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Occurrence Patterns, Habitat Associations, and Potential Prey of the River Dolphin, *Inia geoffrensis*, in the Cinaruco River, Venezuela[1]

Tamara L. McGuire and **Kirk O. Winemiller**

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station Texas 77843-2258, U.S.A.

ABSTRACT

The distribution, habitat association, group size, population structure, and prey availability of river dolphins (*Inia geoffrensis*) were studied from November 1993-June 1994 in the Cinaruco River, a tributary of the Orinoco River that forms the southern boundary of Venezuela's Santos Luzardo National Park. Dolphins were sampled from a boat using modified strip-width transects, for a total of 418 h. The study area was 1.67 km^2, and contained 20 km of water courses. Like other rivers of this region, the Cinaruco River undergoes a seasonal flood cycle. Dolphins were seen most often during the period of falling water (41% of total sightings) and least often during the rising water period (24% of total sightings). Dolphins were seen most often in confluence areas (35% of total sightings) and were seldom seen in side channels (13% of total sightings). The presence of rocks or sandbanks was associated with a greater frequency of dolphin sightings, and sightings increased with habitat heterogeneity. Average group size for the 8-mo study was 2.0 (±1.0) and was largest during the rising water period. Calves were first sighted during the end of the dry season and became more common during the early flood season. Six individuals were photo-identified and resighted with one sighted eight times over 186 d. The fish diversity of the study area was high, with 161 species documented in our samples. The stomach of one *Inia* contained 15 fishes representing at least 4 species.

RESUMEN

Se estudió la distribución, asociación con el hábitat, tamaño de los grupos, estructura poblacional y disponibilidad de presa del delfín de río (*Inia geoffrensis*) desde noviembre 1993-junio 1994 en el río Cinaruco, un tributario del río Orinoco que forma el límite sur del parque nacional venezolano Santos Luzardo. Se tomaron muestras de los delfines desde un bote usando el método modificado de la transecta en banda, durante 418 h de esfuerzo. El área de estudio comprende 1.67 km^2 y contiene 20 km de cursos de agua. Al igual que otros ríos de esa región, el río Cinaruco sufre inudaciones cíclas. Los delfines fueron avistados más frecuentemente durante el período de la bajada del agua (41% del total de los avistamientos) y menos frecuentemente durante el período de crecida del agua (24% del total de los avistamientos). Se vieron más delfines en las áreas de confluencia (35% del total de los avistamientos) y raramente en los canales laterales (13% del total de los avistamientos). La presencia de rocas o bancos de arena estuvo asociada con una mayor frecuencia de avistamiento de delfines, y los avistamientos aumentaron con la heterogeneidad del ambiente. El tamaño promedio del los grupos durante los 8 meses de estudio fue 2.0 (±1.0) y fue mayor durante la crecida de las aguas. Las crías se avistaron primero al final de la estación seca y se hicieron más comunes al inicio de la época de crecida de las aguas. Seis individuos se identificaron con fotografías y se avistaron nuevamente, uno de los cuales fue avistado ocho veces a lo largo de 186 d. La diversidad de peces en el área de estudio era alta, documentándose 161 especies en nuestras muestras. El contenido estomacal de un *Inia* estaba compuesto por 15 peces, representando por lo menos 4 especies.

Key words: black water; conservation; Inia geoffrensis; *llanos; river dolphins; South America; Venezuela.*

River dolphins (*Inia geoffrensis*) inhabit the Amazon and Orinoco River basins of South America (Best & da Silva 1993). Throughout its range, *Inia* has different common names, including *tonina* and *bufeo* (Spanish), *boto* (Portuguese) and river or pink dolphin (English). *Inia* is classified as "vulnerable" by the International Union for the Conservation of Nature (Klinowska 1991), and while not currently subject to direct exploitation, river dolphins are experiencing habitat degradation due to pollution, river traffic, deforestation, hydroelectric dams, and overfishing of their prey by humans (Best & da Silva 1989a). River dolphins are also accidentally killed during human fishing activity, which include gill netting and dynamite fishing (Best & da Silva 1989a). Despite the fact that caimans, piranhas, anacondas, and jaguars share their range, direct evidence of predation on river dolphins is lacking. Taboos preventing humans from harming river dolphins once existed among the native people of the region, but such beliefs are disappearing (Best &

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da Silva 1989a). More recent settlers often regard the dolphins as competitors for fish (Reeves & Leatherwood 1996). In the absence of specific laws that protect river dolphins (Atkins 1989), the best chance for long-term protection may be through the creation and maintenance of river dolphin reserves and national parks. Because little is known about the habitat requirements and population dynamics of these animals, managers must first obtain baseline population data.

River dolphins are restricted to freshwater where they may be found in a variety of habitats (Layne 1958, Magnusson *et al.* 1980), including main river channels, lagoons, below rapids (Best & da Silva 1993), confluence areas (Pilleri & Gihr 1977), and flooded forests (Layne 1958). Many rivers of the Orinoco and Amazon basins undergo annual flood cycles that result in dramatic seasonal changes in both the quantity and quality of aquatic habitats. Dolphins are able to disperse into the flooded forests, smaller tributaries, seasonally-isolated oxbow lakes, and other aquatic habitats of the flood plain (Layne 1958, Best & da Silva 1989a). When flood waters recede during the dry season, habitats for dolphins are reduced (Pilleri & Gihr 1977, Best 1984). There is disagreement in the literature as to the preferred habitat of river dolphins. Layne (1958) found most river-dwelling dolphins in quiet waters near shore or in coves with emergent aquatic vegetation, but most lagoon residents occupied open water. Trebbau and Van Bree (1974) and Pilleri and Gihr (1977) described an affinity for wide lagoons with deep, calm water and shade. In contrast, Best (1984) noted that dolphins seemed to prefer confluences and areas of high turbidity, while Schnapp and Howroyd (1990) found most dolphins along the banks of rivers. Reeves and Leatherwood (1996) observed dolphins most often in areas of sand banks, confluences, or sharp river bends. Some researchers (Pilleri *et al.* 1982, Grabert 1984) have hypothesized that blackwater rivers, due to their characteristically high acidity and low nutrients, are barriers to dolphins. However, this does not appear to be the case as river dolphins occur in the Río Negro of Brazil, the largest blackwater system in the world (Goulding *et al.* 1988).

River dolphins are usually solitary or occur in pairs, although they have occasionally been observed in aggregations of 20–35 individuals (Vidal *et al.* 1993, Best & da Silva 1993, Schmidt-Lynch 1994). However, Schnapp and Howroyd (1990) observed groups of dolphins (2–7 individuals) more often than solitary individuals. The reported calving season is during high and falling water levels. The peak month for births depends on the seasonal flood regime of the region. For example, calving in the upper Amazon occurs during June, July, and August (Best 1984, Trujillo Gonzalez 1990), whereas May-July is the peak calving time in the mid-Amazon (Best & da Silva 1993).

Males reach reproductive maturity at total lengths of 198 cm (Best & da Silva 1984) and 200 cm (Eisenberg 1989). Females mature at 170–183 cm (Eisenberg 1989 and Best & da Silva 1984, respectively). Best and da Silva (1984) found neonate lengths to be 79.4 ± 3.3 cm and estimated the neonatal growth rate at 2.5 cm/mo. Estimated gestation in captivity is 8.5 mo (Caldwell & Caldwell 1972). Based on measurements from the wild, Best and da Silva (1984) predicted a 10.7–11.2 mo gestation period. Eisenberg (1989) reported a gestation of 10.5 and 10 mo.

Food availability is an important component of habitat. River dolphins are top predators (Goulding *et al.* 1988) and could influence fish communities (Lowe-McConnell 1975, 1987) and the structure and function of aquatic ecosystems. River dolphins are known to eat > 50 fish species from 19 families (Best & da Silva 1989a) and occasionally consume smaller amounts of molluscs, crustaceans, and young turtles (da Silva & Best 1982). Dolphin prey range from 50–800 mm total length, with an average total length of 200 mm (Best & da Silva 1993). Best and da Silva (1989a, 1989b) determined that the dolphin's diet is broader during high water, probably because preferred fish are more difficult to locate and catch as the aquatic habitat expands. During the dry season, dolphins may become more selective foragers because prey are more concentrated in space and easier to locate and catch (Best 1984).

Here we examine spatial and temporal patterns of distribution and population structure with respect to habitat type and potential prey availability for *Inia* in the Cinaruco River, a blackwater tributary of the Orinoco River in Venezuela.

METHODS

STUDY SITE.—The Cinaruco River flows east to the Orinoco across the lowland plains (llanos) of Venezuela's Apure state (Fig. 1). The lower portion of the river is particularly sinuous and forms a complex flood plain with numerous lagoons and oxbow lakes. The river is flanked by gallery forests containing diverse vegetation. The river contains diverse habitats that vary in substrate composition, riparian vegetation, water current, and depth. The

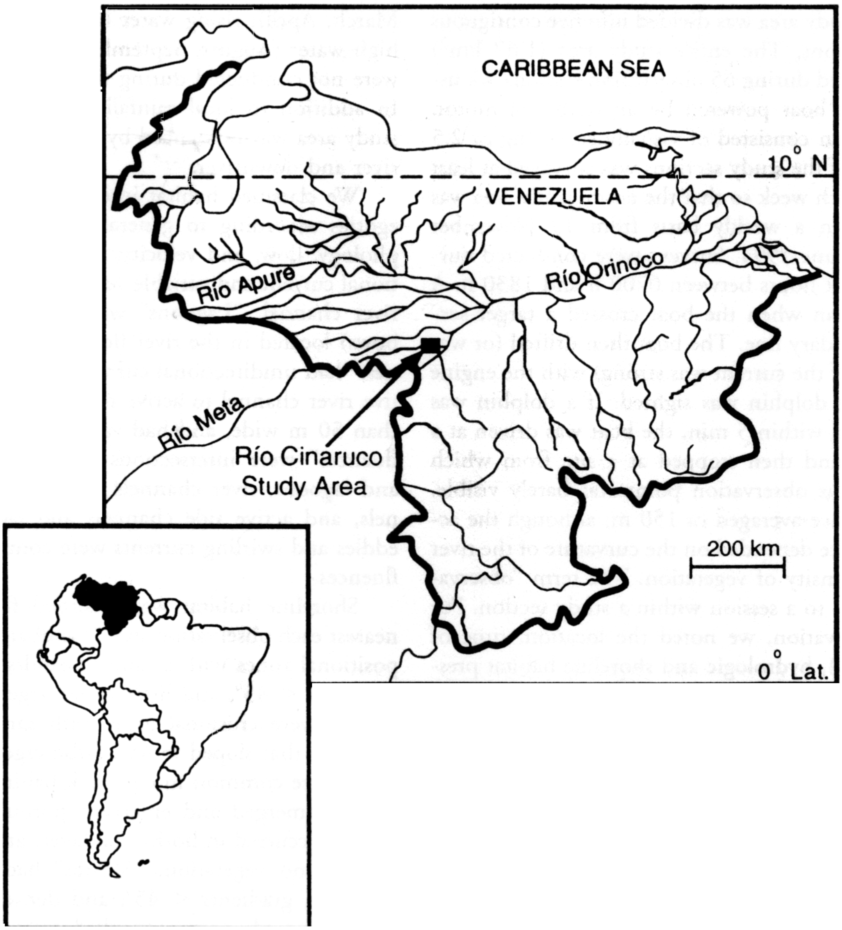

FIGURE 1. Map showing the location of the study area in Venezuela.

river floods the surrounding flood plain from *ca* May-November, then returns to the main channel during the dry season when many lagoons and oxbows become isolated. In one lagoon, water depth increased 3 m between April and June 1994. Water velocity was highest in side channels and absent in lagoons. The Cinaruco River is unusual because it is a blackwater river in a savanna region dominated by whitewater river systems (Taphorn & Barbarino Duque 1993). Blackwaters are usually transparent, nutrient poor, mildly to highly acidic, and stained brown from tannic acids leached from decomposing vegetation (Sioli 1984, Goulding *et al.* 1988).

The study site is *ca* 1.67 km^2 in area and contains *ca* 20 km of water courses. This area lies within one of Venezuela's newest national parks, Santos Luzardo (INPARQUES 1992). During the dry season, ambient temperatures can climb above 45°C (112°F). The llanos are sparsely populated, and the few people who live there historically have made their living from hunting, fishing, and cattle ranching. The Cinaruco River is an internationally recognized location for peacock bass (genus *Cichla*) sports fishing (Taphorn & Barbarino Duque 1993). Many of the local people now make their living as sportfishing guides or camp caretakers. Because dolphins are so conspicuous and have been known to capture and eat hooked or released fish, they are often blamed for perceived degradation of fish stocks.

STUDY DESIGN.—Data collection consisted of surveys of dolphins and habitat, photo-identification of individual dolphins, necropsy and stomach-contents analysis on a single carcass of *Inia*, and sampling of potential prey.

The study area was divided into five contiguous 4-km sections. The entire study area (1.67 km^2) was surveyed during 65 observation sessions/wk using a 5-m boat powered by an outboard motor. Each session consisted of visually surveying *ca* 2.5 ha. Each of the study sections was surveyed at least one day each week so that the entire study area was surveyed on a weekly basis from 19 November 1993–19 June 1994. Surveys were conducted during daylight hours between 0700 h and 1830 h. A survey began when the boat crossed a target section's boundary line. The boat then drifted (or was anchored if the current was strong) with the engine off until a dolphin was sighted. If a dolphin was not sighted within 5 min, the boat was driven at a slow idle and then stopped at a site from which the previous observation point was barely visible. This distance averaged *ca* 150 m, although the actual distance depended on the curvature of the river and the density of vegetation. The term "observation" refers to a session within a study section. For each observation, we noted the location, time of day (TOD), hydrologic and shoreline habitat present, total observation time, and presence or absence of dolphins. The term "sighting" refers to the presence of one or more dolphins during an observation. Sightings were recorded as a dichotomous (*i.e.*, yes/no) outcome variable. The presence of dolphins was determined from visual (*e.g.*, roil, spray, body visible) or auditory (*e.g.*, exhalation, snort) cues. For each sighting, we noted the TOD, sighting duration, location, number of individuals, and dolphin life stage. Individuals were differentiated on the basis of relative body size, coloration patterns, and natural markings. When it was difficult to determine the exact number of individuals present at a sighting, we recorded the most conservative estimate. If a dolphin moved into or out of the study area during an observation, its direction of travel and time within the study site were recorded. A dolphin was not counted as a new sighting if it was obvious that the dolphin had followed the survey boat from the preceding observation site. Attempts were made to photograph all dolphins, but this was not always possible due to weather conditions and the difficulty of predicting precisely where and when dolphins surfaced. The photo frame and film roll number of all images were recorded with all observation and sighting information.

DEFINITION OF TERMS.—We used water levels in the study area to define four seasons: falling water (November, December, January); low water (February, March, April); rising water (May, June, July); and high water (August, September, October). Surveys were not conducted during the high water season. In addition to local rainfall, flooding within the study area was influenced by rising water both upriver and downriver.

We classified habitat into four hydrologic categories according to general features of geomorphology, flow, and velocity. "River" had unidirectional current and variable velocity within the main river channel. "Lagoons" were lentic bodies (oxbows) located in the river flood plain. "Side channels" had unidirectional current that connected active river channel to active river channel, were less than 50 m wide, and had variable velocity. "Confluences" were intersections of the river channel and lagoons, river channels and active side channels, and active side channels and lagoons. Back eddies and swirling currents were common at confluences.

Shoreline habitat was recorded for the bank nearest each observation site. "Sandbanks" were depositional zones with a sand or sand/silt substrate, gradients < 45°, and little to no vegetation. "Cut banks" were erosional areas with sand to clayey substrate that sloped > 45°. Submerged fallen tree snags were common in cut bank habitats. "Rocks" were submerged and emergent porous rocks that usually occurred in horizontal layers and contained little to no vegetation. "Shrubs" had a mud/silt substrate, gradients < 45°, and densely clumped, multistemmed, narrow-trunked trees with heavy, often submerged foliage. Shrub habitats were dominated by guava (*Psidium guineese*) and chiga (*Campsiandra comosa*). "Trees" had a mud/silt substrate, gradients < 45°, and were widely spaced, woody, single-trunked trees. The roots and trunks of trees were often submerged, but not their foliage. We used the sum of the bank types assigned to an observation site as an index of habitat heterogeneity.

We use the term "group" in the same sense that Jefferson (1991) used the term "aggregation" to describe "the total number of animals in the immediate vicinity of a sighting." Thus, we use group to refer to the total number of dolphins sighted during an observation period within an *ca* 150-m radius around the survey boat. This differs from the conventional definition of group, because it implies nothing about social cohesion or interactions of the dolphins in a sighting. When recording group size, we included those dolphins that were initially sighted as well as any that were later sighted during the same observation period.

We assigned dolphins to three life stages. Adults were 1.5–2.5 m total length (snout to tail fluke notch), white to dark gray in color, often with scars, nicks, and lighter gray and pink blotches on the melon and dorsal surfaces, and had a pink belly and underside of the flippers and tail flukes. Juveniles were 1–1.5 m total length, dark gray, and smooth with only a few scrapes and blotches. Calves had total lengths < 1 m and were smooth and uniformly light gray. All lengths were estimated visually, and therefore our life stage designations of "adult" vs. "juvenile" did not necessarily indicate sexual maturity or immaturity.

PHOTO-IDENTIFICATION.—Photographs were taken with 35-mm Canon AE and AV-1 SRL cameras with a 75–200 mm zoom lens. We used black-and-white high speed print film (400 ASA), color print film (200, 100 ASA), and color slide film (100 ASA). Photo-identification followed methods from Würsig and Jefferson (1990). Slides and negatives were examined under a variable-power dissecting microscope and individuals were recognized on the basis of their coloration patterns, scars, and dorsal crest shapes. Suites of images were examined for the designation of type images for each recognizable individual. Resighting information was used to create chronological location maps for individuals.

PREY SAMPLING.—Fishes were collected with seines (0.6 × 4.56 m with 3.17 mm^2 mesh, 0.6 × 6.08 m with 12.7 mm^2 mesh, 0.6 × 15.2 m with 12.7 mm^2 mesh) and an experimental gill net (1.8 m × 50 m with panels of 51, 102, and 152 mm^2 mesh). Smaller seines were used in narrow areas with high vegetation, while the larger seine was used in areas with long, sandy banks. Gill nets were set for 1–2 h in deep water locations and were watched closely to prevent dolphins and other air-breathing species (otters, caimans, aquatic birds) from becoming entangled.

Catch per unit effort (CPUE) was determined for gill net and seine samples. CPUE for seine samples was calculated by dividing the total number of fishes caught (per habitat and season) by the total meters the seine was pulled (per habitat and season). CPUE for gill net samples was calculated by dividing the total number of fishes caught by habitat and season by the total number of minutes the gill net was in the water. We expressed CPUE in terms of number of fishes caught rather than by biomass of fish caught. *Inia* generally does not feed on small (<50 mm) or very large fishes (>800 mm) (Best & da Silva 1993). Therefore, we examined fish numbers by standard length intervals to estimate the abundance of fish within the appropriate prey size range (50–800 mm).

Fishes were either kept alive in fresh water in a plastic tub and released after identification, or preserved in formalin for later identification and measurement. Standard length (snout to terminal vertebrae, in mm) was measured for all fish captured.

NECROPSY.—Following the procedures established in Geraci and Lounsbury (1993), a necropsy was performed on a dead *Inia* encountered on 28 December 1993. The stomach was removed and preserved in 15 percent formalin. Stomach contents were separated, rinsed in water, and examined for diagnostic bones (dentaries) and scales. A dissecting microscope was used to identify contents to the lowest taxon possible. Standard length or nape-to-tail length (first to terminal vertebrae, in mm) was measured. Volume of stomach contents was calculated by the volumetric displacement method (Winemiller 1990).

DATA ANALYSIS.—Observation, sighting, and prey-sampling information was subject to post-stratification by season, habitat, and habitat with season. Group size data were first transformed to the natural log to normalize distributions. Comparisons were made between similar strata using chi-square and ANOVA (Zar 1984). When ANOVA indicated a significant overall difference in a comparison of multiple means, we used a Tukey Studentized Range test for significant mean differences. Results of statistical tests were considered significant at the $P \leq 0.05$ level. Standard deviations about the mean are reported in parentheses following the mean.

A total of 418 h (878 observations) was spent searching for or observing dolphins. The greatest number of observations occurred during low water (192 h), and the fewest during falling water (97.5 h). To correct for the unequal distribution of effort, we standardized survey effort by dividing the number of dolphin sightings by the number of observations, to yield the frequency of dolphin sightings. We expressed survey effort as numbers of observations rather than as the duration of observations. Observation duration depended on the amount of time required to determine the presence or absence of dolphins. The amount of time needed to do so varied with habitat, water conditions, weather, and the presence and activity of other humans in the area. Because of the photo-identification aspect of the study, we tended to observe an area for longer

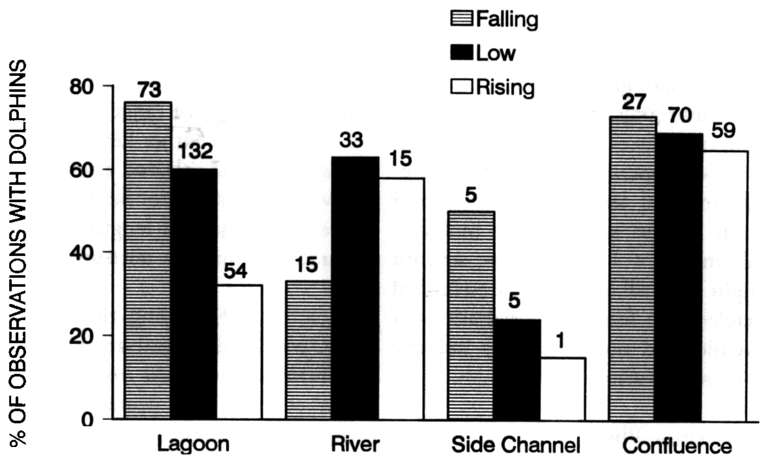

FIGURE 2. Percent of observations with dolphins according to habitat and season. The number of animals sighted seasonally in each habitat is shown over each vertical column.

periods of time if dolphins were present. Expressing dolphin sightings in terms of minutes would imply that frequency of sightings increased as a result of observation time; but this was not the case. We defined lapse time as the average time (min) between the arrival of the observer at a site and the first sighting of a dolphin. Mean lapse time was 2.6 min (± 0.32, $N = 489$). The relationship between lapse time and number of dolphins per observation was not significant ($R^2 = 0.0035$; df = 1, 497; $P = 0.19$). Dolphins were present when the observer arrived for the majority (67%) of sightings. All observations, regardless of lapse time, were included in the analyses.

RESULTS

Dolphins were sighted during 489 of 878 observations (56%). The frequency of dolphin sightings per observation (hereafter referred to as "sightings") was significantly associated with hydrologic habitat ($\chi^2 = 28.27$, df = 3, $P = 0.001$, $N = 489$). Over the 8-mo study, the frequency of sightings was highest in confluence areas (35% of total sightings) and lowest in side channels (13% of total sightings). The frequency of sightings was also associated with season ($\chi^2 = 48.56$, df = 2, $P = 0.001$, $N = 489$). Dolphins were observed most frequently during the falling water period (41% of total sightings), and least frequently during rising water (24% of total sightings).

The frequency of sightings varied seasonally within some habitats (Fig. 2). Within both lagoon and river habitats, sightings were significantly associated with season ($\chi^2 = 52.09$, df = 2, $P = 0.001$, $N = 258$ and $\chi^2 = 10.21$, df = 2, $P = 0.006$, $N = 63$, respectively). Lagoon sightings declined during low and rising water. Fewer dolphins were seen in rivers during falling water than any other season. Side channel sightings were most frequent during falling water. Sightings in confluences were not associated with season ($\chi^2 = 0.470$, df = 2, $P = 0.79$, $N = 156$).

Distribution by shoreline habitat.—For observations pooled across all periods and hydrologic habitats ($N = 878$), "shrub" and "sandbank" were the most commonly observed shoreline habitats. Categories were not exclusive, and 1–5 categories were present at any one observation site. Observations per habitat type were a function of the distribution of survey effort and the percent occurrence of habitat types within the study area. Seasonal changes in observations per habitat type were more pronounced for sandbank, shrub, and trees; the occurrence of rock or cut banks changed little.

The degree of association between frequency of sightings and shoreline type differed by habitat type. Only the presence of rock or sandbank was significantly associated with sighting frequency $\chi^2 = 39.83$, df = 1, $P < 0.0001$, $N = 407$; and ($\chi^2 = 16.43$, df = 1, $P < 0.0001$, $N = 451$, respectively). Dolphins were present at 64 percent ($N = 260$) of all observations made at sites where rock was present ($N = 407$). Of the 451 observations made where sandbank habitat was present, dolphins were present 66 percent ($N = 298$) of the time (Table 1).

TABLE 1. *Percent of observations with dolphins according to shoreline habitat.*

Shoreline habitat	Number of observa-tions	Number of dolphin sightings	Percent observa-tions with dolphins
	696	369	53
	451	298	66
	685	363	53
	407	260.5	64
	567	272	48

There was a strong association of sightings and habitat heterogeneity (χ^2 = 24.87, df = 4, P = 0.001, N = 489). In general, there was a higher frequency of dolphins with increasing habitat heterogeneity, ranging from 33 percent of observations with sightings for a heterogeneity index = 1 (N = 21), to 72 percent for a heterogeneity index = 5 (N = 108).

GROUP SIZE.—For the pooled data set (N = 489 sightings), the mean group size (number of dolphins per sighting) was 2.0 (± 1.0), with a range of 1–8 dolphins. Average group size was influenced by season (F = 6.74, df = 2, 487, $P < 0.0129$, N = 489). Mean group size was 1.7 dolphins (± 0.99, N = 121) during falling water, 1.9 dolphins during low water (± 0.97, N = 240), and 2.3 dolphins (± 1.47, N = 128) during rising water. The relative frequency of group size changed by season as well (Fig. 3).

When we compared the sightings across all seasons (N = 489), differences in group size according to hydrologic habitat were significant only between confluence and river areas (F = 4.28, df = 3, 486, P = 0.005). Groups were larger in the confluence areas (mean group size = 2.2 ± 1.37, N = 154) than they were in the river areas (mean group size = 1.7 ± 1.10, N = 63).

When we combined sightings by season with habitat, the largest groups were found in confluence areas during rising water (mean group size = 2.7±1.78; N = 89), and the smallest groups were in side channels during rising water (mean group size = 1.1 ± 0.03; N = 11; Fig. 4).

POPULATION STRUCTURE.—During the 8-mo study (N = 972 dolphins), 3.7 percent of all dolphins encountered were calves, 7.6 percent were juveniles, and 88.7 percent were adults. Adults and juveniles were encountered throughout the study period. Calves were never seen during falling water, but began appearing near the end of low water (1.5% of all dolphins seen) and comprised 10 percent of all dolphins seen during rising water (Table 2).

The association between the frequency of calf sightings and hydrologic habitat type was not significant (χ^2 = 6.52, df = 3, P = 0.09, N = 36). Eighty-one percent of calf sightings occurred during rising water (N = 29) and 16 percent of calves were seen during low water (N = 7). Calves were never seen during falling water.

Across all seasons, there was a significant association between frequency of juvenile sightings and hydrologic habitat (χ^2 = 8.79, df = 3, P = 0.03, N = 74). Juveniles were sighted most frequently in lagoon areas. Juvenile sightings and season were

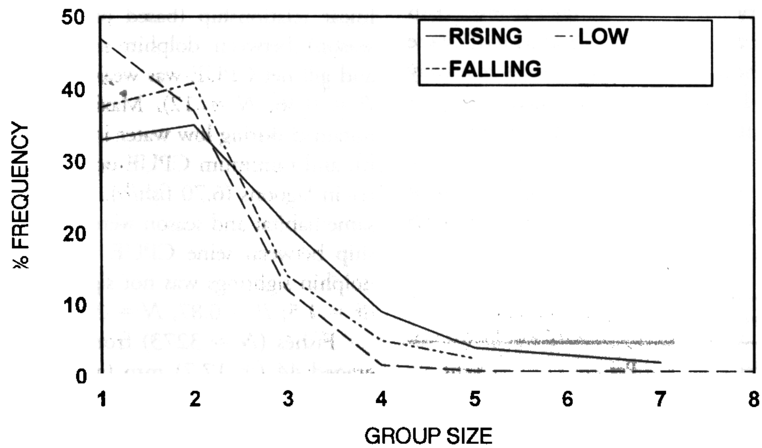

FIGURE 3. Percent frequency of group size by season with all habitats pooled.

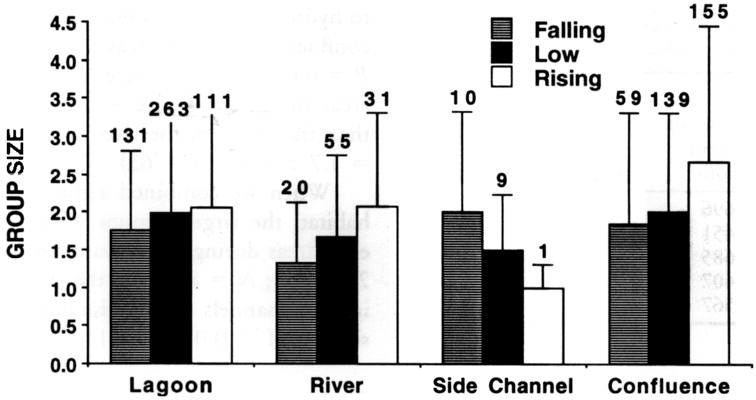

FIGURE 4. Average group size according to hydrologic habitat and season. The number of animals sighted seasonally in each habitat is shown over each vertical column (bars represent SD about the mean).

strongly associated (χ^2 = 9.774, df = 3, P < 0.0008, N = 74), with the majority of juveniles sighted during falling water (Fig. 5).

Sightings of adults were significantly associated with habitat (χ^2 = 32.44, df = 3, P < 0.001, N = 862) and with season (χ^2 = 41.50, df = 2, P < 0.001, N = 862). More adults were seen during the falling water period than any other season. During the falling water period, adults were seen most often in lagoons and confluence areas. During the low and rising water periods, the majority of adults were seen in areas of confluence (Fig. 6).

Photo-identification.—Of 2184 images taken during the study, 1.5 percent (N = 32) of all photographs were of sufficient quality to permit resightings of individuals. Six individual dolphins were positively identified (Table 3) with photographs. Time between resights ranged from 1–186 d. Two dolphins ("Gray nick", "Pink notch") were observed throughout the study area over relatively long periods and four other individuals were resighted infrequently over shorter time intervals.

Potential prey.—We identified 161 fish species in the study area. Fourteen of the identified species have been found in *Inia* stomachs in the Amazon (Best 1984).

On 6 March 1994, one of us (TLM) encountered the carcass of a male *Inia* floating in the upper reaches of a lagoon. Total length (snout to tail notch) of the animal was 1.68 m. We were unable to ascertain the cause of death, but we estimated that it had been dead for 1–2 d. The stomach contained remains of 15 fishes and 25 nematodes. The average standard length (SL) of prey was *ca* 65 mm. We identified at least four different fish species between 40–117 mm (one Serrasalmidae, one Siluriformes, two *Semaprochilodus kneri*, and one Characidae).

The mean CPUE of seine and gill net samples varied by habitat and season. Maximum gill net CPUE occurred during low water in the lagoons (0.28 fish/h), and minimum gill net CPUE was during low water in confluence areas (0.071 fish/h). The linear relationship (based on the same habitat and season) between dolphin sightings per observation and gill net CPUE was weak (R^2 = 0.17, df = 1,5, P = 0.36, N = 12). Maximum seine CPUE was obtained during low water in confluence (70.11 fish/h), and minimum CPUE occurred during rising water in lagoons (6.70 fish/h). When samples from the same habitat and season were compared, the relationship between seine CPUE values and frequency of dolphin sightings was not significant (R^2 = 0.0056, df = 1,5; P = 0.87, N = 23).

Fishes (N = 3273) from the seine samples averaged 44 (± 17.7) mm (all lengths are expressed as SL). The largest fish was 210 mm and the smallest was 13 mm. Small fishes (<40 mm) dominated all but one of the seine samples. The exception was taken during rising water in a side channel, and

TABLE 2. *Percent population structure by season.*

Season	Percent adults	Percent juveniles	Percent calves

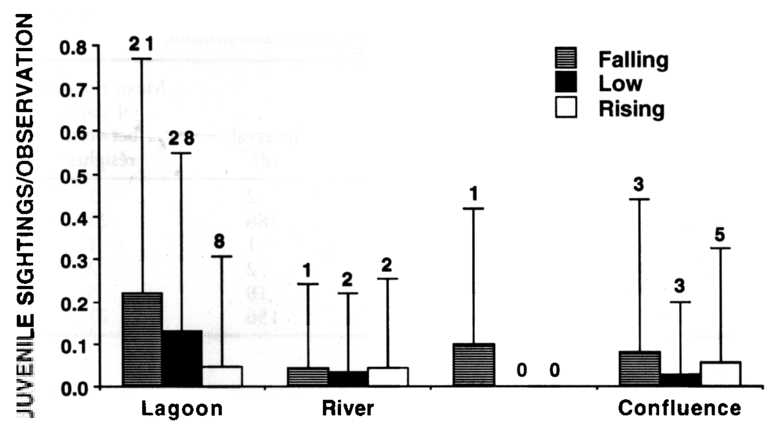

FIGURE 5. Juvenile sightings per observation, according to habitat and season. The number of animals sighted seasonally in each habitat is shown over each vertical column (bars represent SD about the mean).

was comprised primarily of 40–80 mm fishes. Sampling with seines was not uniform across seasons and habitats, only lagoon habitats were sampled during all three seasons. All lagoon samples were dominated by small fishes (10–40 mm), and fishes from larger size classes were more common in low and rising water samples.

Fishes caught in gill nets (N = 157) generally were larger than those from seines. Gill-net caught fishes averaged 199 (± 148.95) mm, with a maximum of 612 mm and a minimum of 100 mm. Average length varied according to season and habitat. Gill net sampling also was uneven across habitats and seasons and only lagoons and confluence areas were sampled during all three seasons. Mean fish length in lagoons increased over the falling water to rising water intervals and fish length in confluence areas was greatest during low water.

DISCUSSION

The strong seasonality of the Cinaruco River influences the local distribution, habitat affinity, group size, and reproduction of *Inia geoffrensis*. Part of this seasonal variation in river-dolphin ecology can be understood in terms of the seasonal fluctuations in the local fish populations. Dolphins were sighted more often in areas of confluence and least often in side channels. In confluence areas, sighting frequency did not change significantly with season, indicating these areas may be favored year-round. Confluence areas provide deep water and may contain high fish densities during certain periods. During falling water, fishes pass through confluences while leaving lagoons and tributaries, and they pass into these areas again during rising water (Lowe-McConnell 1975). Leatherwood (1993) found 63

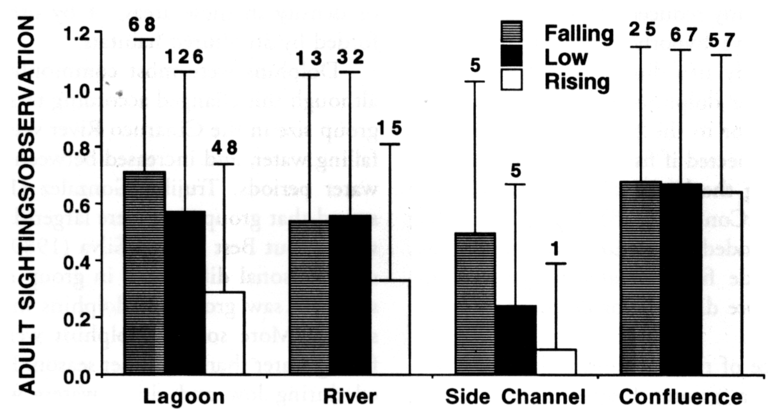

FIGURE 6. Adult sightings per observation, according to habitat and season. The number of animals sighted seasonally in each habitat is shown over each vertical column (bars represent SD about the mean).

TABLE 3. *Resighting record of individual dolphins recognized by photo-identification.*

Name	First sight	Final resight	Interval (d)	Mean number of days between resights	Number of resights
White band	02-05-94	02-07-94	2	2	1
Gray nick	08-12-93	06-02-94	186	25	8
Dorsal mark	06-09-94	06-10-94	1	1	1
Pre-scoop	06-09-94	06-11-94	2	2	1
Scoop	06-09-94	06-19-94	10	5	3
Pink notch	12-28-93	06-02-94	156	27	7

percent of dolphins at or near confluence areas in the upper Amazon. Dolphins may be very sensitive to disturbance from passing boats in long, narrow side channels.

An increase in the aquatic habitat from rising water would by itself result in fewer sightings per observation, because density per unit area declines. By the conclusion of the study, some vertical and lateral expansion had occurred within lagoons, and perhaps the increase in submerged vegetation there made it harder to detect dolphins. However, the total area, water height, and degree of submerged vegetation during late falling water (*i.e.*, during the commencement of the study) is very similar to that during early rising water (*i.e.*, the conclusion of study), so increased area and submerged vegetation cannot alone account for the difference in sightings between these two seasons. If temporal constancy in the number of dolphins within the study area and changes in vulnerability to detection were the only factors affecting sightings per effort, one would expect sightings to be highest during low water, when total aquatic habitat and submerged vegetation are greatly reduced; but this was not the case. An alternative hypothesis is that some dolphins left the study area during rising waters, and that these or other dolphins had immigrated into the study area prior to the period of falling water. This might be expected if fish biomass achieved its maximum during the late rainy and falling water period (Lowe-McConnell 1975). During the rising water period, flooded vegetation may permit dispersal and provide fishes greater refuge, perhaps making them more difficult for dolphins to locate and capture.

The presence of rock or sandbank habitat was associated with a greater frequency of dolphin sightings. Because sandbanks are shallow with a smooth substrate, they might facilitate the detection and capture of prey. Dolphins were often seen swimming at relatively high speeds along sandbanks, apparently pursuing small fishes that were often observed leaping from the water. Sandbanks also may be used by dolphins for other activities. Trujillo Gonzalez (1990) reported that shallow beaches are mating areas for *Inia*. Also, dolphins may be simply more visible to a human observer in sandbank areas, due to the shallower water and high contrast of the body against the white sand. Rock habitats appear to serve as breeding and nursery areas for some fishes (D. Jepsen, pers. comm.), and these areas were popular areas for sportfishing. Rock might have been associated with high sighting frequencies because prey were more abundant there. We had hypothesized that submerged shrubs and trees would be areas of higher dolphin sightings due to the large numbers of fishes that use them for shelter and food (Goulding *et al.* 1988). However, our data did not show this pattern and perhaps dolphins are inefficient in capturing fishes from dense vegetation. Dolphin sightings were associated with greater habitat heterogeneity, a pattern that might be explained by high fish diversity or density in these areas, or by other benefits afforded by structured habitats.

Dolphins were most commonly seen as pairs, although this changed according to season. Average group size in the Cinaruco River was lowest during falling water, and increased between low and rising water periods. Trujillo Gonzalez (1990) also observed that group sizes were larger during the rainy season, but Best and da Silva (1989a) did not observe seasonal differences in group size. In all seasons, we saw groups of dolphins more often than singles. More solitary dolphins were seen during falling water than any other season. Dolphins sighted during low and rising waters were usually in pairs. This seasonal increase in pairs was partially due to the birth of calves, which began at the end of the low water period and peaked with rising water. If *Inia* is monogamous as some researchers have speculated (Best & da Silva 1984) pairs observed during low water may also have been mated pairs. However, Trujillo Gonzalez (1990) observed multi-male mating aggregations during low water, and Beltrán and Trujillo Gonzalez (1993) also reported large mating groups during low water periods. We never observed any obvious sexual activity or mating groups, and therefore cannot provide additional insight into *Inia* mating strategy.

We did not encounter large groups of the size reported by Vidal *et al.* (1993) and Best and da Silva (1993). The largest group we observed was 8 individuals, and this occurred only once. The rarity of very large groups may have been a function of available habitats and the relatively limited spatial scale of the Cinaruco River study area. The largest groups in the Cinaruco River were observed during falling and rising water periods. We had expected maximum group sizes during low water with a concentration of dolphins in the deepest remaining water. The low ichthyomass associated with low water (Lowe-McConnell 1975) might be insufficient to support large groups of dolphins in a limited area. Group sizes were significantly larger in confluence areas than in channel habitats, and the largest group was recorded in a confluence area during rising water. Confluence areas tend to have greater prey densities than river channels (Lowe-McConnell 1975).

One of the most surprising results of this study was the appearance of calves during the periods of low and rising waters. We had expected to see calves during the falling water period because calving in the central and lower Amazon peaks during high and falling water (Best & da Silva 1984). We never sighted calves during falling water. In the Cinaruco River, calves were first sighted on 31 March near the end of the low water period, and they became more common as waters rose. Seasonality of calving has been explained in terms of the relationship of water levels and the availability of fish. It is thought that calves are born throughout the peak and falling water period, the time of maximum fish biomass, because increased availability of fishes may offset the mother's high energetic costs during late pregnancy and lactation (Best & da Silva 1984). The reasons for the difference in the observed reproductive cycle of Amazonian dolphins and Cinaruco River dolphins are not apparent. During rising waters, fish production is just beginning to increase, but fish biomass is greatest during falling water. A female would not only have more fishes available to her 4–6 mo after giving birth, but the fishes would be larger and easier to catch as the waters recede. If an abundance of fishes is important when the calf is several months old and the mother must provision both herself and the calf, there may be an advantage to calving during rising waters. The average age of weaning is undocumented, but a wild-caught mother was observed nursing her calf one year after capture (Caldwell & Caldwell 1972). If gestation is 10–11 mo (Best & da Silva 1984), births during the rising water period would indicate mating during the low water season. Trujillo Gonzalez (1990) and Beltrán and Trujillo Gonzalez (1993) observed mating groups during low water conditions in the upper Amazon River and a Colombian tributary of the Orinoco River, respectively.

Younger dolphins, especially calves, generally approached the survey boat more closely (within 1 m) than adults, and this could have inflated estimates of their relative abundances. Because of their uniform coloration and absence of scars, individual calves could not be distinguished reliably. Calf sightings did not vary according to habitat, but more juveniles were seen during falling water than other times. Since growth rates have been estimated at 2.5 cm/mo for calves (Best & da Silva 1984), smaller juveniles were probably born during the rising water period. Relatively few juveniles were sighted during the rising water period, indicating some larger two-year-olds might have been classified as adults. Eisenberg (1989) reported a 2-yr interbrood. Da Silva and Martin (1995) reported mother-calf bonds of at least 17 mo in the wild. Wells *et al.* (1987) found that juvenile *Tursiops* remained with their mothers after the period of nursing, and speculated that young dolphins need this time to learn the complexities of their social and physical environments. This long period of learning development may exist in *Inia* as well.

Juveniles were most often encountered in lagoons, especially during low water, and were seldom seen in side channels. Juveniles may frequent lagoons because these areas experience less boat traffic than river and confluence areas and provide more deep-water refuges than side channels. Calves also should be sensitive to boat disturbances, yet calves were found in all habitats. We found that during falling and low water conditions, lagoon fishes tended to be smaller than fishes in other habitats; juvenile dolphins might prefer lagoons where smaller fishes are more available.

We identified and resighted six individual adults using a combination of pigmentation patterns, marks, notches, and body size. One individual (Gray nick), was resighted 8 times over a period of 186 d, and was found throughout the study area. Another individual, (Pink notch), was seen 7 times over a 156 d period and was found throughout much of the study area. Both animals were sighted initially during falling water, and then not resighted until the end of the low water or rising water period. Because of our low success rate for photo-identification, a high resighting rate does not demonstrate that a dolphin's range was restricted to the study area, just as a low resighting rate does not indicate that a dolphin had left the study area. Several other dolphins initially identified were never resighted, perhaps due to emigration from the study area, wound healing, or ineffective photo-identification. The low success rate of photo-identification was partially a function of the unpredictable surfacing patterns of dolphins. River dolphins showed two general surfacing patterns. In the first, only the upper melon and blowhole were visible as the dolphin slowly surfaced in a relatively horizontal position. It was nearly impossible for us to identify dolphins when they surfaced in this manner. The second pattern, arch and roll, was more favorable for identification. During arch and roll, the animal's head broke the water first, often with the entire snout visible, then the full dorsal crest became visible. This rolling behavior was relatively uncommon. Trujillo Gonzalez (1994) and Henningsen *et al.* (1995) have successfully photo-identified *Inia* in the upper Amazon, but perhaps the dolphins of the Cinaruco River are more elusive due to frequent confrontations with sportfishers (T. McGuire, pers. obs.).

Like many Neotropical freshwaters, the Cinaruco River has a diverse fish fauna (161 species minimally). Prey size, habitat affinity, and ease of capture are probably more important for dolphins than the taxonomic identity of prey (Best 1984). The stomach from the dolphin carcass we necropsied contained the remains of 15 fishes. The four fish species we identified also were identified from the stomachs of Amazonian dolphins (da Silva *in* Best 1984). Da Silva (Best 1984) found *Inia* prey that ranged from 50–800 mm in length, but we found no fish longer than 117 mm.

Maximum fish CPUE for both gill nets and seines occurred during low water. This index reflects not only the relative abundance of fishes caught, but also the ease of capturing them using these two methods, and should not be interpreted as an absolute density estimate. Fish abundance declines during the late dry season as young-of-the-year and other fishes are either eaten or stranded in shallow, oxygen deficient waters (Lowe-McConnell 1975). Although fish abundance declines during the low water period, fishes are easier for predators to catch because they are spatially concentrated in the reduced water volume. The minimum CPUE for seine samples occurred during the rising water period in lagoons. The dispersal of fish across the flooded forests and plains decreases fish densities per unit area. In addition, fishes gain refuge in submerged vegetation and are possibly more difficult to catch. The relationship between dolphin sightings and fish CPUE was not significant, but our fish samples were very limited, especially with regard to spatiotemporal comparisons. Dolphins probably forage preferentially in areas where migrating fishes and new recruits are abundant and/or vulnerable. Spatial and temporal patterns in the relative abundance of fish size classes were distinguishable. Fishes in lagoons tended to be smaller than fishes in other habitats, and fishes tended to be smaller during falling water than other seasons. As waters receded, young-of-the-year fishes moved out of lagoons and side channels into the river.

Although we have emphasized the availability of prey as an important component of habitat use by *Inia*, food is not the only consideration. Certain habitats may be more energetically favorable due to temperature, shade, and water current. Others may be more attractive because they afford access to mates or refuges from other dolphins or human disturbances. Remote, heterogeneous, prey-rich areas like the Cinaruco River are viable candidates for river-dolphin reserves. Population structure, resource availability, and movement patterns of dolphins should be investigated to estimate the carrying capacities of such areas. These studies should be long enough to encompass major seasonal changes, and large enough to document movement into and out of the system.

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