SOUNDS AND BEHAVIOR OF CAPTIVE AMAZON FRESHWATER DOLPHINS, *INIA GEOFFRENSIS*

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ABSTRACT: Twelve types of phonations, placed in four major categories, were recorded in 688 minutes of listening to eight captive *Inia geoffrensis* (Blainville). These sounds are discussed and sonograms of typical ones are presented. Both juveniles and adults were studied under a variety of circumstances. In general, the phonations are less varied, lower in intensity, and of slightly lower frequencies than those observed in most other odontocete cetaceans. Included among the phonations are click trains which when correlated with observed behavior suggest an ability by this species to echolocate. However, the use of this ability may be dependent on learning. Evidence is presented to indicate that vision is the preferred method of environmental exploration, but some tactile sense may also be employed. Data are included to indicate for *Inia* frequent and precocious sexual play, a general lack of competitive feeding behavior, and a lower incidence of fear responses than demonstrated by the much studied Atlantic bottlenosed dolphin.

INTRODUCTION

Dolphins of the family Platanistidae are considered the most primitive of the living odontocete cetaceans (Simpson, 1945: 100). For the purposes of comparison with certain of the more advanced dolphins, of the family Delphinidae, we were especially interested in learning something of the phonations, and more particularly of possible echolocation ability, in the Platanistidae. To our knowledge, only one of the four species of platanistids, the Amazon freshwater dolphin, *Inia geoffrensis* (Blainville), is available presently for study in the United States. We recorded the phonations along with observed concurrent captive behavior of eight animals and the behavior of two others was observed but no recordings were attempted. Other behaviors, not necessarily related to sound production, were also studied. Amazonian animals, one each held captive at the Toledo Zoo, Ohio (see Hofmeister, 1964), and at the John G. Shedd Aquarium, Chicago, Illinois, were not studied directly, but enough was learned of their behavior (from Max Hofmeister at Toledo; and from William P. Braker at Chicago) to indicate that it did not

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differ significantly from that of the animals we did study. The behavior and sonic display of two Amazonian males held captive at Silver Springs, Florida, was discussed by Layne and Caldwell (1964), Schevill and Watkins (1962), Layne (1959), Allen and Neill (1957) and Phillips (1964: 95 ff.). As this paper goes to press we have also learned that an Amazonian *Inia* was kept for a short time at the Crandon Park Zoological Garden, Miami, Florida (Gordon Hubbell, *pers. comm.*). From time to time other *Inia* have been and are held captive at the compounds of animal importers, mostly in Florida. Most notable of these is the Tarpon Zoo at Tarpon Springs, where, through the courtesy of Fred Penman, individuals were observed from time to time. We have had no reports from various observers of behavior by these miscellaneous animals not duplicated in our own observations on the animals listed below.

The species *Inia geoffrensis* is found in the Amazon and Orinoco rivers of South America and their tributaries and adjacent lakes. During times of flood, the animals may also be found throughout the flooded forest floors and may remain in the lakes near the rivers after the floods subside even though in some cases a connection to the rivers no longer remains. After capture, animals to be imported into the United States are usually held in South America for varying lengths of time until it is determined that they are in good health and that they will feed in captivity. The period of time that they are held in South America varies, but usually it is at least a week and sometimes as much as several months before they are flown to the United States. Frequently the importer does not know the exact length of time that the animals have been held. Consequently, even if they are observed at the moment of their arrival in the United States, they cannot truly be called naive as they have become adjusted to captivity to some degree, to the eating of dead fish and to the presence of humans.

None of the animals we studied had been subjected to any known reinforcement of vocalizations, although (as noted below) all had been trained to take food from a human hand and some had been subjected to more complicated training procedures.

ACKNOWLEDGMENTS

Access to the captive animals was made through the generous cooperation of a number of people in charge, as indicated in the list of study sites included below. We wish to express our sincere appreciation to all of these people, most of whom gave us considerable information on the captive history and behavior of the animals in their care, and some of whom gave much of their own after-hours time in making our studies more profitable. Marie Poland Fish, William H. Mowbray and Paul Perkins of the Narragansett Marine Laboratory, and William E. Schevill and William A. Watkins of the Woods Hole Oceanographic Institution kindly gave us copies of recordings they had made, independently, of captive *Inia* and they both also made many helpful comments and suggestions on a late version of our manuscript. Financial support for certain phases of the work came from the National Science Foundation (grant no. GB-1189), the National Institute of Mental Health (grant no. MH-07509-01), the American Philosophical Society (grant no. 3755-Penrose), and the Museum Associates of the Los Angeles County Museum of Natural History. Technical support for certain parts of the study came from the Naval Ordnance Test Station, China Lake, California. William E. Sutherland of the Lockheed-California Company, Los Angeles, provided helpful technical advice. The photographs of the live animal are by Fred Jenne and are used here through the courtesy of Earl S. Herald, Steinhart Aquarium. Photographs of the sonagrams are by Armando Solis and Mike Hatchimonji, Los Angeles County Museum of Natural History.

Study Sites and History and Description of Animals Studied

1. One juvenile male (47.5 inches, 121 cm., in snout to caudal-notch length on first recording session; 52.5 inches, 133 cm., in snout to caudal-notch length on second recording session). Recorded and observed through the courtesy of Earl S. Herald, Robert P. Dempster and Thomas Green at the Steinhart Aquarium, California Academy of Sciences, San Francisco, Cali-

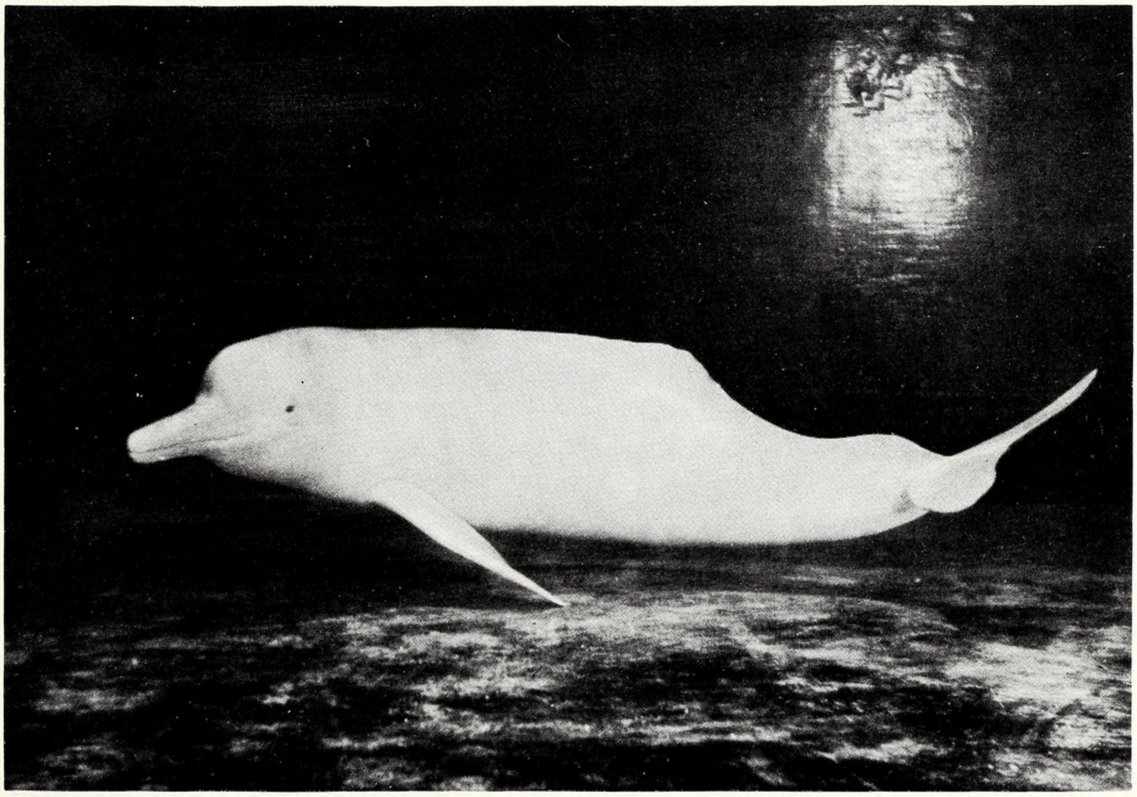

Figure 1. Inia geoffrensis. Juvenile male ("Whiskers") from the Amazon River drainage near Iquitos, Peru, at the Steinhart Aquarium in late 1964.

fornia, on 30 September 1964 (six days after its arrival there) and on 5 May 1965. This animal was also observed on several intervening and subsequent occasions when the recording of phonations was not attempted. The animal was originally captured in the Amazon drainage near Iquitos, Peru, and was held in Florida for some six weeks before it was received in San Francisco. On our first recording session, it had not been subjected to any training other than to take dead food fish from the hand. By the second recording session this training had been supplemented with exposure to a large and a small ball and a small hoop. Recordings were also made in April, 1965, by Dr. Fish and her associates. Some historical and behavioral observations on this animal (Figs. 1 and 10) were presented by Herald and Dempster (1965), Dempster (1965), Richardson (1965), and Caldwell, Caldwell and Evans (*In press*).

2. One juvenile male (49.2 inches, 125 cm., in snout to caudal-notch length). Recorded and observed through the courtesy of John A. Moore at the Monte Vista Zoological Park, Bloomington, California, on 12 September 1964, after being there for at least six weeks and possibly for as long as two months. The animal was originally captured in the Amazon drainage near Iquitos, Peru, and was flown directly to California. It had not been subjected to training other than to take dead food fish from the hand.

3. Two subadult males (about 69 and 73 inches, 175 and 185 cm., in snout to caudal-notch length). Recorded and observed through the courtesy of Kent Burgess, David W. Kenney and Donald D. Zumwalt at Sea World, San Diego, California, on 17 April 1965 (10 days after their arrival there) and on 18 and 19 February 1966. During the first session we had a flat (± 2 db) recording capability of 40 to 20,000 cycles per second; and during the second (two-day) session this was increased to a flat response (± 2 db) of 110,000 cps, with a useable response of 150,000 cps. The animals were originally captured in the Amazon drainage near Iquitos, Peru, and were flown directly to California. They had not been subjected to training other than to take dead food fish from the hand, but on occasion they had been allowed to play with small objects placed in their tanks. Recordings were also made in April, 1965, by Fish, Mowbray and Perkins from the Narragansett Marine Laboratory. Some preliminary results of our studies with these animals have been described by Caldwell, Caldwell and Evans (*In press*).

4. Two subadult to adult males (69 and 76.5 inches, 175 and 194 cm., in snout to caudal-notch length). Recorded and observed for 70 minutes through the courtesy of Winfield H. Brady at the Aquarium of Niagara Falls, New York, on 8 April 1966 after being in captivity for approximately five months. The animals were originally captured in the Amazon river about 60 miles from Manaos, Brazil, and were flown directly to Niagara Falls. They had not been subjected to training other than to take dead food fish from the hand.

These animals were contained in a tank with a 49.3-inch (125-cm.) male *Sotalia* sp. from near Manaos. Consequently, inasmuch as we cannot be sure which animals produced which sounds, this 70-minute listening period is not included in Table 1. However, no sounds were recorded, which we suspected originated from the *Inia*, that we had not recorded elsewhere under uncontaminated conditions. Schevill and Watkins had recorded these same three animals under these conditions about one week previous to our visit, with similar results. The behavior of the two *Inia* at Niagara Falls was similar to that observed for captive *Inia* elsewhere.

5. One adult male (about 85 inches, 216 cm., in snout to caudal-notch length) and one adult female (about 75 inches, 191 cm., in snout to caudal-notch length). Recorded and observed through the courtesy of Lawrence Curtis and Gary T. Hill at the James R. Record Aquarium, Fort Worth Zoological Park, Fort Worth, Texas, on 26 June 1965. The male had been captive there for 34 months and the female for 37 months, and both had been held in Florida for an unknown period of time prior to their arrival at Fort Worth. The animals originally were captured in the Amazon near Leticia, Colombia. They had been subjected to simple training procedures, which included taking dead food fish from the hand, jumping clear of the water in a vertical manner for food, and jumping and grasping a ball in order to raise a flag. Most of the activity other than simple feeding was performed by the male. Some historical and behavioral data on these animals were presented by Curtis (1962), Walker (1964: 1089), Phillips and McCain (1964), Hill (1965), and Caldwell, Caldwell and Evans (*In press*).

6. One adult and one juvenile of undetermined sex and size (very approximately, about 60 and 70 inches, 152 and 178 cm., in snout to caudal-notch length) were observed but no recordings were attempted on 28 June 1964, at Homosassa Springs, Florida. The animals were originally captured in the Amazon near Leticia, Colombia. They had not been subjected to any training, as far as we could determine, other than to take dead food fish.

PHONATIONS

All of the recordings resulting in Figures 2 through 9 and in Table 1 were made at a tape speed of 7.5 inches, 19 cm., per second with a Uher 4000 Report-S recorder, which at that tape speed had a flat frequency response of 40 to 20,000 cycles per second. An Atlantic Research Corporation model LC-57 hydrophone was used, with a special preamplifier designed and built for the system by William E. Sutherland of the Lockheed-California Company. Sonagrams (sound spectrograms) were prepared on a Kay Sona-Graph model 6061A Sound Spectrum Analyzer calibrated from 85 to 8000 cps. When the recorded tape speed is reduced by half, and then fed into the analyzer, the

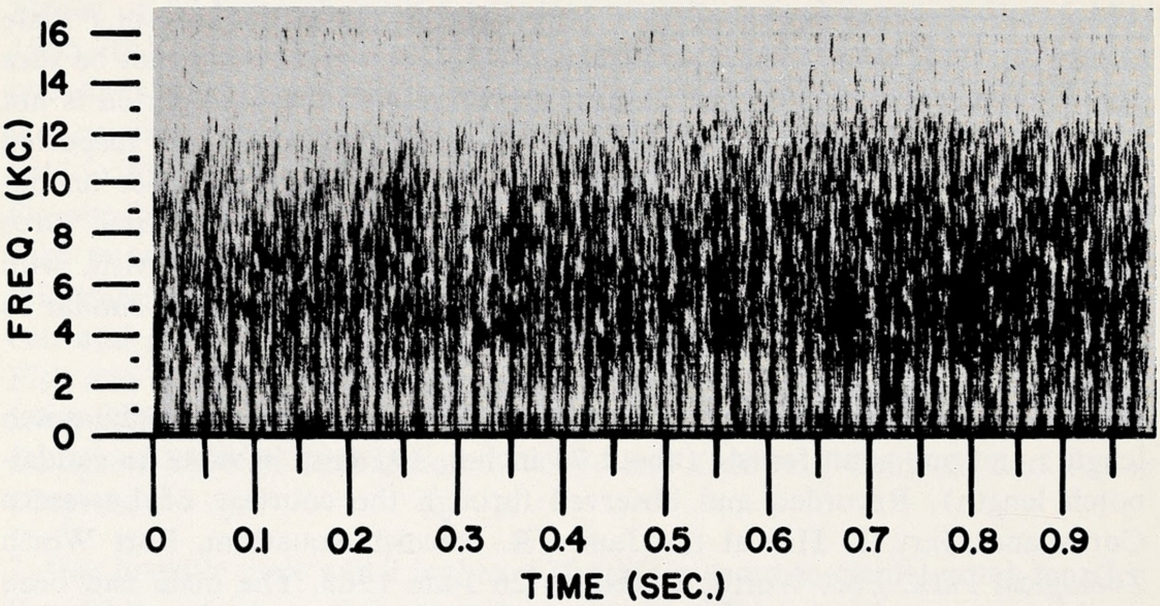

Figure 2. Phonation of *Inia geoffrensis.* Echolocation-like run on solid object (hydrophone) by a large adult of undetermined sex. Clicks emitted in darkness at the Fort Worth Zoo, June 26, 1965.

response of the latter is increased to 16,000 cps. The effective filter band width used in all of the analyses was 600 cycles.

Sounds were recorded with this system when the animals were resting or swimming leisurely, when swimming rapidly, during feeding both in isolation and in competitive situations, when both strange and familiar objects

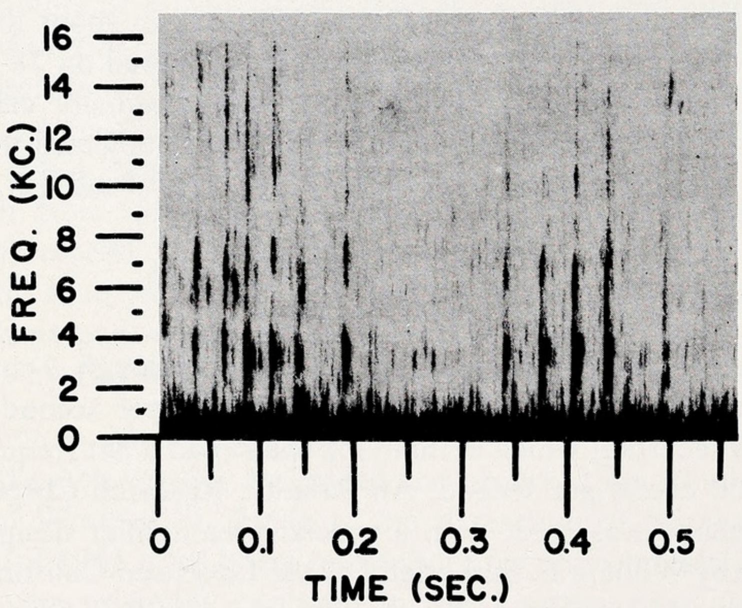

Figure 3. Phonation of *Inia geoffrensis.* "Grate." No stimulus observed. Emitted in daylight by an isolated juvenile male at the Steinhart Aquarium, September 30, 1964.

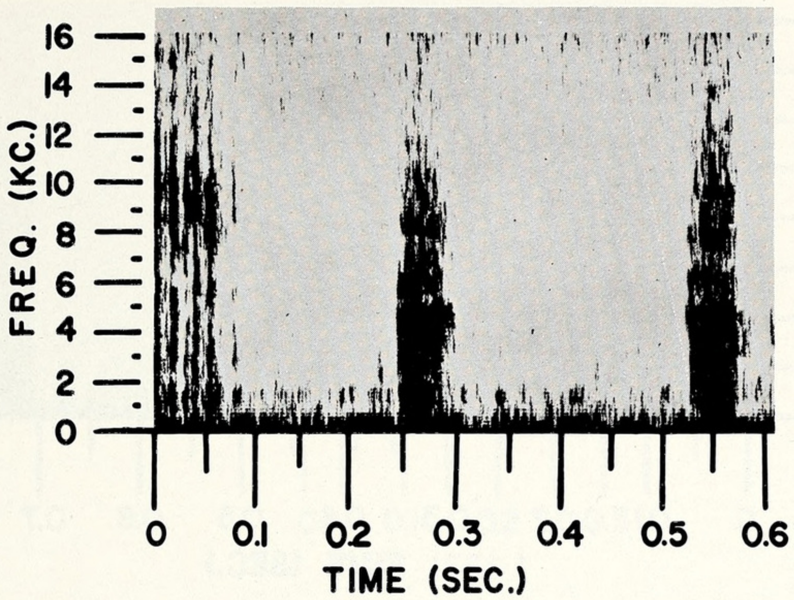

Figure 4. Phonations of *Inia geoffrensis.* "Squawks." No stimulus observed. Emitted in daylight by an isolated juvenile male at the Steinhart Aquarium, September 30, 1964.

were presented, during exposure to sudden loud noises and to lights flashed out of darkness, in isolation and with another animal of the same species of the same or opposite sex, in light and darkness, and with another *Inia* of the same sex as well as another animal of the same sex (all males) belonging to a different cetacean family (*Sotalia* sp., family Delphinidae).

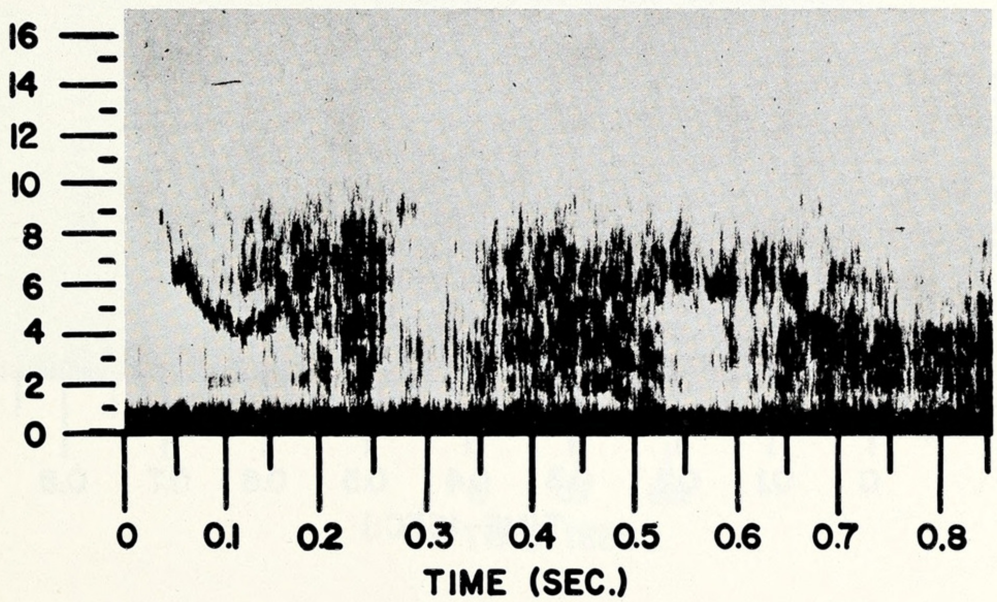

Figure 5. Phonation of *Inia geoffrensis.* "Screech." No stimulus observed. Emitted in daylight by an isolated juvenile male at the Steinhart Aquarium, September 30, 1964.

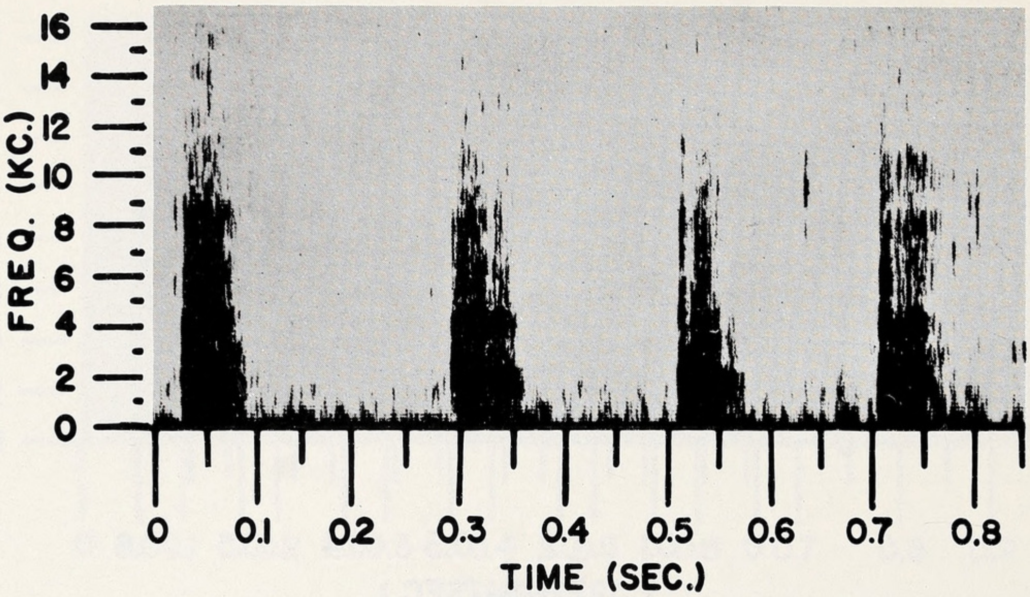

Figure 6. Phonations of *Inia geoffrensis*. "Barks." No stimulus observed. Emitted in daylight by an isolated juvenile male at the Steinhart Aquarium, September 30, 1964.

All of the *Inia* phonations we have observed consist of trains or bursts of impulsive broad-band clicks, characteristic of most of the odontocetes recorded to date. The major difference in *Inia* clicks, versus those of other delphinids, is the apparently limited frequency content of individual clicks (little energy above 10 KC). In contrast, *Steno bredanensis* clicks contain

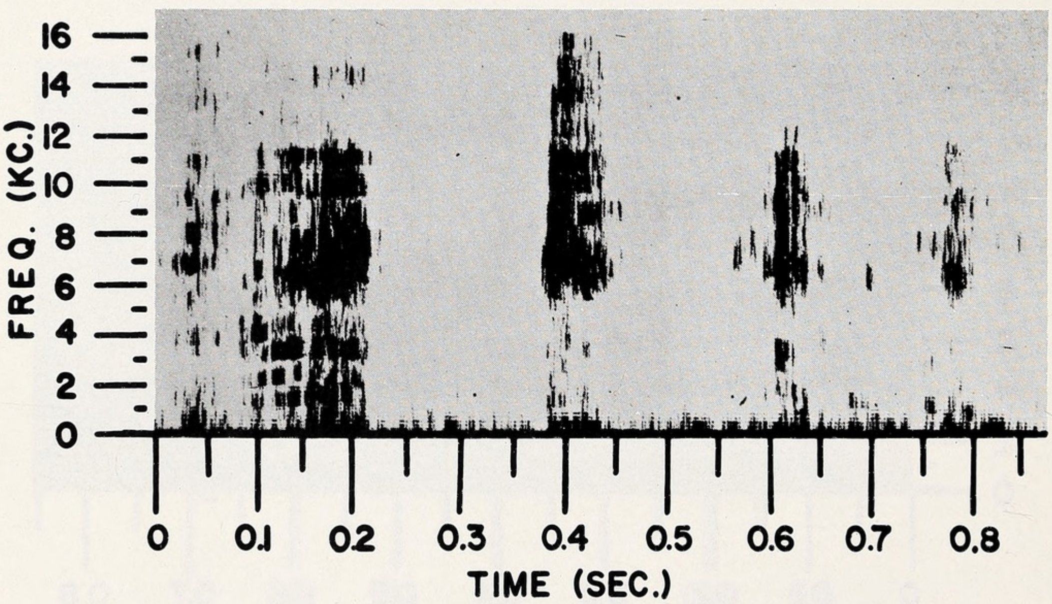

Figure 7. Phonations of *Inia geoffrensis*. "Whimpers." No stimulus observed. Emitted in daylight by an isolated juvenile male at the Steinhart Aquarium, September 30, 1964.

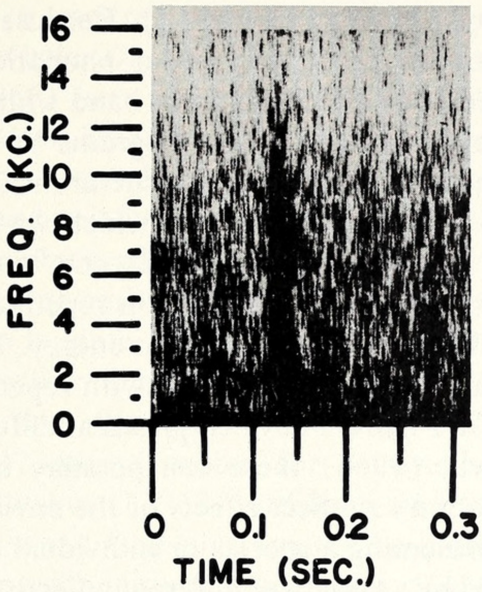

Figure 8. Phonation of *Inia geoffrensis*. "Crack." Emitted in the dark when a bright light was suddenly flashed into the eyes of an adult animal, sex not observed, at the Fort Worth Zoo, June 26, 1965. This "crack" immediately followed a train of clicks.

energy at frequencies in excess of 100 KC (Norris and Evans, 1966). Whether this lower frequency limit is due to a characteristic of the species or an instrumental limitation remains to be tested.

The *Inia* clicks recorded were of three types: click trains at repetition rates of 30 to 80 clicks per second, single intense clicks, and sounds of the

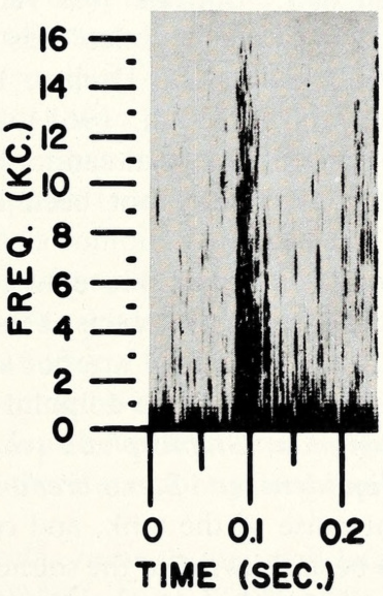

Figure 9. Phonation of *Inia geoffrensis*. Jaw "snap" or "click." Made in daylight by a mature animal, sex not observed, as it caught a small live goldfish at the Fort Worth Zoo, June 26, 1965.

burst-pulse type described by Watkins (1966). Because of the extremely fast repetition rates involved in the latter type of phonation and the resolution limits of the analyzer determined by the filter band width used (600 cps) this group of sounds is characterized on the sonagrams by having a complicated harmonic structure. The complexity of this structure is indicative of repetition rates involved (Figs. 4, 5, 6, 7). The sounds which we have listed in Table 1 as "squawk," "squeal," "squeaky-squawk," "screech," "bark," and "whimper" are all of this burst-pulse type, but vary only in repetition rate and frequency (in KC) of energy, and particularly of greatest energy. The click trains shown in Figures 2 and 3 are representative of those with repetition rates of 30 to 80 per second. The pulses in Figure 3 have emphasis at different frequency bands. As suggested by Schevill (1964) these can possibly be ascribed to uneven response of instrumentation or reflect effects of the environment and structure in the actual sound representing a species or individual characteristic (voice).

Although described by a variety of different adjectives, *e.g.*, "echolocation-like run," "grate," "squeal," "squawk," "screech," "bark," etc., all of these audible sounds consist of trains or bursts of clicks which occur at various repetition rates. Clicks occurring at rates of 10 to 20 per second can be resolved by the observer to consist of individual pulses or clicks and thus have a grating or clicking quality. Clicks occurring at faster repetition rates (40 per second and more) are not recognized by the human ear as separate clicks but rather the whole train takes on a tonal quality and thus becomes an "echolocation-like run," "creaking door," "buzz," or a "screech," depending on the click rate. This same explanation holds for "squawks" and "barks" which are short bursts of clicks (0.05 to 0.3 second duration) at relatively high click repetition rates (150 per second and up). "Squeals" (as referred to by Schevill and Watkins, 1962; Schevill, 1964) and "whistles" (as referred to, for example, by Evans and Prescott, 1962; Evans and Dreher, 1962; Lilly, 1962; Dreher and Evans, 1964; Caldwell and Caldwell, 1965) are tones, pure and most often with a simple harmonic structure, that cannot be resolved into individual clicks. Signals of this latter type have not been observed to be produced by *Inia*.

In considering the numbers of audible emissions in each category described (Table 1) it is well to note two facts. First, that the phonations of *Inia* are of such low sound level that they are not as readily audible as those observed by us in several species of marine dolphins (*e.g., Tursiops truncatus, Tursiops gilli, Stenella plagiodon, Globicephala scammoni, Pseudorca crassidens, Lagenorhynchus obliquidens,* and *Steno bredanensis*). Thus some sounds may be lost in the ambient noise of the tank, and our counts may err on the low side. In addition, it has been shown that the sound field of certain delphinids is extremely directional, and therefore if the animals making them happened to be facing away from our non-directional hydrophone, the sound might not have been recorded at its full intensity, if at all. William E. Schevill and William A. Watkins (*pers. conversation*, April, 1966) have found that there is a marked decrease in low-frequency sound intensity when soniferous individuals of the killer whale, *Orcinus orca*, turn away from the hydrophone. Norris and Evans (1966) have observed a similar effect with high-frequency sounds produced by *Steno bredanensis*, *Stenella attenuata* and *Stenella* sp.[4]

Keeping these facts in mind, however, Table 1 does represent a reasonable picture of the types and relative numbers of the audible sounds emitted by *Inia geoffrensis* as we observed them under a variety of captive conditions. The maximum number of emissions per animal per hour observed with this species was 52.5. This is quite low in comparison with sound emission rates in *Tursiops truncatus*, which in many cases will exceed 180 emissions per hour, and somewhat lower than the approximately 88 emissions per animal per hour recorded in a 47-minute session for captive belugas, *Delphinapterus leucas*, by Fish and Mowbray (1962), although we have observed the general behavior of captive *Inia* and *Delphinapterus* to be quite similar. It should also be noted that sound emission in some species (*e.g.*, *Tursiops truncatus*, *Stenella attenuata*, and *Stenella* sp.[4]) has been found by Powell (*In press*) to be very periodic with quite regular cycles of vocalization and nonvocalization. It is thus difficult to quantify the "vocalness" of *Inia* in comparison to marine dolphins, but in general it is safe to say that *Inia* is less vocal, at least in the audible range, than most marine delphinids observed to date.

As noted above, no pure-tone "whistles" were recorded, nor have any of the attendants with whom we have talked reported an audible whistle from any of the *Inia* in their charge. In this regard it is interesting to note that two delphinids which are considered by many workers to be the more primitive members of the family, or even in a separate family, also have been reported not to produce sounds other than bursts and trains of clicks. Busnel, Dziedzic and Andersen (1963, 1965) and Busnel and Dziedzic (1966) reported on recordings of captive *Phocoena phocoena* and Evans (unpublished findings) has recorded captive *Phocoenoides dalli*.

A "screech," (Fig. 5), a harsh raucous sound, was recorded on only one occasion. This is a burst-pulse type sound with a high pulse repetition rate which on a sonagram forms a contour similar to, but not directly related to, the pure-tone whistle contours of many delphinids. Similar "click contours" have been illustrated for *Phocoena phocoena* by Busnel, Dziedzic and Andersen (1963) and Busnel and Dziedzic (1966: figs. 45, 47 and 49). The "screech" that we figure here was recorded with the gain on the recorder turned up sufficiently high to pick up the faint sounds emitted by the species. When this single loud sound was recorded, therefore, the system was somewhat overloaded.

[4]We have not applied a specific name to the small long-snouted Hawaiian spinner porpoise discussed here. However, F. C. Fraser (*pers. comm.* to D. K. Caldwell, 1965) has suggested that the name *Stenella roseiventris* (Wagner) be applied. Published precedence for the use of this name, also based on Fraser's personal remarks to the authors, may be found in Brown, Caldwell and Caldwell (1966) and Morris and Mowbray (1966).

TABLE 1. Types and relative frequency of occurrence of non-extraneous phonations by six captive *Inia geoffrensis*. See text for details of animals and study sites. Two additional animals were recorded for 70 minutes at the Aquarium of Niagara Falls, but contamination in the form of a young *Sotalia* sp. was present and thus we have not tried to include the possible *Inia* sounds here. Numbers in parentheses indicate number of each phonation per animal per hour.

Study Site	Number of Animals	Number of Minutes Recorded	Echolocation-like Run[1] (Fig. 2)	Creaking Door[1]	Grate[1] (Fig. 3)	Squawk[2] (Fig. 4)	Squeaky-squawk[3]	Squeak[3]	Screech[3] (Fig. 5)	Bark[3] (Fig. 6)	Whimper[3] (Fig. 7)	Crack[3] (Fig. 8)	Total number of Phonations
Steinhart	1	283	2 (.42)		2 (.42)	61 (12.9)	107 (22.7)	9 (1.9)	3 (.64)	4 (.85)	60 (12.7)		248 (52.5)
Bloomington	1	60	1 (1.0)	1 (1.0)	26 (26.0)			1 (1.0)					29 (29.0)
Sea World	2	135			11 (2.4)	4 (.88)		3 (.67)		10 (2.2)		2 (.44)	30 (6.7)
Fort Worth	2	140	63 (13.5)		3 (.64)	2 (.43)						1 (.21)	69 (14.8)
Totals	6	618	66	1	42	67	107	13	3	14	60	3	376

[1] Contain audible pulses at ⅛ recorded tape speed.
[2] Although at recorded tape speed these all sounded the same, at ⅛ recorded tape speed some did and some did not contain audible pulses.
[3] Do not contain audible pulses at ⅛ recorded tape speed.

An *Inia* "squeal" was reported to us by Earl Herald and by Lawrence Curtis, usually made when the animals in their charge were taken out of the water. A "squeal" was also reported to Layne and Caldwell (1964: 102), made by an animal out of water during transport in an airplane, and by an animal (possibly the same one) in water at Silver Springs, Florida. While we have no recordings of any of these "squeals," it is possible that the sound which we have described as a "screech" is involved. We had first used the term "squeal" to describe it in our notes, and the fact that it has a somewhat contoured quality on a sonagram may be further evidence that the same sound was heard by the observers noted above.

Schevill and Watkins (1962) did not attempt to apply word descriptions to the *Inia* sounds they included on their record. However, upon listening to the record we hear the sounds which we list in the present report as "echolocation-like run," "whimper," and "bark." The sonagram which Schevill and Watkins (1962: fig. 4) included appears to be the lower portion of a "bark" (see our Figure 6). Although they only show frequencies to four kilocycles per second, it appears that the frequency range for the sound illustrated by Schevill and Watkins actually extends higher, as it does in the "barks" we recorded (Fig. 6).

Adults: For the two adults at the Fort Worth Zoo we were able to correlate three audible sounds with observed behavior. These were low-frequency click trains made on the unfamiliar hydrophone (Fig. 2) and on live food fish; indistinct low-frequency clicks followed by a loud "crack" elicited by suddenly flashing a bright light in their eyes out of darkness (Fig. 8); and a jaw "snap" or "click" that was produced when one of the animals caught and bit down suddenly on a live goldfish (Fig. 9). This last was not made when the *Inia* chewed, but only as they caught the fish in one quick jaw snap.

Pulsed sounds have been experimentally demonstrated to be echolocation devices in only one, or possibly two, cetaceans: *Tursiops truncatus* (see Kellogg, 1961; Norris, *et al.*, 1961) and *Phocoena phocoena* (see Busnel, Dziedzic and Andersen, 1965). However, such sounds are known to be produced by, and are strongly suspect of being echolocation devices in many other odontocetes (see Norris, 1964). We were interested then in knowing first whether this pulsed sound as recorded by Schevill and Watkins (1962) is characteristic of *Inia geoffrensis* and secondly to learn whether it is utilized as an echolocation device by this primitive species. Layne (1958: 16) suggested that this may be so because of the ability of wild *Inia* to avoid nets. Layne and Caldwell (1964: 95) included behavioral observations on two captive animals that suggested their use of echolocation in environmental exploration. Based on observations and correlations with behavior, our conclusion is that the low-frequency pulsed sounds described as "echolocation-like runs," "creaking door," or "grate" are probably utilized by the adult *Inia* in echolocation. Both males and females demonstrated this ability. The use of the more rapidly-pulsed sounds such as the "squawk" (Fig. 4) for echolocation is more doubtful.

The low-frequency echolocation-like runs were made most frequently as the animal approached the hydrophone (Fig. 2). We were able to observe this visually in both daylight and artificial light. The aquarium in which we worked with the adults was constructed so that we could obtain almost total darkness, and therefore we were able to record the adults under this condition also. We could not see the animals at the time, but the tapes make it apparent that the audible trains of clicks almost invariably precede the sound of the animals rubbing against the listening gear. When we introduced live fish into the tank in darkness, audible click bursts, and the subsequent jaw "click" associated with fish captures were also produced.

Trains of audible clicks were emitted both in light and darkness. Quantitatively, however, the number produced in darkness was 25.3 per animal per hour, as opposed to 6.9 per animal per hour in daylight or artificial light.

The "crack" elicited under stress (Fig. 8) is virtually the same as that produced by *Tursiops truncatus* under the same fright stimulus (Caldwell, Haugen and Caldwell, 1962). However, we cannot state positively that this is not a jaw clap as we heard it only momentarily as the light was flashed.

The jaw "click" or "snap" produced (Fig. 9), apparently by the teeth hitting together, when an animal caught a small fish, is loud enough to be heard by a diver underwater, as the trainer, Gary Hill, reported having noted this sound when he was doing underwater feeding of the Fort Worth animals.

No audible phonations accompanied sexual behavior that resulted in an erection by the male. None occurred when the *Inia* were presented with familiar objects.

Inasmuch as no *Inia* whistles have been recorded, it is therefore likely that *Inia* makes use of clicks in communication as well as in echolocation, much like *Physeter* and *Phocoena*.

A puzzling loud "gurgling growl," obviously not of extraneous (to the tank) origin, was recorded several times from these adults. Evans (unpublished) has recorded these sounds emanating from captive *Tursiops truncatus* during feeding and accompanying defecation, and it is suggested that they are the sounds of digestive processes within the animal and the nature of the sound lends itself to this explanation.

Subadults and Juveniles: Although the two subadult males at Sea World were capable of creating a train of audible pulses or clicks (Table 1), we were unable to elicit them, either in daylight or dark, on a specific stimulus such as feeding dead fish, or by the presentation of strange or familiar objects. Even when obviously startled by loud noises or having objects suddenly thrown at their heads they did not vocalize audibly but only jerked and swam violently away. None of the audible sounds by these animals listed in Table 1 were correlated with any stimulus that we could note. Dr. Fish and her associates recorded audible clicks from these two animals when the water was murky. In addition, those workers recorded audible sounds described by them later as "chirps" and "squawks." Upon listening to copies of their tapes, we would have listed the "chirps" as "squeaks" and the "squawks" we would have listed as "squeaky squawks."

The audible vocalizations of the young males at Bloomington and at the Steinhart Aquarium were similarly unrelated to observable stimuli. When the Steinhart animal was 52.5 inches (133 cm.) long, we worked with him intensively at night attempting to obtain a positive correlation of audible click trains and feeding. We were totally unsuccessful, although we were able to work in a dark building with only low-intensity ambient light from a nearby window. Dead fish were first thrown into the tank with a splash and varying amounts of time allowed to elapse before turning on the lights to see whether the fish had been found. The animal usually found the fish in six seconds or more, but failed in four seconds or less. No phonations were heard and we have no explanation for his ability to locate the sinking fish in the dark after the initial cue of the splash unless his hearing is so acute that he could actually hear it falling through the water, his tactile sense so well developed that currents generated by the falling fish could be detected at close range after the animal had generally located the fish from the initial splash, or he (and all *Inia*) has the ability to echolocate in the high-frequency (inaudible to humans) range.

Layne and Caldwell (1964: 96) discussed the probable sensory function of the structurally-complicated snout bristles of *Inia,* and the young animal under study was so well endowed with them that he was given the name "Whiskers." Gustatory cues are probably ruled out by the fact that if the fish were silently either slipped into the tank and allowed to drop or if quietly hand held in the tank, the animal failed to find it in several minutes. If in fact he was able to hear or "feel" the fish falling through the water after the attention-getting cue of the initial splash when a fish was thrown, then in the latter experiments without the splash it follows that although the fish falling through the water would make the same sound or generate the same currents as before, the splash must be necessary to draw his attention. The fact that this animal is obviously able to emit audible sounds that we normally consider echolocation bursts, but did not do so in these experiments, makes for a puzzling picture. One possibility that suggests itself is an investigation of the factor of learning in this species. Although audible pulsed phonations are obviously present in the very young, *i.e.,* the four-foot (122 cm.) male at Bloomington, California, the use of these same phonations to echolocate objects may require experience. Fish, Mowbray and Perkins told us in early 1966 that they recorded good audible click trains (over 60 in a 22-minute period) from the Steinhart Aquarium young male. These observers suspected that the click trains were emitted in response to spectator activity, insertion of the hydrophone and fish, movement of large garfish *(Lepisosteus spatula)* in an adjacent and connected enclosure, movements of the scientific investigators, and perhaps spontaneously. However, like us, these investigators apparently did not record click trains produced concurrently with a specific situation which would seem to call for the use of echolocation.

The possibility that the animal was echolocating in the very high-frequency ranges, inaudible to the human ear, cannot be discounted, but our studies on this possibility have been inconclusive (see Caldwell, Caldwell and Evans, *In press*).

VISUAL ACUITY

The eyes of *Inia* are so small that doubt has been raised as to their being functional. However, Layne (1958: 16) concluded that vision, at least above the surface of the water, seemed good in this species in the wild. Layne and Caldwell (1964: 93) suggested that in captive animals it is also good under-water as well as above. The behavior of the eight animals that we observed intensively leads us to believe that vision is not only acute but is the preferred or primary device for environmental investigation. Although animals tend to use any sensory device available, there is usually a tendency to rely on one in preference to the other if the preferred sensory input is available. Since our work was done in aquaria, good visibility by the animals was usually present during daylight hours. All of the eight animals visually inspected any change in their environment, including new sounds, when they visually inspected the source. They visually inspected food offered them, and if the food was dropped or thrown into the tank, they searched for it visually. Only rarely in the two adults at Fort Worth were click trains added to visual inspection in daylight. Tiny bits of left-over food were found visually. As mentioned earlier, no echolocation-like bursts either day or night were heard from the juveniles or subadults during observed episodes of environmental investigation. They were also rare in the adults if sufficient light was available for us to observe. It was noted that the eyes of the adults at Fort Worth demonstrated a pink eye shine in the dark, which is indicative of good vision in low light intensities (Walls, 1963). Unfortunately, the degree of night vision has not been investigated in any cetacean, but our evidence suggests that in *Inia* it is excellent.

Good vision in this species is apparently less hampered by the reduced size of the external opening of the eye (the eye itself is comparatively large and well-enervated) than by the large bulging cheeks. These cheeks are so enlarged that they apparently prevent the animals' seeing much below the horizontal plane of the eye. This problem is solved by their turning over and swimming upside down, whereby a good field of vision is opened up below the animal. The small male at Steinhart Aquarium always visually checked the bottom of his tank after feeding by swimming upside down around the tank and recovering the small bits of fish debris lost during feeding. If he dropped a fish on the bottom he immediately turned over and swam upside down around the tank until he apparently saw it and then recovered it. He also swam upside down when pursuing live fish near the bottom of his tank. Upside down swimming in this species in semi-wild conditions has been noted as occurring often (Layne and Caldwell, 1964: 88f.; Allen and Neill, 1957: 328) and increased visibility to the *Inia* is the probable explanation. Although we did not always see them actually find food or other objects on the bottom, we observed this upside down swimming in all of the animals we studied, including the two at Homosassa Springs, Florida, and the two at the Aquarium of Niagara Falls. Mr. Brady told us that more of this upside down swimming occurred when the latter animals were first captured than when we observed them some five months later, suggesting that it is a natural behavior that for some reason began to be abandoned by the captives.

Layne (1958: 19) noted that on one occasion the gaping jaws of a wild *Inia* appeared above the surface of the water under circumstances which suggested that it was feeding. That this was probably the case is suggested by our underwater observations of the Fort Worth *Inia* during a sequence in which they were being fed live goldfish. The small fish swam near the surface, and in slowly pursuing them, the *Inia* positioned themselves at about a 45° angle just under the surface with the jaws extending out of the water. In attempting to catch the fish, which they eventually did, the *Inia* opened and closed their jaws in a manner similar to that described by Layne. As the upside down swimming position seems to permit better vision for objects on the bottom, so did the upright angled position appear to make vision over the bulging cheeks more practical for observing a small target just beneath the surface and just ahead of the *Inia*—more so than would a direct horizontal head-on approach to the target. We have also noted that *Inia* fed from the surface at the side of their tank also assume a similarly angled attitude, in which they are obviously visually observing the feeder, and then open and close their jaws as if begging from the attendant.

MISCELLANEOUS BEHAVIOR

Curiosity and Manipulation: It is impossible not to compare the striking difference in the intensity and duration of fear in this species with what we have noted in the Atlantic bottlenosed dolphin. A naive animal of this latter species requires many hours or days to acclimate to strange objects (McBride and Hebb, 1948; Caldwell and Caldwell, 1964). Although young animals and captives of long duration may adjust more quickly to strange objects than the recently captured adults, it usually takes several days for any individual *Tursiops* to approach unusual objects in its environment without reinforcement of approach behavior.

None of the *Inia* ever showed any fear of the hydrophone. Within minutes after introduction of the listening gear they often were using it as a play object, tactual stimulant or sex object. Loud tapping against the walls of the aquaria caused immediate approach toward the direction of the noise. With the initial fear so evident in the bottlenosed dolphin, the curiosity and playfulness of *Inia* became immediately evident. The small male at the Steinhart Aquarium demonstrated a duration of three hours almost continuous play with the hydrophone, which he had approached immediately on its being introduced. We have never observed such behavior by any *Tursiops* of any age, sex or acclimation to captivity. The play by the *Inia* was discontinued only when the hydrophone was removed.

Sexual play: Although the Steinhart Aquarium animal was only 52.5 inches (133 cm.) long at the time just noted above, he had several erections while playing with the gear when it rubbed against his genital area. This same animal had previously been observed masturbating against the net webbing which divided his tank (Earl S. Herald, *pers. conversation,* 1965, and motion picture films in his and the Caldwells' files), and along the corner of the tank where the wall met the floor (Edward Mitchell, *pers. conversation,* 1965; observations by the Caldwells May, 1966).

The animal also once displayed an erection that lasted several seconds immediately following defecation.

Mitchell (*pers. conversation,* 1965) also reported observing the same animal in January, 1965, at the Steinhart Aquarium as it tried to "eat" drops of water which were falling into its tank from an unseen source high above. Mitchell noted that the *Inia* attempted to "eat" the drops about once every minute and that the dolphin became progressively more agitated on each attempt. After the procedure continued for about five minutes, the *Inia* pulled away from the area of the dripping water and clumsily bumped into a wall of netting that divided his tank. At this time he had an erection and proceeded to masturbate against the corner of the tank as noted above. Mitchell reported that while masturbating the *Inia* would rub the tip of its snout against the net and sporadically rotate its body and thus its snout while still in contact with the net. The dolphin's eyes reportedly were open during all of the observed display. This behavior was essentially the same as that recorded in the film noted above which was made at about the same time. After the sexual display observed by Mitchell, which lasted for about 10 to 15 minutes, the *Inia* lay on the bottom of the tank on his right side or upside down without actively moving, or else slowly swam around the tank and surfaced to breathe very slowly and apparently with his eyes closed.

We have also observed this animal assume the upside-down stance while it was resting or sleeping on the bottom of the tank. The position (Fig. 10) is so unusual that we were startled when we first saw it, and a number of visitors to the aquarium have been overheard to comment that the animal seemed to be dead. Such a position must be associated with the apparent reduced fear responses of *Inia,* because in nature it would seem to leave the animal open and vulnerable to attack. However, according to available reports, when one considers that in nature *Inia* apparently has no predators other than man on rare occasions, and that it normally lives in an oft-times shallow and rather

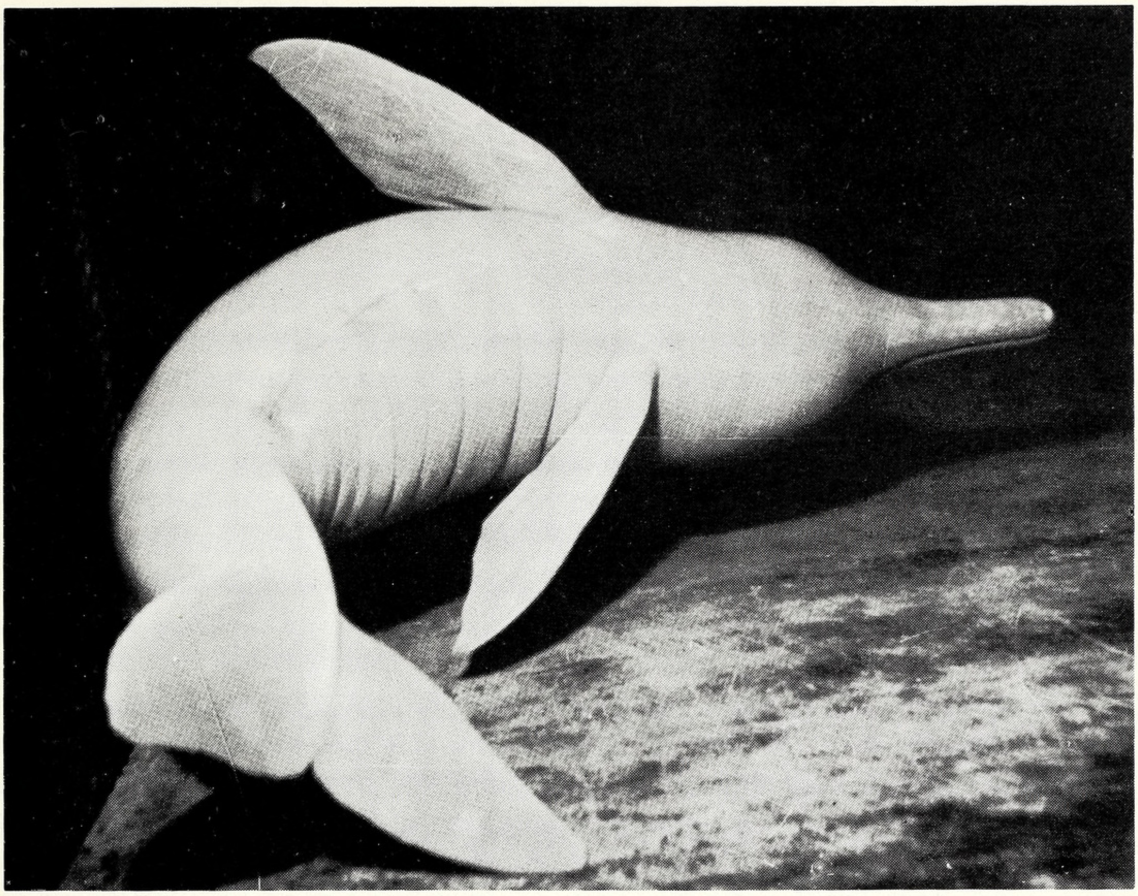

Figure 10. Inia geoffrensis. Juvenile male ("Whiskers") in a typical upside-down sleep position at the Steinhart Aquarium in late 1964. Also note the bulging cheeks.

protected and less hostile environment than that provided by the open sea, this attitude of rest should be advantageous because it would seem to permit a deeper sleep, if only for a brief period, than that achieved by marine cetaceans which apparently only lightly doze while resting near the surface or while actually on the move.

We suggest that the reduced fear response toward strange objects may also be related to the conditions in the natural environment of *Inia.* It lives in areas where it might encounter many more strange objects than a marine dolphin. Not only does *Inia* venture into small streams, lakes and even into flooded forest areas where there might be much debris as well as standing vegetation, but the main stream of the Amazon itself is noted for the great amount of floating debris that it continually carries. Evans (unpublished) has noted a similar lack of fear toward strange objects by harbor seals *(Phoca vitulina)* in California. Like *Inia, Phoca* lives in areas such as lagoons, coastal rivers and bays where there may be more strange objects than more oceanic marine mammals normally encounter.

With further regard to sexual behavior, on one occasion during our observations at the Aquarium of Niagara Falls, the small male *Sotalia* in the tank with the two male *Inia* frequently rubbed the top of its head as if trying to scratch it. This behavior included rubbing against the sides of the tank, and swimming upside down to rub the top of its head along the floor of the tank. During this same period, one of the *Inia* was seen rubbing his genital region on several projecting pipes near one bottom corner of the tank. Shortly thereafter, the three animals were swimming together in a normal upright position when the *Sotalia* rose beneath the same *Inia* just noted and began to rub the top of its head against the underside of the *Inia,* including the genital region of the latter. The *Inia* had a full erection shortly thereafter which lasted for nearly a minute while the two animals remained together. During this time, and while both were swimming in a regular circular pattern around the tank, the *Inia* appeared to use the *Sotalia* as a sexual stimulus and even tended to force the smaller animal toward the bottom in an apparent attempt to masturbate against it. The *Sotalia* apparently had only accidentally stimulated the erection by the *Inia* when it rubbed against the underside of the larger animal, and it immediately appeared to try to escape the attentions of the *Inia* when the erection occurred.

In no case have we seen one of the masturbating *Inia* effect an ejaculation.

As noted above, we observed one attempt at intromission by the adult male *Inia* with the adult female at Fort Worth. The technique was similar to that we have often observed in captive marine delphinids. The male approached in an essentially upside down position beneath the female, at about a 30- to 45-degree angle to her, and attempted intromission from the inverted position. Lawrence Curtis, Gary Hill, and Gary K. Clarke, the latter now Director of the Topeka (Kansas) Zoological Park, have observed the breeding behavior of the Fort Worth pair in much greater detail and have photographed much of it. We understand that these observations are to be prepared for publication.

COMPETITIVENESS

With one exception, we observed none of the competition for food between the two sets of subadult males, at Sea World and at Niagara Falls, or the adult male and female, at Fort Worth, that is so prominent in Atlantic bottlenosed dolphins. *(T. truncatus)* during feeding. However, the number of *Inia* in each of the competitive situations was limited to two, and they were at all times well fed. Because of the expense of air-shipping these animals from South America, they are treated with even more exquisite care than the bottlenosed dolphins in that they are not subjected to difficult training programs or show procedures in order to secure their food. The dominant male at Fort Worth, in fact, jealously dominates the simple show there and will no longer allow the smaller female to perform. However, this does not appear to be a matter of competition for food because both animals are always fed to satiation.

The one observed exception to lack of food competition took place on 9 January 1966 at Sea World in San Diego. One of the subadult males, the least active one, had just taken a dead food fish from the hand of a feeder and was slowly swimming away with the limp fish trailing outside the side of its mouth. The other subadult male, usually more active, slowly swam up alongside the first *Inia,* head to head going in the same direction, and very deftly snipped off the trailing fish about midway the length of its long jaws and very close to the jaws of the first animal. This incident took place early in the day, before the animals had received much food from the public which is allowed to feed the *Inia,* and such behavior was not even suggested later on in the day after the animals had been well fed by the public. Earlier in the day when the competition had been observed, both the animals had very actively "begged" for food by swimming up to the side of the tank and opening their jaws to the observers standing there. While the *Inia* continued to accept food later in the day, they did not appear to actively "beg" for it and their general attitude was one of much less interest in food than it had been earlier.

Layne and Caldwell (1964: 103) noted two brief instances of food competition between a large and a small male; in one case the activity was very similar to that noted above at Sea World.

No food or other competition was noted between the two male *Inia* at Niagara Falls or between them and the smaller male *Sotalia* housed with them in a relatively small tank, although the *Sotalia* seemed to be hesitant about feeding from the hand of the attendant while the *Inia* were being fed.

On the other hand, Kent Burgess told us in May, 1966, that he has observed apparent competition for human affection between the two male *Inia* at Sea World.

SUMMARY

Adult *Inia geoffrensis* have an audible pulsed phonation that is concurrent with investigation and search situations. This apparent echolocation device is more frequently employed when visibility is poor but may be employed when visibility is good. Juveniles and subadults of the same species have a similar audible pulsed phonation, but in work on four animals of this class, we have not been able to demonstrate a correlation of the audible phonation and a situation that would indicate that it was used as an echolocation device.

Although an echolocation device apparently is available to at least the adults of the species, in our observations in aquaria it was not the sensory system of choice. Vision was apparently the preferred sensory device.

No pure tone whistles were recorded, but several other phonations are included in their repertoire.

Fear is less easily precipitated in this species than in the Atlantic bottlenosed dolphin, and it is of shorter duration. Curiosity, playfulness, and early and frequent sexual play are also characteristic of this primitive species.

Competitive feeding behavior so familiar in the Atlantic bottlenosed dolphin was not usual in the *Inia* studied.

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