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Seasonality of Reproduction in Amazon River Dolphins (*Inia geoffrensis*) in Three Major River Basins of South America

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ABSTRACT

Reproduction of Amazon River Dolphins, *Inia geoffrensis*, is generally reported to be highly seasonal; however, this conclusion is based on studies from only one area of *Inia* distribution from throughout the Amazon and Orinoco river basins. Our observations of live dolphins from the Orinoco, Amazon, and Mamoré river basins (in Venezuela, Peru and Bolivia, respectively) indicate that reproduction in *Inia* often occurs year-round, with seasonal peaks varying according to geographic location. *Inia* neonates in Peru and Bolivia were seen in all seasons, and were observed most often in falling water (season was defined by relative water level). Conversely, neonates in Venezuela were seen at the end of low water and in rising water, yet were never observed during falling water. *Inia* mating behavior in Peru was observed in all seasons, while mating was observed only during falling and low water in Bolivia. Our review of the literature from throughout the range of *Inia* indicates variation in reproductive seasonality, with year-round reproduction in some areas. Seasonality of peaks in births varied according to study area, and may be more closely associated with local environmental and prey conditions than with taxonomic relatedness, relative seasonal differences in water levels, or broad geographic distribution.

RESUMEN

La reproducción del delfín de rió Amazonico, *Inia geoffrensis*, es reportada como altamente estacional; si embargo, esta conclusión sólo se basa en estudios de un área en toda la distribución de *Inia* en las cuencas del Amazonas y del Orinoco. Presentamos los resultados de observaciones de delfines en las cuencas de los ríos Orinoco, Amazonas y Mamoré (en Venezuela, Perú y Bolivia), los cuales indican que la reproducción de *Inia* es todo el año, con picos estacionales variando de acuerdo a la localidad geográfica. Los neonatos en Perú y Bolivia fueron observados durante todas las estaciones, pero más a menudo en el descenso de agua (la estación fue definida por el relativo nivel del agua). La reproducción en Venezuela fue más estacional, los neonatos fueron observados al final de aguas bajas y en aguas creciendo, pero ninguna vez durante el descenso de agua. El apareamiento de *Inia* en Perú fue observado en todas las estaciones, mientras que en Bolivia el apareamiento fue observado solamente durante aguas en descenso y bajas. La revisión bibliográfica de todo el rango de *Inia* indica que hay una variación en la estacionalidad reproductiva, y que en algunas áreas la reproducción ocurre todo el año. Los picos estacionales de nacimientos variaron de acuerdo a las áreas de estudio y pueden estar asociados con condiciones ambientales y de disponibilidad de presa más que una relación taxonómica, la relativa diferencia estacional en los niveles de agua, o la amplia distribución geográfica.

Key words: Amazon; *Inia;* Mamoré; Orinoco; reproduction; river dolphins; seasonality; South America.

REPRODUCTION IN ODONTOCETES (a suborder of cetaceans that includes dolphins and porpoises) ranges from highly seasonal to year-round. In many species, reproductive seasonality is related to geographic distribution; for example tropical *Stenella* reproduce year-round (Barlow 1984), while at high latitudes, reproduction in *Phocoena, Monodon,* and *Delphinapterus* is highly seasonal (Leatherwood & Reeves 1983, Read 1990). Extreme latitudes may influence reproduction via extreme seasonal differences in photoperiod, water temperature, and prey abundance. Reproductive seasonality in some odontocetes however, such as *Tursiops,* has been shown to be flexible and inherent to populations, rather than correlated with latitude (Urian *et al.* 1996).

The Amazon River Dolphin, *Inia geoffrensis,* occurs in freshwaters of the Amazon and Orinoco river basins of South America, in the countries of Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela (da Silva 1994). Most of the published literature about Amazon River dolphin reproduction comes from the central Brazilian Amazon (Best 1984; Best & da Silva 1984; Brownell 1984; Best & da Silva 1989*a*, *b*, 1993; da Silva 1994; da Silva & Best 1996), where *Inia* births have been reported to be highly seasonal. Published information about seasonality of reproduction in *Inia* in other regions of its approximately 8 million km^2 range is scarce, but indicates geographic variation in timing and degree of reproductive seasonality, and year-round reproduction in some areas (McGuire 1995, McGuire & Winemiller 1998, Aliaga-Rossel 2002).

Inia occurs in the Neotropics, where water temperature and photoperiod remain almost constant throughout the year; seasonal differences are primarily between rainfall (wet and dry seasons) and corresponding river water levels (low, rising, high, and falling). Changes in water levels affect not only the quantity and quality of aquatic habitat available to fish, but also available to *Inia*. Fish reproduction and migrations are highly seasonal, although the timing of these events varies according to species (Goulding 1980). *Inia* are piscivores, and therefore prey biomass and availability are largely determined by seasonal water levels. *Inia* births in the Central Brazilian Amazon have been reported to occur during the local period of high water and the beginning of falling water, and Best and da Silva (1989a) hypothesized that these births coincided with increased

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access to prey fish, which become vulnerable as habitat and cover from previously inundated vegetation decrease with falling water levels. We were interested in determining if this hypothesis could be applied to *Inia* throughout its range, and if geographic differences existed. In this paper, we review published and unpublished *Inia* literature and present results of our own investigations of seasonality of *Inia* reproduction in Venezuela, Peru, and Bolivia.

METHODS

STUDY AREAS.—Between 1993 and 2001, river dolphin surveys and behavioral observations were conducted in freshwaters of Bolivia, Peru, and Venezuela (Fig. 1; Table 1). All three study areas contain main stem rivers, tributaries, confluences, and oxbow lakes, which can further be divided into whitewater and blackwater habitats (differentiated by turbidity, nutrient load, pH, and origin (Sioli 1984)). Four seasons can be assigned based on relative water levels: high water, falling water, low water, and rising water. Seasons are of approximately equal duration, and differ among study areas with respect to month of the year (*e.g.*, April generally falls during the high water season in Peru and during low water season in Venezuela; Fig. 1), and sometimes within a study area (*e.g.*, high water in Peru may begin in mid-March of one year, and in April of the next). Water levels of Neotropical river systems are dependent on season and are influenced by local rains, snowmelt from the Andes, and water levels both upstream and downstream. The Peruvian study area is classified as lowland tropical rain forest, whereas the Bolivian and Venezuelan study areas are characterized as tropical savannas with gallery forests (Cox & Moore 1993).

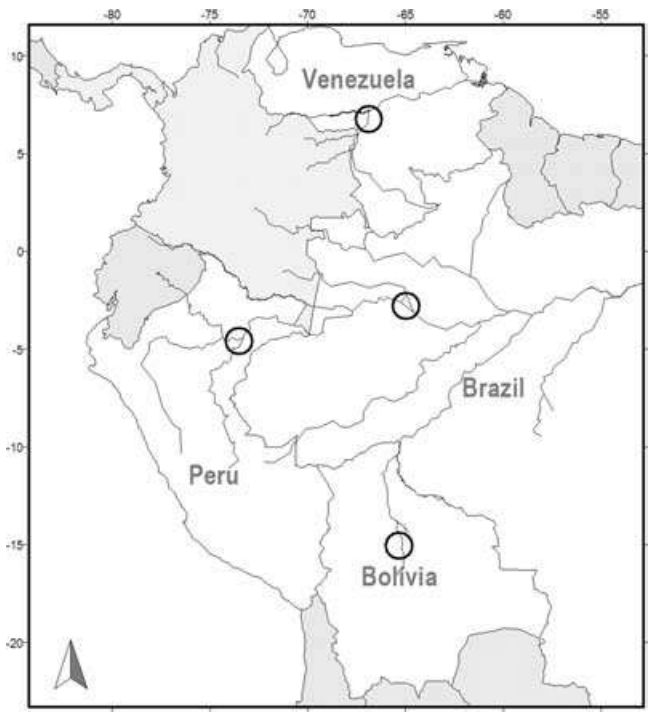


FIGURE 1. Location of study sites.

FIELD SAMPLING.—During boat-based surveys in rivers, tributaries, lakes, and confluences (for detailed methods see McGuire 1995, Aliaga-Rossel 2000, and McGuire 2002) river dolphins were assigned to one of two age/size classifications. Age classifications were based on visual estimation of total length and divided into two categories of *neonates* (<1 m), and *other* (>1 m). Neonates were further identified by their uncoordinated swimming and surfacing behavior, and fetal folds (when possible). The *other* category included older calves, juveniles, subadults, and adults, and was not further subdivided as it was often difficult to visually differentiate size-class of intermediate sized animals. Age, sexual maturity, and sex are not clearly differentiated based on length alone in these dolphins (da Silva 1994).

Mating behavior was opportunistically recorded. Season, date, time of day, and description of the behavior were recorded for each mating bout. An interaction was categorized as mating if ventral-to-ventral contact between two or more dolphins was observed. Opportunistically encountered dead dolphins were examined to determine sex, stomach contents, pregnancy and/or lactation of females, and tooth eruption of neonates and calves.

LITERATURE REVIEW.—We reviewed the published and unpublished literature; the unpublished literature consists of project reports, licenciatura and masters theses, doctoral dissertations, and conference abstracts. These works are written in English, Spanish, Portuguese, and German.

RESULTS

NEONATE SIGHTINGS AND REPRODUCTION.—*Inia* neonates were observed year-round in Peru and Bolivia, although seasonal peaks in sightings of neonates occurred during falling water in both of these study areas (Table 2). In Venezuela, neonates were never observed during falling water, but began appearing at the end of the low water season and peaked during rising water (high water was not sampled due to logistical constraints). Seasonal calving peaks in each of the study sites were defined as the season with not only the maximum total number of neonates, but also as the season with the maximum ratio of neonates relative to all *Inia* seen during a season, and with the maximum ratio of neonates relative to hours of seasonal sampling effort. *Inia* mating behavior in Peru was observed in all seasons (Table 2), but was observed only during falling and low water seasons in Bolivia. Mating was not observed in Venezuela.

NECROPSY.—One *Inia* neonate was necropsied 13 August 1997 during low water in Peru. The animal was a female, 82.5 cm total length (straight length, tip of snout to tail notch), with fetal folds. The teeth had not yet erupted but were visible just below the surface of the gums. The stomach was empty, although the intestinal contents indicated a milk diet. Based on its total length and da Silva's (1994) estimates of neonate growth rates, it was estimated to be <1-mo-old, and born between falling and low water. Dead females

TABLE 1. *Dates, locations, and seasons of field observations. Flux is defined as the difference between highest and lowest water levels.*

Country	Location	River Basin	Long/Lat	Year	Effort (hr)	Seasons	Flux (m)	Reference
Bolivia	Tijamuchi River	Amazon, Mamoré Sub-basin	65°W, 14°S	1998 1999 2001	213	Falling: April–June Low: July–September Rising: October–December High: January–March	7	Aliaga-Rossel 2000, 2002
Peru	Pacaya-Samiria National Reserve	Amazon	74°W, 5°S	1996–2000	1636	Falling: July–September Low: October–December Rising: January–mid-March High: mid-March–June	7	McGuire 2002
Venezuela	Cinaruco River, Santos Luzardo National Park	Orinoco	67°W, 6°N	1993–1994	420	Falling: November–January Low: February–April Rising: May, June High: not sampled	5	McGuire 1995, McGuire and Winemiller 1998

that were pregnant or lactating were not encountered. Permit restrictions prevented us from collecting reproductive organs.

LITERATURE REVIEW.—A review of published and unpublished studies from Bolivia, Brazil, Colombia, Ecuador, Peru and Venezuela indicate geographic variation in seasonality of *Inia* reproduction (Table 3).

DISCUSSION

Our findings of year-round births and geographic variation in reproductive seasonality were unexpected. In comparing the differences in our results to predictions based on the prevailing published literature, we consider possible sources of variation due to: phylogeny, geographic distribution according to river basin or latitude, relative seasonal differences between high and low water levels of the study areas, prey, and methodology.

PHYLOGENY AND DISTRIBUTION ACCORDING TO RIVER BASIN.—*Inia* is generally considered to be a single species, *I. geoffrensis*, with three subspecies: *Inia g. humboldtiana* in the Orinoco River Basin, *Inia g. geoffrensis* in the main Amazon River Basin, and *Inia g. boliviensis* in the Bolivian subbasin of the Amazon (Rice 1998, Reeves *et al*. 2003). However, some researchers have proposed classifying *I. boliviensis* as a separate species, based on genetic and morphologic differences (D'Orbigny 1834, Pillieri & Gihr 1977, da Silva 1994, Hamilton *et al.* 2001, Banguera *et al.* 2002). Because the current subspecific classification of *Inia* is determined by distribution according to river basin, the possible effects of differences in phylogeny are essentially indistinguishable from differences in broad geographic

TABLE 2. *Total neonates, total* Inia, *mating behavior, neonate encounter rates, and sampling effort, according to study area and season. X indicates not sampled.*

Study area	Season	Effort (hr)	No. of neonates	No. of *Inia* (all age classes)	No. of neonates/no. of *Inia*	Neonate encounter rate (no. of neonates/hr)	No. observed mating behavior
Venezuela	Falling	99	0	399	0	0	0
	Low	192	5	335	1.5%	0.03	0
	Rising	129	23	233	9.9%	0.18	0
	High	X	X	X	X	X	X
Peru	Falling	334	10	224	4.5%	0.03	4
	Low	300	2	266	0.8%	0.01	2
	Rising	709	4	167	2.4%	0.01	3
	High	293	1	172	0.6%	0.00	2
Bolivia	Falling	53	36	670	5.4%	0.68	5
	Low	60	12	290	4.1%	0.20	9
	Rising	51	7	466	1.5%	0.14	0
	High	49	8	496	1.6%	0.16	0

TABLE 3. *Summary of the literature on seasonal reproduction in* Inia. *Seasonal comparisons are based on water levels and not month of the year, as peak water levels vary by river basin and latitude. Flux is defined as the difference between highest and lowest water levels.*

Country	River basin	Neonates/calves	Mating	Authors	Flux (m)
Bolivia	Amazon (Mamoré sub-basin)	year-round (peaks during falling water)	falling and low	Aliaga-Rossel 2000, 2002	7
Brazil	Amazon	high and early falling	no information	Best 1984, Best & da Silva 1984, da Silva 1994	13
Colombia	Amazon	year-round (few seen during rising)	no information	Hurtado 1996	10–15
Colombia	Amazon	year-round, (peaks during high water)	no information	Galindo 1998	10
Colombia	Amazon and Orinoco	falling (Amazon Basin) no info (Orinoco Basin)	low (Amazon and Orinoco basins)	Beltrán & Trujillo 1993. Trujillo *et al.* 1998	no info
Ecuador	Amazon	falling/low water (other seasons not sampled)	no information	Herman *et al.* 1996	no info
Peru	Amazon	year-round (fewest during high water)	no information	Henningsen 1998	7
Peru	Amazon	rising and falling water (other seasons not sampled)	no information	Leatherwood 1996	7
Peru	Amazon	year-round peak during falling	year-round	McGuire 2002	7
Venezuela	Orinoco	end of low water	rising	Caranto & Gonzalez-Fernandez 1998	no info
Venezuela	Orinoco	rising water and end of low water never during falling water (high water not sampled)	not observed	McGuire 1995, McGuire and Winemiller 1998	5

distribution. When we associate study area with subspecies (*i.e.*, *I.g. humboldtiania* in Venezuela, *I.g. boliviensis* in Bolivia, and *I. g. geoffrensis* in Peru and Brazil,) no clear patterns emerge with respect to synchrony of reproduction. In fact, there is more similarity in the patterns of seasonality of reproduction in dolphins from the Peruvian and Bolivian study areas (*I. g. geoffrensis* and *I. g. boliviensis*, respectively) than between *I.g. geoffrensis* from the Peruvian and Brazilian study areas from the same river basin. Although sample sizes are small, two separate studies from Venezuela (McGuire 1995, Caranto & Gonzalez-Fernandez 1998) suggest *I.g. humboldtiania* may differ from the other subspecies in that the calving peaks during low water, and does not occur year-round.

LATITUDE.—Based on the patterns of reproductive seasonality found in other odontocetes, we were interested in exploring if the degree of seasonality of reproduction in *Inia* increases with distance from the equator. If so, we would predict little to no seasonality in da Silva and Martin's Brazilian study site (3°S) and strong seasonality in the Bolivian study site (14°S), with intermediate levels in Peru and Venezuela (5°S and 6°N, respectively); however, this was not the case, and no clear patterns emerged.

SEASONAL FLUX OF WATER LEVEL.—Might degree of reproductive seasonality in *Inia* be related to relative differences between high and low water levels? Are differences in reproductive seasonality more pronounced where seasonal differences in aquatic habitat are most extreme? In general, differences between high and low water levels not only increase with latitude, but also along the course of a river. Compared to the rest of South America, seasonality is minimal in the northwestern Amazon Basin (Lewis *et al.* 1995). The Amazon River is just a few degrees south of the equator, where its seasonal flux is generally not as extreme as those rivers located at higher latitudes. In addition, there is an east/west gradient of seasonal changes in water level. For example, the difference between maximum and minimum waters in the Peruvian study area is 7 m, but downriver in central Brazil it is almost twice that amount (Martin & da Silva 2004); *Inia* reproduction is year-round in the first study site and seasonal in the second. This model does not readily apply to our other study sites, however, as Venezuela had the smallest difference between high and low waters, yet *Inia* reproduction was seasonal. Further testing of this hypothesis requires more data from throughout the vast geographic range of *Inia*, and a refinement of our definition of seasonal changes in habitat (*e.g.*, measure not only differences in water depths, but also the amount and type of habitat lost and gained throughout a complete flood cycle).

PREY.—The mostly widely published interpretation of reproductive seasonality in *Inia* is based on studies from the Brazilian Amazon, which investigated the seasonality of calving (Best & da Silva 1984) and the diet of river dolphins (da Silva 1983). *Inia* births in this

region were reported to occur during the local period of high water and the beginning of falling water, and Best and da Silva (1989a) hypothesized that births coincide with increased access to fish prey that become vulnerable as habitat and cover from inundated vegetation decrease with falling water levels. The majority of lactating female *Inia* were observed during falling and low water, and da Silva (1994) hypothesized that because lactation is a more energetically expensive period of the breeding cycle than pregnancy, it benefits the mother to lactate during the dry season when foraging efficiencies are presumably greater, as fish are concentrated in shallow water. The above hypothesis does not appear to apply to all *Inia* populations, as we have observed variability of reproductive seasonality in other regions, and even a lack of seasonality in some. Perhaps in some regions, fish generally are not a scarce resource for *Inia*, and thus do not necessarily dictate seasonality of breeding. Given the high biomass and diversity of fishes in the Neotropics (*e.g.*, 171–625 species in the Peruvian Amazon, Guerra 1995; and 327 species in the Mamoré Basin, Poulli *et al.* 2004), it is likely that dolphins could utilize different prey species at different times of year, depending on local taxon-specific fish reproduction and migration schedules, which vary among fish species (Lowe-McConnell 1987, Ribeiro & Petrere 1990). The da Silva (1983) diet study indicated that *Inia* are generalists, feeding on as many as 43 species of fishes from 19 families. Solitary and shoaling fish were taken in almost equal numbers, and 51 percent of fishes were pelagic, 33 percent were benthic, and 9 percent lacustrine (Best & da Silva 1989*a*). In addition, dolphins in the study were collected from the whitewater Amazon and its large tributaries. It would be useful to collect diet data, such as stomach contents and prey availability indices from other regions and habitats to help interpret reproductive patterns of these different geographic areas.

METHODOLOGICAL CONCERNS.—Determining age-class based on visual estimation of total length of a free-ranging aquatic mammal is difficult, and especially so given the turbid waters and shallow-surfacing profiles of river dolphins. The definition of neonate as a dolphin <1 m in length was somewhat arbitrary, but was based on the following information: *Inia* have a mean length at birth of 80 cm (Best & da Silva 1984), and there are records of nursing calves between 80 and 114.5 cm total length without erupted teeth, and other calves between 123 and 154 cm with erupted teeth feeding on a diet of mixed milk and fish (da Silva 1994). Harrison and Brownell (1971) also report two lactating females with calves sized 115- and 114-cm long, but did not state if teeth had erupted, or specify the diet of the calves. By specifying a maximum of 100 cm, we increased our confidence that animals under 100 cm were nursing animals with unerupted teeth. We may have missed larger neonates, and likewise, may have included smaller calves older than a few months, but this could not be prevented with observational techniques. We did not attempt to classify animals >1m as older calves, juveniles, or subadults, because there is too much potential overlap in size classes for visual differentiation in the field (a nursing calf has been measured at 154 cm and a mature female at 160 cm; da Silva 1994). Total length of adult dolphins varies throughout their range (da Silva 1994) and it seems likely that size of neonate also varies. We encourage future studies to develop site-specific growth curves.

Reports of seasonality of calving vary within regions as well, as demonstrated by some of the different results obtained by different studies within the same study areas (Leatherwood 1996, Heningsen 1998, McGuire 2002). Part of this discrepancy may be due to differences in sampling techniques and definition of age classes. For example, Leatherwood's (1996) definition of a neonate included close proximity to an adult presumed to be the mother. We observed that neonates rarely made physical contact with larger dolphins, and were often >4 m away from the presumed mother. Many of the researchers listed in Table 3 simply reported animals as "calves," without defining the term; therefore, they could have been referring to a day-old newborn or a 2-yr old nursing calf.

Differences in survey vessel and speed undoubtedly contributed to differences in neonate detection rates. We do not have sufficient data to quantify the effect of vessel height on number of nonadults recorded, but we found that neonates were easier to classify from a skiff with a low observer-eye height than from a higher platform (although dolphins were easier to detect from higher platforms). In addition, age-class determination was more difficult from a rapidly moving boat than from a slow-moving or stationary boat; different researchers have used very different boat speeds, and this may have influenced results among studies.

MATING.—Observations of mating offer little insight into seasonal reproduction of *Inia*, because mating was rarely observed, difficult to classify, and sometimes may have been social in nature. Mating by *Inia* was observed in all seasons in Peru, during falling and low water in Bolivia, and not at all in Venezuela. In general, categorizing an activity as mating was subjective. Little of the animals were visible above the surface of the water and this made classification and description of behavior difficult. It was impossible to determine how much of the behavior described as mating was truly reproductive in nature, and how much was other social behavior such as play, aggression, sexual behavior without copulation, or dominance displays. Caldwell *et al.* (1989) reported that heterosexual and homosexual behaviors were very common in captive *Inia*, regardless of season. Based on examination of dead animals**,** male *Inia* do not appear to exhibit seasonality in reproductive condition (Best & da Silva 1984).

CONSTRAINTS OF OBSERVATIONAL METHODS.—More necropsies would have provided additional information about reproductive and developmental state, and age/length curves. Due to the low human populations of our study sites, there was little incidental capture in fishing nets. Furthermore, dead dolphins were sometimes hidden rather than reported (Reeves *et al.* 1999). It was rare for us to encounter dead dolphins, and in remote tropical areas, carcasses were usually in advanced stages of decomposition with significant loss to scavengers.

It would have been informative to determine the sex of the animals, but we were rarely able to do so. To date, only one research group has reported success in sexing free-ranging river dolphins, by using visual estimates of the relative distance between the anal

and genital slits (Trujillo *et al.* 1998). Waters in our study areas were not sufficiently transparent to achieve this. Also, dolphins did not usually display their undersides, and distances between observers and dolphins were too great to determine sex based on visual inspection of genital slit length. Males are larger than females, but this sexual dimorphism cannot be used to visually determine sex in free-ranging animals, as size also is related to age.

Our studies were observational in nature, but studies that have employed live-captures yield more accurate age, length, sex, and reproductive state data (Martin & da Silva 2004).

Seasonal reproduction in other river dolphins.—There is little information on the seasonality of reproduction in other river dolphin species. *Lipotes* is reported to mate in the spring and calve in the winter and spring (Zhou & Zhang 1991). *Platanista* is thought to have a bimodal calving and reproductive season (Kasuya 1972, Shresta 1989). *Pontoporia* is reported to give birth during the austral spring and early summer of higher latitudes (Harrison *et al.* 1981, Danilewicz 2003), with year-round births at slightly lower latitudes (Ramos 1997).

Although usually not classified as a river dolphin, *Sotalia fluviatilis* is found in fresh water and shares much of the range of *Inia,* although it does not occur in our Bolivian or Venezuelan study sites. In Peru, neonate *Sotalia* were observed in all seasons, with a slight peak during high water (McGuire 2002). In contrast, *Sotalia* in the central Amazon of Brazil were reported to give birth during low water (Best & da Silva 1984). Da Silva (1983) reported *Sotalia* feed primarily on pelagic schooling fish, which Best & da Silva (1984) reasoned would be most concentrated and easiest to catch during extreme low water, and therefore concluded that calving season coincides with the periods of greatest availability of prey for these dolphins. As we have previously discussed in this paper, published information about diet of *Inia* and *Sotalia* is based on one study (da Silva 1984), limited in sample size and geographic scope, and may not reflect the potential diversity and flexibility of diet of these river dolphins throughout their range.

Application to conservation.—The conservation status of *I. geoffrensis* is listed as vulnerable (Reeves *et al.* 2003). Better understanding of the reproductive seasonality of *Inia* could contribute to the conservation of this species, primarily by enhancing fisheries management. Restrictions on certain fishing practices in critical reproductive seasons and habitats may be warranted in some areas. For example, Bolivian fishermen report that dolphins are most likely to become incidentally entangled in fishing nets during the periods of low and falling water, as fish abundance in lagoons and tributaries is generally highest during this season and fishermen place their nets across the mouths of lagoons and tributaries in efforts to catch fish leaving with the falling water. Moreover, more calves are born during this season and in these habitats, and curious, naive young dolphins are more likely to approach nets than are older dolphins (McGuire & Aliaga-Rossel, pers. obs.). Fishermen along the Tijamuchi River of Bolivia stated that in 1 yr they accidentally netted three calves, two juveniles, and one adult *Inia,* and two of the three calves were captured during falling/low water (Aliaga-Rossel 2002).

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