

Vocalizations of Amazon River Dolphins, *Inia geoffrensis*: Insights into the Evolutionary Origins of Delphinid Whistles

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Abstract

Oceanic dolphins (Odontoceti: Delphinidae) produce tonal whistles, the structure and function of which have been fairly well characterized. Less is known about the evolutionary origins of delphinid whistles, including basic information about vocal structure in sister taxa such as the Platanistidae river dolphins. Here we characterize vocalizations of the Amazon River dolphin (*Inia geoffrensis*), for which whistles have been reported but not well documented. We studied *Inia* at the Mamirauá Sustainable Development Reserve in central Brazilian Amazônia. During 480 5-min blocks (over 5 weeks) we monitored and recorded vocalizations, noted group size and activity, and tallied frequencies of breathing and pre-diving surfaces. Overall, *Inia* vocal output correlated positively with pre-diving surfaces, suggesting that vocalizations are associated with feeding. Acoustic analyses revealed *Inia* vocalizations to be structurally distinct from typical delphinid whistles, including those of the delphinid *Sotalia fluviatilis* recorded at our field site. These data support the hypothesis that whistles are a recently derived vocalization unique to the Delphinidae.

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Introduction

Cetaceans produce a diversity of vocalizations, used in a broad range of contexts including orientation, navigation, and communication (e.g. Payne and Webb 1971; Ford 1989; Au 1993). Tonal whistles of the oceanic dolphins (Odontoceti: Delphinidae) have been a topic of particular interest. Observational and experimental studies, largely of the bottlenose dolphin (*Tursiops truncatus*), indicate that delphinid whistles may provide cues about individual identity (Caldwell and Caldwell 1965; Caldwell et al. 1973, 1990; Sayigh et al. 1995), may

maintain group cohesion (Janik and Slater 1998), and are shaped in structure by social context and learning (Tyack 1986; Sayigh et al. 1990; Smolker and Pepper 1999; Janik 2000a). Comparative studies indicate that whistles vary in structure across populations and species (Steiner 1981; Ding et al. 1995; Rendell et al. 1999), with whistle divergence perhaps facilitating species recognition and speciation (Steiner 1981). Overall, the study of delphinid whistles is beginning to influence our understanding of mammalian vocal learning and communication (Tyack and Sayigh 1997), although much remains to be learned.

One class of open questions about dolphin whistles concerns their evolutionary origins and subsequent patterns of diversification. For instance, did whistles arise *de novo* in delphinids, or were they modified from an ancestral vocal form? Was the origin of whistles catalyzed by the evolution of a novel vocal mechanism? To address such questions, it is helpful to consider dolphin phylogenetic relationships and patterns of vocal behavior across species. A key point here is that all delphinid species studied to date, with the exception of the four *Cephalorhynchus* species, produce whistles (e.g. Steiner 1981; Ding et al. 1995; Rendell et al. 1999; Matthews et al. 1999; V. Janik, pers. comm.). Those delphinid whistles that have been described are diverse but share basic structural similarities: they are highly tonal (with acoustic energy expressed in narrow ranges of frequencies), and are often frequency-modulated. Further, as noted by Ding et al. (1995) and Matthews et al. (1999), whistle frequency in delphinids scales with body size, with large species producing whistles with comparatively low frequencies. The structural uniformity and scaling of delphinid whistle features suggest a common vocal mechanism for whistle production, synapomorphic to the group (see Cranford et al. 1996). A satisfactory explanation of dolphin whistle origins thus requires attention to taxa outside of the Delphinidae.

The sister families of the Delphinidae, the Phocoenidae (porpoises) and Monodontidae (white whales and narwhals; see Hamilton et al. 2001; Fig. 1), appear not to produce whistles (Evans 1987). This finding supports the hypothesis that whistles are a uniquely derived character within the Delphinidae. Studies of another related taxon, *Inia geoffrensis* (see Fig. 1), however, have offered apparent contradictory evidence. To elaborate, early studies of captive *I. geoffrensis* documented a diversity of vocal types but no whistles (Caldwell et al. 1966; Caldwell and Caldwell 1970; Norris et al. 1972; Evans 1973). However, Nakasai and Takemura (1975), in field work near Iquitos, Peru, reported on the occurrence of whistles in *Inia*. The validity of this report was compromised by the authors' failure to provide information about sampling methods and the acoustic structure of recorded vocalizations (e.g. Best and da Silva 1989). A more recent field study described the acoustic structure of *Inia* vocalizations from tributaries of the Marañon and Tigre Rivers, Peru (Ding et al. 1995, 2001). Although acoustic analyses revealed these vocalizations to be distinct from whistles expressed by delphinids, particularly in frequency measures, they were still classified as whistles (Ding et al. 1995, 2001).

The question of whether *I. geoffrensis* produces whistles holds implications for delphinid whistle evolution. Confirmation of whistle occurrence in *Inia*,

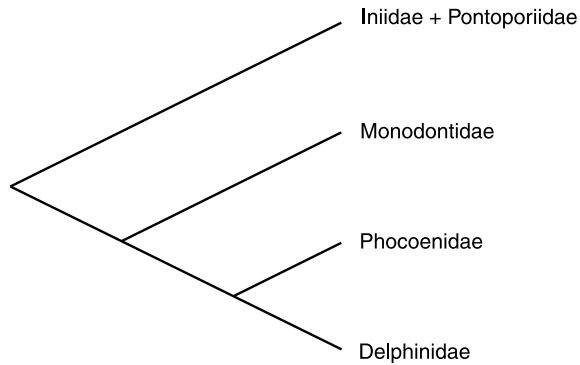


Fig. 1: Phylogenetic tree of dolphins and allies, from Hamilton et al. (2001). The 'true' dolphins (Delphinidae, comprised of 32 species), porpoises (Phocoenidae, six species), and white whales and narwhals (Monodontidae, three species) form a monophyletic clade, the Delphinioidea (Hamilton et al. 2001). The South American river dolphins (*Inia geoffrensis* and *Pontoporia blainvillei*) are sister taxa to the Delphinioidea

together with evidence of homology to delphinid whistles (e.g. Lauder 1986), would support an origin of whistles in or before the common ancestor of the Iniidae and Delphinidae. The lack of whistles in Phocoenidae and Monodontidae would then be attributed to secondary losses. Refutation of whistle occurrence in *I. geoffrensis* would, by contrast, support a more recent origin of whistles in the common ancestor of the Delphinidae. This question is of interest to dolphin biologists given the present role of whistles in delphinid social interactions and learning; information about the phylogenetic origins of whistles might help to specify the ecological factors and selective pressures that favored the evolution of whistles and associated traits.

The primary goal of the present study is to further document *Inia geoffrensis* vocal behavior as it occurs in the wild, both in usage and acoustic structure. We provide data based on 40 h of systematic acoustic sampling of a wild population of *Inia* in the central Brazilian Amazon. We also analyze the acoustic structure of whistles of the delphinid species *Sotalia fluviatilis*, recorded at our study site, as a point of comparison with *Inia* vocalizations.

Methods

Our study was conducted at the Mamirauá Sustainable Development Reserve, in the central Brazilian Amazon (Ayres 1995). The Mamirauá Reserve, comprising 1.1 million ha, is situated at the juncture of the Amazon and Japurá rivers. The reserve lies within the Amazon floodplain and is subject to a seasonal flood of 10–12 m amplitude. During the low water season, Mamirauá is a mostly low-lying, forested land with a network of lakes and water channels. At high water the reserve is transformed into a vast inland sea, much of which is covered by forest canopy. The reserve supports high densities of fish, and attracts fish-

eating predators including *Inia geoffrensis*. The *Inia* of Mamirauá have been studied intensively since 1994. Research activities have included marking individual dolphins using freeze-brands and tracking their movements using radio and satellite telemetry (da Silva and Martin 2000). Tracking data (Martin and da Silva 1998) indicate that some *Inia* are year-round residents of Mamirauá, whereas others travel out of tracking range during the high-water season. We limited our sampling in the current study to dolphins in the Mamirauá lake and channel sub-system, spanning approximately 28 km near the eastern-most point of the reserve. Few motor-powered vessels are permitted in this sub-system, thus providing excellent observation and recording conditions.

Our goal was to document vocalizations and associated behavior in this population. Data were collected between 28 Sept. and 9 Oct. 1997, which corresponds to the low-water season. During this season dolphins are restricted to the main river and its channels and lakes. Each morning (06:00–12:00 h) and afternoon (15:00–18:00 h) *Inia* were located using small motor-powered canoes or Zodiac boats. Underwater sounds were monitored and/or recorded using single or paired High Tech HTI-94-SSQ Series 2 wire marine hydrophones and Sony TC-DM5 or Marantz PMD-221 portable cassette recorders. These recording systems have flat frequency responses up to 15–18 kHz, suitable for detecting and recording many delphinid social signals (although not suitable for complete documentation of other dolphin sounds, notably echolocation clicks). Pilot observations and acoustic monitoring revealed a rich diversity of waterborne sounds, including distinct low-frequency sounds that occurred only in the presence of *Inia*. Three additional lines of evidence make us nearly certain that these sounds were produced by *Inia*. First, in several cases, individual *Inia* passed directly under the boat, and we heard the source of these sounds shifting in the corresponding direction and with the corresponding timing (detected as changes in the onset between left and right-positioned hydrophones). Secondly, the amplitude of these sounds corresponded closely to the proximity of individuals; in particular, the highest-amplitude calls always occurred with *Inia* alongside our boat. Thirdly, throughout the entire study and during a subsequent field excursion, these distinctive sounds were never detected in the absence of *Inia*.

Behavioral observations were conducted by three observers during 480 5-min blocks (40 h total). We disengaged boat engines during observation blocks to limit background noise. Blocks always commenced with one or more *Inia* in sight. During each block vocal behavior was monitored and, during most blocks, recorded. At the start of each block, we estimated *Inia* group size as the number of individuals visible within a radius of about 100 m. The identity of marked individuals was noted when possible. Patterns of *Inia* activity at the surface were tallied, following Layne (1958) and Layne and Caldwell (1964). Specifically, we classified all surfacing events as either 'horizontal surfaces' or 'rolls'. During horizontal surfaces, animals break the surface of water with their heads or with their heads and dorsa together. They remain at the surface for some seconds to breathe and then slowly submerge (Layne 1958). Rolling surfaces are more rapid, and appear to be a preliminary step in deeper-angle diving. During rolls, dolphins

normally expose only their dorsi; they contract their body into a c-curve and quickly 'roll' forward. Behavior below the surface could not be observed because of high turbidity.

We conducted sound analyses using SIGNAL V. 3.1 software (Beeman 1999). Tapes were reviewed and 240 *Inia* vocalizations with high signal-to-noise ratios were chosen for analysis. We digitized (25 kpts) these recordings on an IBM laptop computer using SIGNAL and a DART PCMCIA digitizing card. A majority of *Inia* vocalizations were found to contain multiple notes, often with dynamic shifts in frequency and with significant harmonic content (Fig. 2). Our analyses aimed to characterize a diversity of timing and frequency features. Across multiple note calls we measured call duration (using oscillograms), numbers of notes produced, and dominant frequencies of first and last notes. Dominant frequencies were identified as those frequencies with the highest amplitudes. We conducted frequency analyses

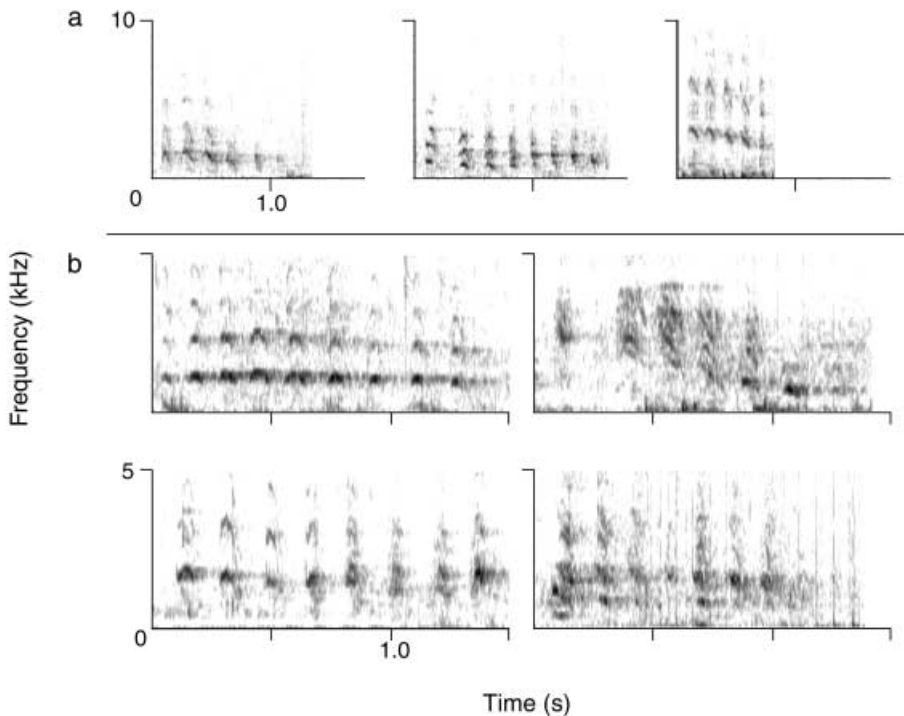


Fig. 2: Example sound spectrograms (shown at two scales) of *Inia geoffrensis* vocalizations. *Inia* vocalizations consist of multiple, heterogeneous notes. (a) The frequency range of vocalizations generally did not exceed 5 kHz, although harmonic overtones were occasionally expressed between 5 and 10 kHz. (b) Diversity in vocal structure. Some vocalizations maintained a consistent frequency during calls (upper left), whereas others showed reductions in frequency as calls progressed (upper right). Temporal structure also varied among vocalizations (compare upper left and lower left spectrograms). The spectrogram on the lower right illustrates a vocalization accompanied by low-frequency components of echolocation clicks. All spectrograms were calculated at 256 FFT (sample rate = 25 kpts, frequency resolution = 98 Hz, Hanning windows)

using amplitude spectra calculated across entire notes (FFT of 32 kpts, smoothed to a frequency resolution of 100 Hz). From vocalizations with multiple notes we selected single notes for further analysis. For these notes, and for single note vocalizations, we measured note duration and note dominant frequency.

Sotalia fluviatilis, a delphinid dolphin with riverine populations, was present in moderate numbers at Mamirauá during our study. *Sotalia* produces high-frequency whistles that are distinguished easily by ear from *Inia* vocalizations. These whistles were detected only when *Sotalia* was in sight. We recorded, digitized (50 kpts) and analyzed 50 *Sotalia* whistles (e.g. Fig. 3). From each whistle we measured five variables: duration, start frequency, end frequency, minimum frequency, and maximum frequency. Duration was measured from oscillograms, and frequency measures from spectrograms using an on-screen cursor.

Results

Inia group size ranged from 1 to 14 individuals ($\bar{x} \pm SD = 6.87 \pm 3.02$). Groups were often comprised of two or more smaller aggregates, as described by Best and da Silva (1989). We recorded 1612 *Inia* vocalizations over the 480 observation blocks. Vocal activity was low, with an average of one vocalization per individual per 10.1 min. Over half of all vocalizations occurred during <10% of blocks, and no vocalizations were recorded during 40% of blocks. Across all observation blocks, vocal activity correlated positively with group size ($r = 0.179$, $p < 0.001$) and with both types of surfacing activity (horizontal surfaces, $r = 0.126$, $p < 0.01$; rolls, $r = 0.195$, $p < 0.001$). When group size was taken into account, vocal activity (vocalizations/individual) still correlated with rolling surfaces (rolling surfaces/individual, $r = 0.113$, $p < 0.05$) but not with horizontal surfaces (horizontal surfaces/individual, $r = -0.041$, $p > 0.35$).

Structurally, *Inia* vocalizations were diverse in temporal, frequency, and harmonic features (Fig. 2, Table 1). The number of notes per vocalization ranged widely, from 1 to 16 (4.18 ± 2.35 ; Table 1). Of the 240 vocalizations analyzed, 216

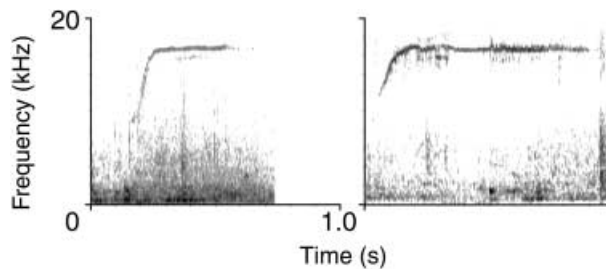


Fig. 3: Sound spectrograms of two *Sotalia fluviatilis* whistles, calculated at 256 FFT (sample rate = 50 kpts, frequency resolution = 195 Hz, Hanning windows). *Sotalia* vocalizations are narrow band (frequencies concentrated within a narrow range), frequency modulated, and relatively stereotyped (invariant across renditions)

Table 1: Summary values of acoustic characteristics of *Inia geoffrensis* vocalizations (n = 240 vocalizations)

	Multiple note calls				Single notes ^a	
	No. of notes	Duration (s)	f _d first note (kHz)	f _d last note (kHz)	Duration	f _d
\bar{x}	4.18	0.720	2.90	2.45	0.103	2.57
SD	2.35	0.453	1.50	1.41	0.070	1.26
CV (%)	56.3	62.9	51.7	57.5	67.5	48.9

^aIncludes single note vocalizations and single notes selected from within multiple note vocalizations.

f_d (dominant frequencies) were defined as those frequencies with maximal amplitudes. CV is the coefficient of variation (\bar{x}/SD).

contained multiple notes. Individual notes ranged widely in duration, from 0.037 to 0.534 s, and in dominant frequency, from 0.40 to 7.92 kHz. Dominant frequency tended to decline over the course of multi-note vocalizations, both on an average basis (Table 1) and for 142 (65.7%) of 216 multi-note vocalizations. Dominant frequency increased over the course of 69 (31.9%) of multi-note vocalizations, and there was no change in dominant frequency for an additional five multi-note vocalizations. Many notes expressed multiple harmonic frequencies (e.g. Fig. 2). Coefficients of variation (i.e. \bar{x}/SD) for analyzed vocal features ranged from 48.9 to 67.5% (Table 1).

Sotalia appeared during 70 (14.6%) of our observation blocks, and vocalized during 66 (94%) of these blocks. The most common vocal type produced by *Sotalia* were whistles (Fig. 3), which were uniformly tonal and frequency modulated. Measurements of *Sotalia* whistle features are summarized in Table 2; coefficients of variation for *Sotalia* whistles ranged from 15.9 to 50.8%. These results are similar to those reported by Ding et al. (1995) for a riverine population of *Sotalia* in north-east Peru.

Discussion

Our study aimed to characterize vocal behavior in *I. geoffrensis*, a sister taxon to the Delphinoidea (Fig. 1). At our study site, we also secured recordings of the

Table 2: Summary values of acoustic characteristics of *Sotalia fluviatilis* whistles (n = 50 whistles)

	Duration (s)	Start frequency ^a	End frequency	Minimum frequency	Maximum frequency
\bar{x}	0.630	9.70	14.64	9.18	15.65
SD	0.320	3.64	2.66	3.05	2.49
CV (%)	50.8	37.6	18.2	33.2	15.9

^aAll frequency measurements are in kHz.

delphinid species *S. fluviatilis*. Analyses of *Sotalia* whistle production illustrate typical delphinid vocal patterns, on five fronts. First, *Sotalia* produced whistles nearly continuously, in 94% of observation blocks in which they occurred. High rates of vocal activity have similarly been documented in other delphinids (Evans 1987). Secondly, *Sotalia* whistles expressed energy in narrow ranges of acoustic frequencies, and were normally frequency modulated (Fig. 3). This is consistent with whistle structure in other delphinid species, including *Tursiops truncatus* (e.g. Sayigh et al. 1995; Matthews et al. 1999). Thirdly, *Sotalia* whistles increased in frequency over the course of individual whistles (Table 1, compare start vs. end frequency). Of 15 delphinid species analyzed by Steiner (1981) and Ding et al. (1995), 10 expressed a similar pattern of rising frequency. Fourthly, all coefficients of variation for *Sotalia* frequency features (15.9–37.6%) and duration (50.8%) fell within ranges of coefficient of variation expressed by other delphinids (Ding et al. 1995, their Table 1b–f). Fifthly, frequency values of *Sotalia* whistles map closely onto a family-wide scaling relationship between frequency and body size (Fig. 4).

Vocal behavior of *I. geoffrensis* stands in sharp contrast. In overall vocal activity, *Inia* was comparatively quiet, producing an average of only one vocalization per individual per 10 min. Further, *Inia* produced no vocalizations in 40% of observation blocks. When *Inia* vocalized they did so in bouts. Over half of recorded vocalizations occurred in less than 10% of observation blocks. Accounting for group size, vocal activity correlated significantly with the frequency of rolling surfaces but not with horizontal (breathing) surfaces. Rolling surfaces occur as *Inia* engage in deep dives, and *Inia* normally execute deep dives when feeding (Layne 1958, Best and da Silva 1989). These observations collectively suggest that *Inia* vocal behavior is associated temporally with feeding. In further support of this suggestion, we observed on two occasions *Inia* feeding as a group during bouts of vigorous vocalizing. Our observations of feeding behavior in these instances were of dolphins clustering near the riverbank and apparently 'cornering' groups of fish; from within these clusters, fish could be seen jumping out of the water. Yet, we recorded many vocalizations during times that this behavior was not observed.

Inia vocalizations also proved to be distinct from delphinid whistles in structure. The most notable feature of *Inia* vocalizations in our population is that they normally consist of heterogeneous series of short-duration notes (Fig. 2); by contrast, most delphinid whistles consist of single notes (e.g. Fig. 3). Caldwell and Caldwell (1970), working with *Inia* in captivity, recorded and illustrated a call that contained multiple notes. This vocalization is similar in appearance to *Inia* vocalizations at Mamirauá. The reports of Ding et al. (1995, 2001), by contrast, suggest that *Inia* vocalizations consist of single notes.

Pairwise comparisons of *Inia* and delphinid vocal features reveal substantial differences (e.g. compare Tables 1 and 2). Dominant frequencies of *Inia* vocalizations (1.41–2.90 kHz, mean values) fell below all delphinid frequency parameters including minimum frequency (5.45–6.49 kHz mean values across six species, Ding et al. 1995). Other frequency measures of *Inia* were consistent with those reported by Ding et al. (1995, 2001). Dominant frequencies of *Inia* notes

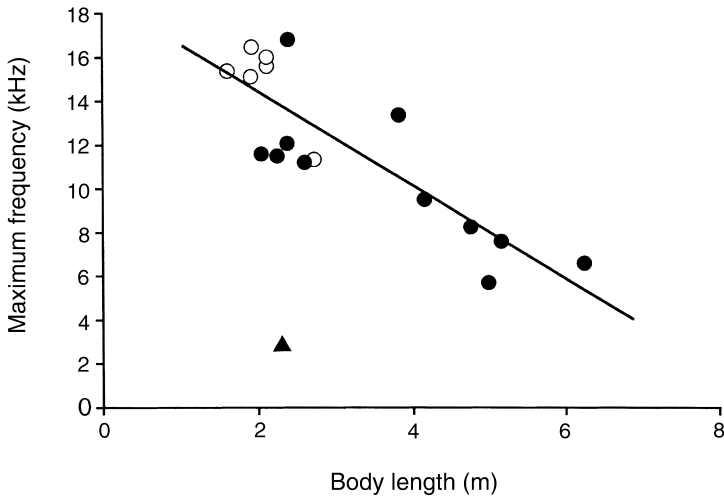


Fig. 4: Maximum fundamental frequency of vocalizations as a function of body length for 17 delphinid species (circles) and for *Inia geoffrensis* (triangle). Maximum frequency was used here because this is the most widely available frequency variable in the literature on dolphin vocalizations. All body size data from Evans (1987). Acoustic frequency data from Ding et al. 1995 (open circles), Matthews et al. 1999 (filled circles); and the present study (triangle). Within the delphinids, fundamental frequency regresses positively on body size (solid line; $r = 0.851$), suggesting a common size-dependent production mechanism. A test of significance of this regression awaits further clarification of delphinid species-level phylogenetic relationships. The likelihood of a phylogenetic effect is enhanced by the fact that the cluster of points on the upper left of the graph (body size < 3.5 m), with the exception of the leftmost point, *Sotalia fluviatilis*, are in one subfamily, the Delphininae, while the remaining points (with the exception of *Inia*) are in another subfamily, the Globicephalinae. The data point for *Inia* is located far off the Delphinidae regression, suggesting a distinct production mechanism

tended to decrease over the course of calls. *Inia* notes also expressed significant harmonic content (Fig. 2), more than occurs in many delphinid vocalizations. Overall, *Inia* features were more variable than were delphinid parameters, as determined by the coefficient of variation (CV). The CV of *Inia* call duration (62.9%) exceeded those for all delphinids (38.8–58.7%), and CVs for *Inia* frequency features (48.9–57.5%; Ding et al. 1995, 2001) similarly exceeded those for all delphinids (10.89–44.56%; Ding et al. 1995, 2001). Finally, *Inia* vocal frequencies fell well below values expressed by the delphinids when accounting for body size (Fig. 4).

The functions of delphinid whistles have begun to be elucidated. For instance, whistles appear to function in mother–calf communication (Sayigh et al. 1995) and social group interactions (e.g. Smolker and Pepper 1999; Janik 2000a). Our study provides little direct insight into the function of *Inia* vocal behavior. Even if *Inia*'s vocal behavior co-occurs with feeding, as our data suggest, the question of vocal function still remains open. Vocalizations during feeding bouts might be used to facilitate co-operative hunting, or might be used

to stun or confuse prey (Janik 2000b). Alternatively, they might occur as an incidental outcome of feeding behavior and serve no function at all. Pilot playback and observational data suggest that *Inia* vocalizations do not serve other obvious communication functions. For instance, mothers and calves did not vocalize as they reunited after temporary separation, and we failed to document responses to playbacks of *Inia* vocalizations (recognizing probable limits on the quality of our playback system; Podos, da Silva and Rossi-Santos, unpubl. data).

We have demonstrated here that *Inia* vocalizations and delphinid whistles are distinct entities, with divergent acoustic structures and patterns of usage. This finding, along with a lack of evidence for delphinid-like whistles in the Phocoenidae and Monodontidae (Evans 1987), lends support to the hypothesis that whistles are a unique, derived feature of the Delphinidae. As a caveat, the possibility remains that these (or other closely related) taxa do produce delphinid-like whistles, but that such vocalizations have eluded detection. Statements that animals do not behave in certain ways are always probabilistic. For *Inia*, the 40 h sampling regime reported here was bolstered by an additional 20 h of formal observation at Mamirauá in Nov.–Dec. 1997, without detection of delphinid-like whistles (Podos, da Silva and Rossi-Santos, unpubl. data).

The phylogenetic proximity of *Inia* and the Delphinidae raises the question of whether vocalizations retained by *Inia* could have provided a structural precursor for delphinid whistles. For instance, low-frequency pulses characteristic of *Inia* might have given rise to high-frequency whistles in early delphinids through the augmentation of pulse rates (see Murray et al. 1998). As an alternative, delphinid whistles may have evolved de novo, utilizing a distinct vocal mechanism. Two lines of evidence support the latter interpretation. First, the delphinid *Tursiops truncatus* produces a class of vocalizations ('barks' or 'brays'; Evans 1973; Schultz et al. 1995; Janik 2000b) that is structurally similar to the *Inia* vocalizations in our sample. Similarities between these vocal forms imply that low-frequency vocalizations have been evolutionary conserved. A second, more compelling line of evidence is the marked deviation of *Inia* from the delphinid scaling relationship (Fig. 4). This deviation suggests that delphinid whistles and *Inia* vocalizations are produced by distinct mechanisms. This is because the scaling of vocal frequency in vertebrates is presumed to occur through size-dependent effects on a common vocal apparatus (e.g. Ryan 1988), for which deviations from scaling relationships would perhaps indicate an independent proximate mechanism.

In conclusion, our understanding of the origins of delphinid whistles awaits further advances in dolphin vocal mechanics, for which even the basic question of sound source identity remains unresolved (but see Cranford et al. 1996). Identification of distinct vocal sources for *Inia* vocalizations and delphinid whistles would, for example, indicate an absence of homology among the vocal forms (e.g. Patterson 1982; Lauder 1986), to a greater extent than could be provided by acoustic descriptions or phylogenetic interpretations alone. In the interim, our acoustic analyses herein support the hypothesis that whistles are a unique, derived feature within the Delphinidae.

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