table 3). Calves presented higher values for all the acoustic variables except in the number of harmonics. Females had higher values for signal duration and mean, maximum, and minimum fundamental frequencies compared to males, but they presented fewer harmonics and a lower mean peak frequency. No significant difference in fundamental frequency range between males and females was observed.

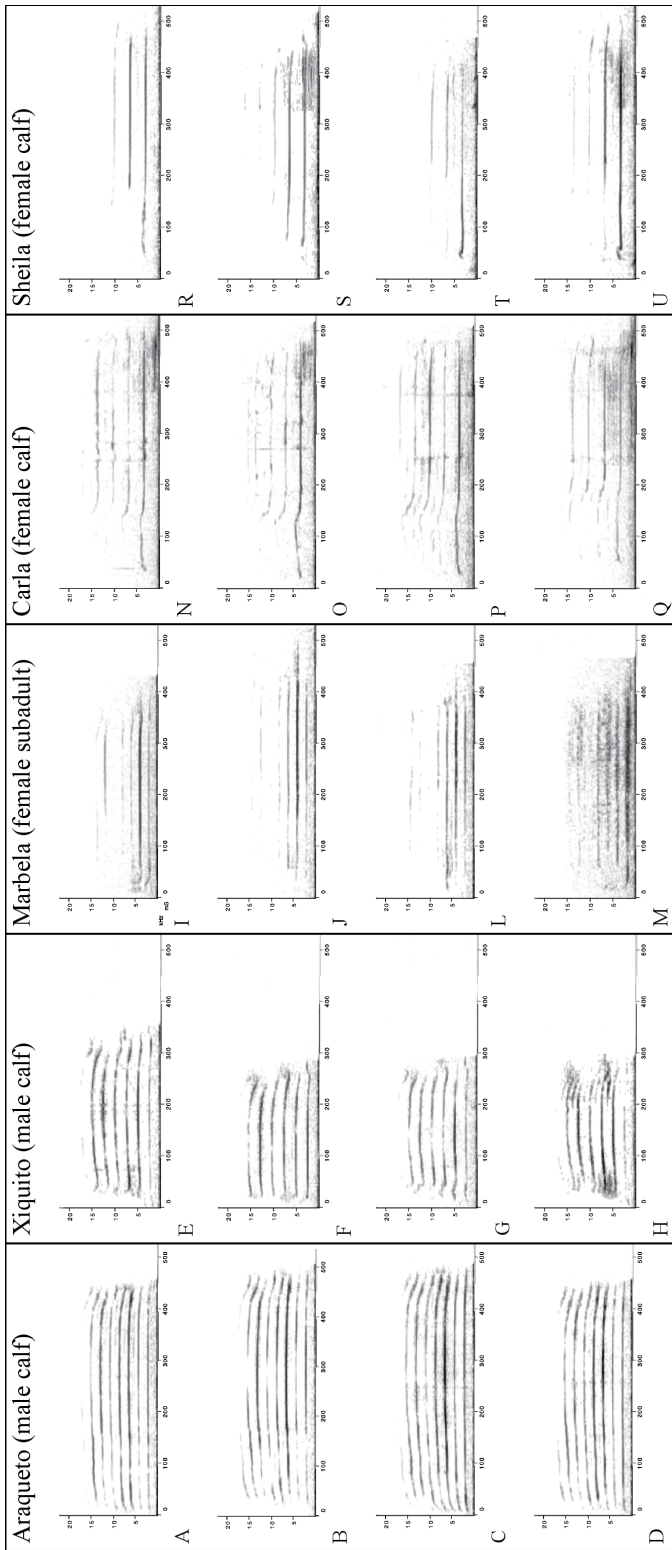


Figure 1. Four examples of isolation call spectrograms from five different Antillean manatees; time on the X axis (0 to 500 ms) and frequency on the Y axis (0.0 to 20.0 kHz). “Carla” and “Sheila” are twin sisters; note their calls’ similarity.

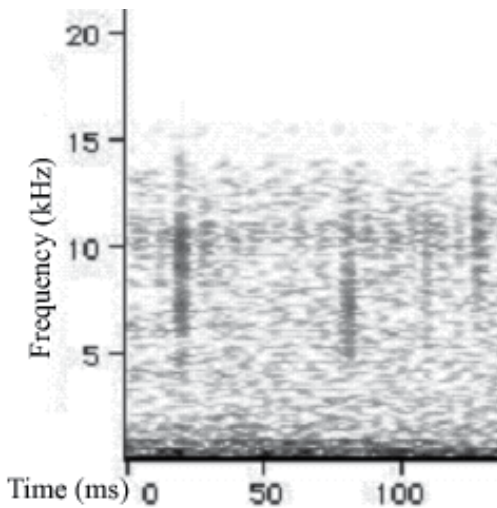


Figure 2. Example of clicks produced by Antillean manatees

Significant inverse relationships were found between total body length and both the fundamental frequency range ($F_{1,13} = 5.49$; $r = -0.54$; $p = 0.038$) and the peak frequency ($F_{1,13} = 9.03$; $r = -0.65$; $p = 0.008$) (Figures 4 & 5).

Discussion

Sound Repertoire

Sound analysis and description can be a very subjective exercise. For example, some authors measure slightly different things such as mean fundamental frequency vs the absolute value of the fundamental frequency at some point along the duration of the call. Thus, in order to avoid further artifacts, we made our comparisons by using only quantitative data provided in the literature.

Our data on the Antillean manatee vocal repertoire adds to the data gathered by Sonoda & Takemura (1973) and Nowacek et al. (2003). The first authors recorded two captive Antillean manatees and found “click-like,” “frog-like,” and “multi-layer” vocalizations and described clicks as very short signals with a main frequency range from 2.0 to 7.0 kHz. We recorded clicks that reach peak frequencies up to 14.0 kHz (Figure 2). Nowacek et al. (2003) recorded several individuals and did not report clicks in wild manatees. Clicks and vocalizations have also been recorded in semi-captivity in Brazil (approximately 250 h of recordings by Sousa-Lima, unpub. data). There is no information about how the click sounds described for this species are produced. Although speculative, we believe that the click sounds may be generated by teeth movements rather than by a specific anatomical structure as in cetaceans (Cranford et al., 1996).

Sonoda & Takemura’s (1973) “frog-like” and “multi-layer” vocalizations are similar to the calls recorded by Nowacek et al. (2003) and those in Figure 1. Sonoda & Takemura (1973) indicated durations of less than 200 ms and a main frequency range of 2.0 to 4.0 kHz, while a more recent paper describing these vocalizations (Nowacek et al., 2003) indicates a wider range for the duration (32 to 217 ms). The shortest call recorded in Brazil was 110 ms (Sousa-Lima, 1999), and the duration limits we found in this study were 180 to 480 ms. To summarize, taking account of all the information available, Antillean manatee vocalizations have durations as short as 32 ms (Nowacek et al., 2003) and as long as 480 ms (this study).

The range of the fundamental frequency reported here (1.07 to 4.98 kHz) is consistent with the data available in the literature (Sonoda & Takemura, 1973; Nowacek et al., 2003). The mean peak frequency range (3.7 to 5.7 kHz) was also consistent with the range (3.18 to 7.08 kHz) reported by Nowacek et al. (2003). To our knowledge, no other data have been published on the repertoire of Antillean manatees, and there are no obvious differences in the vocalizations produced by manatees from Florida and Belize (Nowacek et al., 2003). Additionally, *T. manatus* is considered a paraphyletic species (Catanhede et al., 2005; Vianna et al., 2006); therefore, we also examined the data available for manatees from Florida.

Steel (1982) reported duration limits of 80 to 470 ms for Florida manatees, while Schevill & Watkins (1965) found limits of 150 to 500 ms. Fundamental frequency values are very similar between our study and that of Steel (1.08 to 5.00 kHz). Schevill & Watkins reported a lower limit for the fundamental frequency (0.6 kHz). Peak frequencies range from 1.0 to 12.0 kHz (Steel, 1982). No click-like sounds have been reported for the Florida manatee. Despite differences in measurement methods and populations, we can reasonably conclude that West Indian manatees have vocalizations that range from 32 to 500 ms in duration, with a fundamental frequency of 0.6 to 5.0 kHz and peak frequencies ranging from 1.0 to 12.0 kHz.

It is not yet clear how the nonharmonic frequency bands in the vocalizations are produced and, in some cases, there is a suggestion of two different sources of sound production (Figure 1: N, R & S) (also noted by Mann et al., 2006). Manatees (both the Antillean and the Amazonian species) contract the muscles dorsal to the maxilla and caudal to the nostrils while maintaining the nostrils closed when vocalizing (Sousa-Lima, pers. obs.). It is possible that the contraction of those muscles (probably the naso-labial or the maxillo-labial muscles described for West African manatees [*T. senegalensis*] by Saban, 1975) might

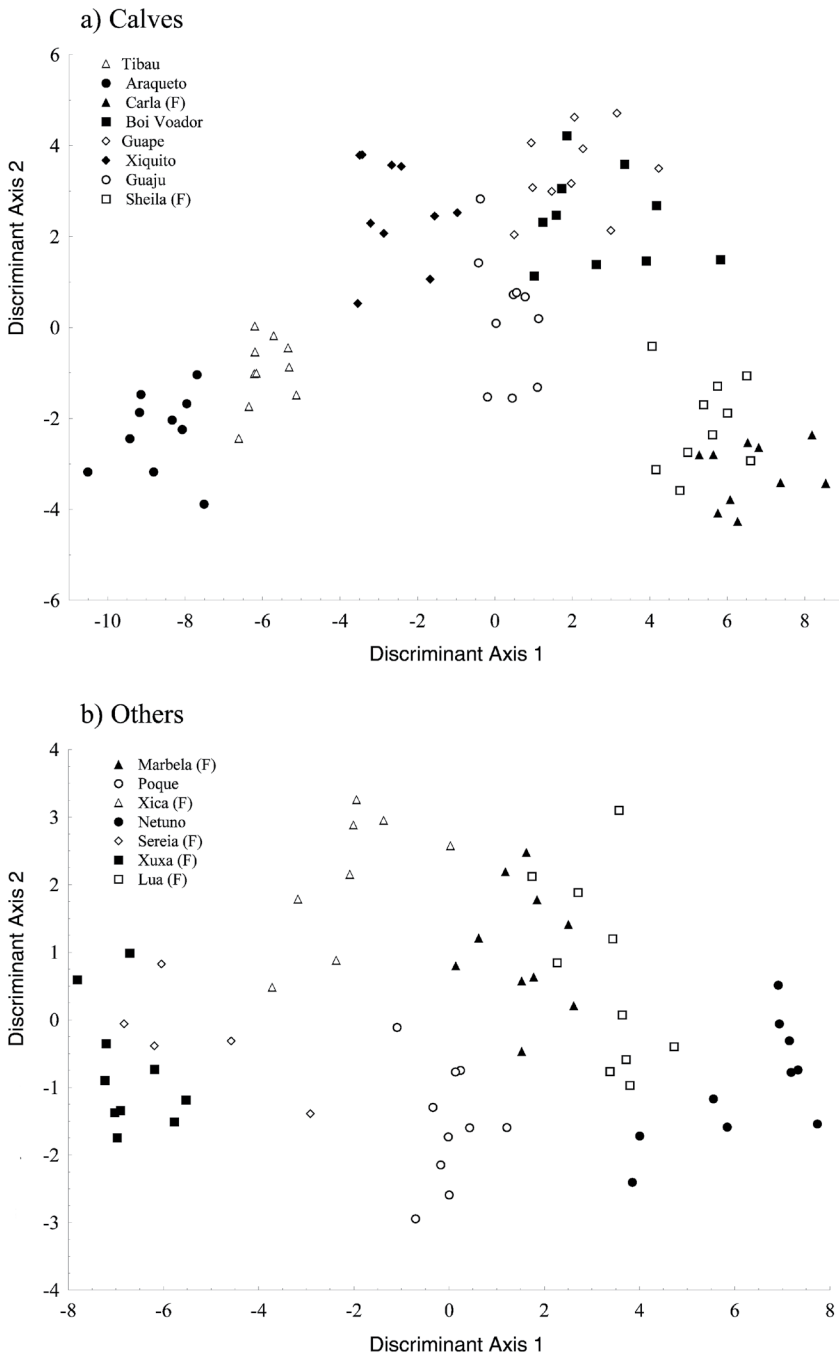


Figure 3. Plot of the first two DFA axes: Discriminant Axis 1 is related to frequency and number of harmonics; Discriminant Axis 2 is related to signal duration and peak frequency (function of the relative intensity contribution of the harmonics). Calves (a) and Others (b) were plotted separately to enable better visualization of individual groupings.

contribute to the acoustic characteristics of the sounds produced.

Sex Differences in Acoustic Behavior and Mating Strategies

We found significant differences between sexes in

Table 3. Results of the nested MANOVA, mean \pm SD, and multivariate F-test between age classes and sexes of each variable; all variables, except that “signal duration” was log-transformed for the statistical analysis. The mean values presented are in the original linear scale.

Variable	Age class (Wilk's $\lambda = 0.103$; $F_{7,122} = 152.2$; $p < 0.001$)				Sex (Wilk's $\lambda = 0.290$; $F_{7,122} = 42.6$; $p < 0.001$)			
	Calves ($n = 80$)	Others ($n = 63$)	$F_{1,128}$	p -level	Males ($n = 80$)	Females ($n = 63$)	$F_{1,132}$	p -level
Signal duration (ms)	371.9 \pm 80.4	323.9 \pm 78.6	25.0	< 0.001	320.7 \pm 82.4	388.8 \pm 66.5	56.3	< 0.001
Number of harmonics	6.2 \pm 1.5	7.1 \pm 1.4	50.6	< 0.001	6.9 \pm 1.4	6.2 \pm 1.6	36.1	< 0.001
Harmonic with most energy	2.2 \pm 1.4	1.8 \pm 1.2	6.1	0.015	2.3 \pm 1.2	1.7 \pm 1.2	18.8	< 0.001
Mean fundamental frequency (kHz)	2.7 \pm 0.5	2.1 \pm 0.4	1,042.0	< 0.001	2.4 \pm 0.5	2.6 \pm 0.6	114.7	< 0.001
Maximum fundamental frequency (kHz)	3.3 \pm 0.7	2.5 \pm 0.6	231.7	< 0.001	2.8 \pm 0.7	3.1 \pm 0.8	39.4	< 0.001
Minimum fundamental frequency (kHz)	2.2 \pm 0.5	1.8 \pm 0.4	109.8	< 0.001	1.9 \pm 0.5	2.1 \pm 0.5	50.3	< 0.001
Fundamental frequency range (kHz)	1.2 \pm 0.5	0.7 \pm 0.3	60.2	< 0.001	0.9 \pm 0.4	1.0 \pm 0.5	0.4	0.530
Peak frequency (kHz)	5.7 \pm 2.9	3.7 \pm 2.2	26.6	< 0.001	5.4 \pm 3.1	4.1 \pm 2.2	11.1	0.001

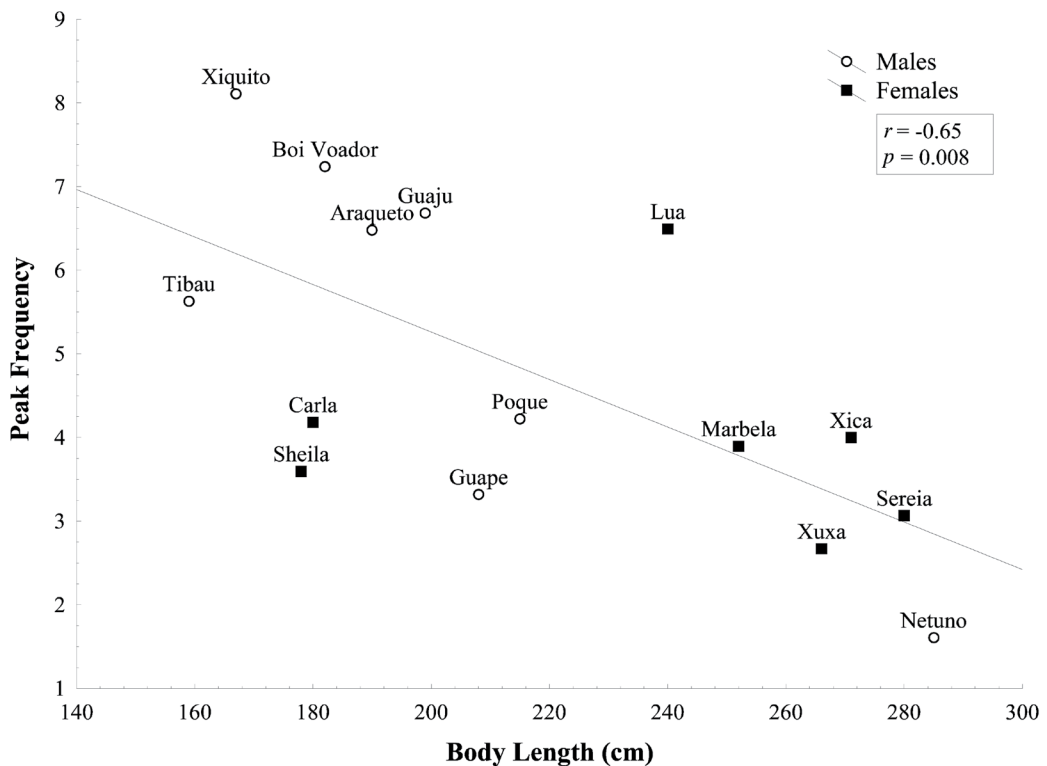


Figure 4. Regression between total body length and peak frequency of calls made by Antillean manatees

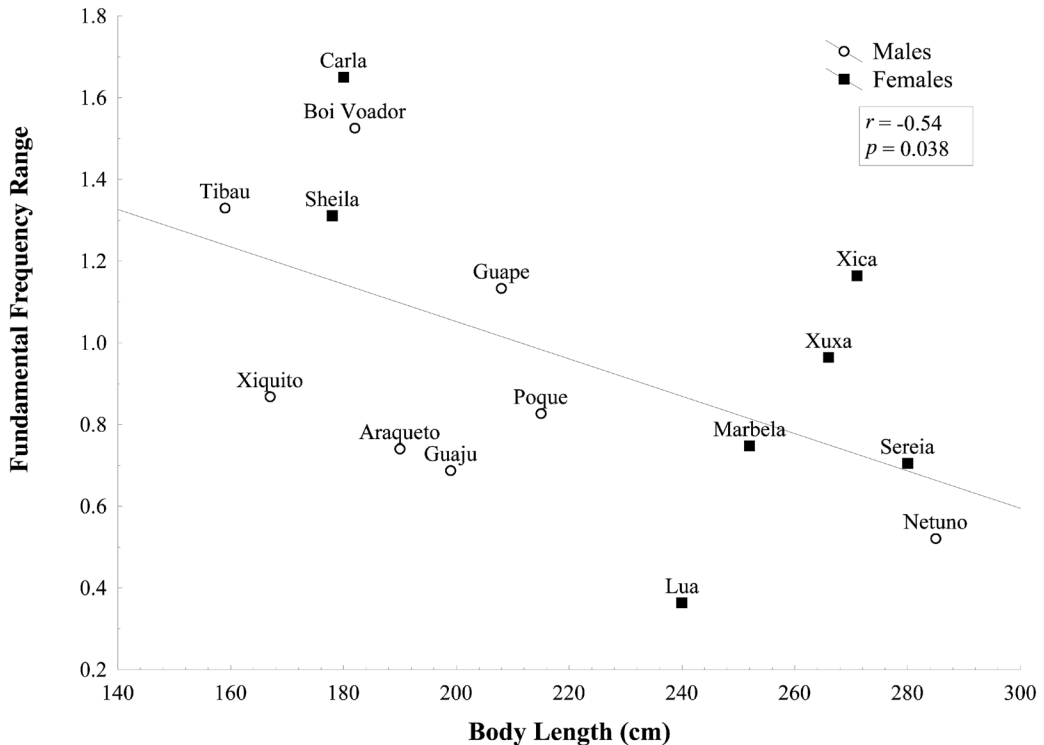


Figure 5. Regression between total body length and range of fundamental frequency of calls made by Antillean manatees

Antillean manatee calls. Females emit calls with higher fundamental frequencies but lower peak frequencies than males. Also female calls are longer in duration than male calls. Steel (1982) reports higher pitched calls (higher fundamental and peak frequencies) for male Florida manatees. However, Steel was unable to confirm the identification or location of the vocalizing individual, which could have resulted in misidentification of the animal producing the sound. Nonetheless, sexual vocal differences suggest that the emission of calls may have a function in reproduction.

Anderson (2002) lists gaps in information about the manatee's sexual strategies and indicates that one of these is "how males recognize estrous," suggesting that estrous females may advertise their receptiveness acoustically. Bengston (1981) showed that adult male Florida manatees establish regular search circuits in areas frequently used by females in a supposed attempt to assess female reproductive status. We suggest that frequent calling between mother and calf pairs might aid roving males in locating females. This presumption is based on observations by Hartman (1979) and O'Shea & Hartley (1995) that Florida manatee females with young calves are harassed

by "mating" herds of males and that that could be considered as a form of infanticide to induce subsequent estrous.

Morton's (1977) motivation-structural rules suggest that increased emission rates and higher frequency calls are both characteristics of signals that elicit the approach of receivers. We can speculate that females could be using their high frequency calls to attract males to their location. In the Antillean as well as in the Amazonian manatee (Sousa-Lima et al., 2002), females present greater fundamental frequency values than males (i.e., they tend to emit higher frequency vocalizations despite their bigger size). Furthermore, female Antillean manatees emit longer isolation calls than males. Although we do not know if the individuals recorded were in estrous, we speculate that females could also be altering other parameters in their calls (such as signal duration or intensity) to inform males of their receptiveness. Female estrous vocal cues, such as increased call intensity, have been reported in elephants (*Loxodonta africana*) (Poole et al., 1988).

Age Differences

Signaling strategies such as increased emission rates and higher frequency calls are also widely used in parent-offspring interactions in mammals and birds (Morton, 1977). In isolation, Amazonian manatee calves vocalize more than adults: 6 calls/min vs 1 call/min (or not at all) during a 25-min recording session (Sousa-Lima et al., 2002). We found no difference in calling rates between age classes or sexes in Antillean manatees recorded in isolation (3 calls/min); however, context and stress levels may influence call emission rate in Antillean manatees. Individuals recorded by us in isolation present a higher calling rate than individuals in the wild recorded by Nowacek et al. (2003) (0.09 to 0.75 calls/min). Individual calling rates in the wild Florida manatee are also lower, ranging between 0.25 to 4.75 calls/5 min (Bengston & Fitzgerald, 1985; Phillips et al., 2004; Miksis-Olds, 2006). Furthermore, other environmental characteristics, such as elevated noise levels, increase the Florida manatee's calling rate (Miksis-Olds, 2006). Manatee calves might have different species-specific strategies to call conspecific attention (mainly their mothers'). Amazonian manatee calves increase the number of vocalizations emitted (Sousa-Lima et al., 2002), while the calves in the Antillean species emit longer and higher pitched calls (this study).

The inverse correlation between the fundamental frequency range of the calls and total body length in Antillean manatees indicates that maturity has an effect of decreasing this vocal parameter. As noted elsewhere (Sousa-Lima et al., 2002), it appears that as the manatee grows older, the fundamental frequency range decreases, thus, the most important parameter that confers vocal identity (fundamental frequency) is better defined as the animal ages. This phenomenon is observed in adolescent male humans and in birds such as penguins (*Aptenodytes patagonicus*) as they prepare to leave the nest (Robisson, 1992).

Interindividual Discrimination

Some of the most important variables for individual vocal discrimination in Antillean manatees are related to the fundamental frequency as also has been found for pinnipeds (Insley, 1992; Charrier et al., 2003; Insley et al., 2003). Nevertheless, DFA function 2 (related to signal duration; Figure 3) also contributed to the isolation of individual vocal patterns. Signature information in Antillean manatees can also be contained in the frequency modulation of the calls (not analysed in detail here). Nevertheless, vocal identity involves the more easily measured features of duration; number of harmonics; and minimum, maximum, and mean fundamental frequency.

Other characteristics of the signal may carry additional identity information but could not be included in the quantitative analysis because they did not conform to the test assumptions or were not measured. One of these characteristics is the energy distribution across frequency bands, which gives a distinct timbre or tonal quality to the call (Marler, 1969). This unaccounted vocal feature can be observed in Figure 1 and may also be perceived as an identity cue by the manatees. Therefore, individual differences can be present in both quantitative and qualitative characteristics of the signal. At this point, we cannot say which characteristics the animals use in the process of discrimination/identification, but probably the signal is perceived as a whole and differences in qualitative and quantitative features are taken into account during recognition.

Holekamp et al. (1999) demonstrated that female hyenas (*Crocuta crocuta*) identify cubs as their own vs others based on long distance vocalizations; whereas vervet monkeys (*Cercopithecus aethiops*) can identify third-party relationships, showing an impressive level of social cognition (Seyfarth & Cheney, 1994). Although manatees are also long-lived mammals that bear few offspring, which require a long period of dependence on the mother, they are subject to less selective pressure to recognize conspecifics within their less social system in such a way that vocal discrimination may not be so extreme. If similar benefits can be derived by employing a simpler coding scheme with lower costs, one would expect selection to favour the simpler scheme (i.e., binary recognition task) (Bradbury & Vehrencamp, 1998). Indirect evidence of the binary recognition hypothesis for mother-calf manatee pairs comes from the vocal similarity observed between the twins, Carla and Sheila (Figure 1). The mother (Sereia) would nurse either individual by recognizing only one vocal pattern as "own calf." The question of whether or not Antillean manatees may be able to recognize the voices of multiple individuals within their species is beyond the scope of this paper. Interindividual discrimination can be further considered in two different ways: (1) the level of stereotypy within an individual's call and (2) the level of discrimination among the calls of different individuals (i.e., how similar the calls are from a particular individual and how different they are in comparison to the calls of conspecifics).

If selective pressures result in a greater stereotypy in the individual calls of a species, we cannot expect that manatee isolation calls would be as readily discriminated as bat pup calls (100% of calls classified correctly in Scherrer & Wilkinson, 1993). Bats are subjected to a much greater selective pressure because of their spatially

confined nursery colony with hundreds of pups in close proximity. In an aquatic environment, animals are consistently more isolated from each other so that there is ultimately less selection on vocal patterns. Inasmuch, the degree of selective pressure within aquatic species may also vary, favouring more or less individual call stereotypy. Different levels of call stereotypy were found in fur seal species of the genus *Arctocephalus* as a result of differential selective pressure on mother-pup recognition (Page et al., 2002).

Similarities and Differences Between Kin

Related individuals had similar acoustic parameters in their vocalizations. Carla and Sheila have very close values of DFA factors 1 and 2 (Figure 3). Note also the similar spectrogram contours and fundamental frequency values of these two individuals (Figure 1). Xica and Xiquito also have similar values of both DFA axes (Figure 3). The first two individuals are twin sisters and the other two are a mother and calf pair. There seems to be a strong genetic component in the vocal pattern expressed by an individual manatee, which also has been suggested for the Amazonian species based on one case of mother-calf similarity (Sousa-Lima et al., 2002). Nevertheless, there were no similarities between the twins' vocal patterns and their mother's (Sereia; Figure 3).

Bottlenose dolphin (*Tursiops truncatus*) infants develop their own signature whistle within their first few months of life (Caldwell & Caldwell, 1979), and there is accumulating evidence that the development of signature whistles is strongly influenced by vocal learning (Janik, 1999). Captive bottlenose dolphin calves often develop whistles that are similar to the whistles used by the human trainer or similar to whistles of their pool mates but not to those of their mothers (Tyack, 1997). If manatees are capable of vocal learning, manatee calves in captivity that are exposed to vocal templates of unrelated individuals might develop a vocal pattern different from the primarily inherited one. Carla and Sheila were raised in a communal pen with several other individuals, while Xiquito was rejected by its mother and bottled in an isolated pen. It is possible that because Xiquito was isolated from other individuals, he retained his mother's vocal pattern as his template (also observed in Amazonian manatees by Sousa-Lima et al., 2002). The influence of vocal learning might be a likely explanation; however, vocal similarity between mothers and their male calves may also be the result of an inbreeding avoidance mechanism as suggested for bottlenose dolphins (Sayigh et al., 1995) and fur seals (*Arctocephalus australis*) (Phillips, 1998).

Intraindividual Variation

Individual Antillean manatees have their own characteristic vocalization patterns, with minor variations within an individual's vocal signature. The intraindividual vocalization repertoire in Antillean manatees is formed by a continuum of signals that vary slightly and that may carry different or additional information. Anderson & Barclay (1995) identified several types of vocalizations produced by another sirenian species—the dugong. These authors also showed that the dugong call repertoire is a continuum rather than a set of discrete types, with gradation between one general type of sound to the other. Noisier sounds have been attributed to Florida manatee calves (Steel, 1982). These results contrast with our findings for Antillean manatees, which, regardless of age class, may emit noisy or clear sounds as part of their repertoire.

Conservation Implications

Studies of captive animals in parallel with efforts in the wild can provide measures for use in the conservation of the sirenians. Our results could form the basis for the development of alternative techniques for management and conservation of the Antillean manatee in Brazil. Acoustic surveys of wild populations may provide an additional means by which to assess the population's status along the coast, estimated to be less than 300 individuals (Lima, 1997). The application of vocal identity in assessing population estimates and structure in the wild should be explored as a potential tool in the conservation of this species, which is considered the most endangered mammal in Brazil (listed as "critically endangered"; IBAMA, 2001).

An improved understanding of the natural variation found in manatee calls might be useful in developing acoustic detectors to warn boaters of the presence of manatees. The development of passive acoustic detectors of manatee calls (see algorithms tested in Niezrecki et al., 2003) and other improvements on this technology (Yan et al., 2005) would decrease the number of boat strikes, which cause the injury or death of these highly threatened animals.

In addition to more accurately estimating population size and structure, and helping avoid boat strikes, another pressing conservation issue along the Brazilian coast is the increasing rate of stranded calves (IBAMA, 2001). Lima (1997) suggested that females are no longer able to give birth inside sediment-filled estuaries due to erosion; therefore, calving must occur in the sea where breaking waves might make it more difficult for calves to maintain close contact with their mothers and which might mask their isolation calls due

to greater ambient noise levels, preventing their location and reunion after separation.

Mothers may stay in the vicinity of the area where the lost calf was stranded for periods of over 12 h (Sousa-Lima, pers. obs.). Playbacks of vocalizations of stranded calves that have been rescued may help attract their mothers and allow the release of the calf *in loco*, significantly decreasing the costs of rehabilitation in captivity and promoting the maintenance of the wild population without complicated and costly reintroduction efforts. Manatees may be “ecologically trapped”—that is, they may present poor habitat choice based on cues that formerly correlated to habitat quality (Schlaepfer et al., 2002). Manatee mothers choosing to give birth inside calmer waters of estuarine rivers might be experiencing reduced reproductive success in an environment that has been altered by humans. The adaptive value of the evolution of isolation calls as means of identification, location, and proximity maintenance between mothers and calves may have decreased as a consequence of habitat destruction.

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