Chapter 19
Cetacean Sociality in Rivers, Lagoons, and Estuaries

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Abstract Cetaceans of rivers, lagoons, and estuaries are isolated or partially isolated from marine species and have evolved in habitats with typically low predation pressure, but particularly high fluctuating physical and biological environments. In this chapter we explore if life in these generally murky, restricted habitats has affected the evolution of grouping and sociality in seven cetacean taxa: *Platanista*, *Pontoporia*, *Inia*, *Lipotes*, *Neophocaena*, *Orcaella*, and *Sotalia*. We suggest that there is a gradual increase in social complexity and communication as we move from the obligate or true river dolphins to the more facultative estuarine/brackish-water species.

Keywords Dolphins · Rivers · Lagoons · Estuaries · Sociality · Behavior · South Asia · South America · Southeast Asia · *Platanista* · *Pontoporia* · *Inia* · *Lipotes* · *Neophocaena* · *Orcaella* · *Sotalia*

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19.1   Introduction

Sociality is a complex outcome of interactions between evolutionary traits and more proximate biological (life history) and environmental factors. Cetaceans of rivers or lagoons are isolated or partially isolated from sympatric marine species. River and lagoon cetacean species and populations have evolved in environments characterized by spatial limitation, fluctuating prey availability, often a lack of predation pressure, and seasonally dynamic physical and biological environments. In rivers, the linear nature of habitats, patchiness of food resources at confluences and in deep pools, and highly variable water depth are three key factors that could influence movement, grouping, and social behavior. To understand if these differences influence sociality, we review available information from seven cetacean taxa (*Platanista*, *Pontoporia*, *Inia*, *Lipotes*, *Neophocaena*, *Orcaella*, and *Sotalia*) across parts of South America, South Asia, and Southeast Asia.

Fox et al. (2017) offered that encephalization (a brain to body weight ratio) in dolphins is a correlate of sociality and grouping behavior. The diversity of communication signals might also promote sociality under specific conditions, such as the importance of communication while under predation risk (Morisaka and Connor 2007). We review small-bodied cetaceans (adult body size usually less than 2.5 m), reaching sexual maturity between 7 and 10 years and calving about once every 3 years (Taylor et al. 2007). Natural changes in water area, seasonal flows, natural flood pulsing, and prey distribution across dry and wet seasons are common features of their habitats. They generally appear to have few natural predators (Hoy 1923; Pilleri 1972; Stacey and Arnold 1999), although there may be unrecognized predation by freshwater sharks, caiman, etc. on dolphins that venture into salt water, i.e., Irrawaddy dolphins, Guiana dolphins (Khan et al. 2011; Santos et al. 2009), and franciscana in the coastal waters of South America (Di Beneditto 2004) that are more susceptible to predation pressure. We explore grouping, sociality, and sociosexual behaviors across these seven taxa in ascending order of their currently accepted ages of divergence, i.e., from most basal to most recent (based on Yan et al. 2005; Costeur et al. 2018).

19.1.1   Platanista

Platanista is one of the most basal odontocetes and includes the Ganges River dolphin or Susu *P. g. gangetica* and the Indus River dolphin or Bhulan *P. g. minor* distributed across the Indus-Ganga-Brahmaputra (IGB) rivers and their tributaries. The species as a whole is listed as "Endangered" on the IUCN Red List (Braulik and Smith 2017), but despite numerous dams and barrages fragmenting river flows across their ranges, populations have persisted at high densities in some reaches (e.g., 1600–1800 Indus dolphins in 700 km of the Indus; Braulik et al. 2015). Ganges dolphin populations are estimated at 3000–3500 in about 5000 river kms of

the Ganga Brahmaputra basin (Sinha and Kannan 2014). The taxonomy of *Platanista* is in flux, and we expect that the two subspecies may be separated into two species in future.

Given the murky, sediment-rich rivers they evolved in, *Platanista* are "almost blind" due to evolutionary regression of the optic nerve and eye lens (Herald 1969; Waller 1983). There are no confirmed records of predation on *Platanista*. It has also not been possible to observe *Platanista* underwater in the wild, the primary reason for their poorly known social behavior. Observations on captive Indus and Ganges dolphins kept in aquaria in the USA, Switzerland, and Japan in the late 1960s and 1970s (Herald 1969; Pilleri et al. 1971a, b; Pilleri 1974) showed that there was frequent body rubbing, stroking and caressing, chasing, biting (near dorsal hump, pectoral fins, and tail flukes), and rostrum-body contact, especially in young and subadult animals (Pilleri et al. 1971a, 1980; Gihr et al. 1976). Males, whose ranges were relatively larger than young females, also displayed more affiliative behaviors. Sexually excited behaviors (chasing, male biting female's rostrum) occurred at the start of April (in Switzerland: Pilleri et al. 1971a). Pilleri et al. (1980) documented basic play behaviors in captive animals.

In their natural habitat, *Platanista* are generally solitary (Reeves and Brownell 1989), except for mother-calf associations, mating pairs, and nonsocial feeding aggregations (up to 30–40 animals) in deep pools with high prey availability (Smith and Reeves 2012; Nowak 2003; Moreno 2004; Lal Mohan and Kelkar 2015). Sexual dimorphism is limited to body size and shape, adult females being slightly longer and with more curved rostra than adult males. Most descriptions of mating wild *Platanista* are from the peak dry season and pre-monsoon (March–June; Pilleri 1972; Sinha and Kannan 2014; Lal Mohan and Kelkar 2015), extending to August in the Brahmaputra River (Kasuya and Haque 1972; Haque et al. 1977). Pilleri (1972) suggested that a female might mate with up to three males, but it was not clarified how males were identified. In river areas with high dolphin densities, mating aggregations form—and *Platanista* are then more acrobatic (breaching high, tail slapping) than usual. Kelkar and others observed a mating pair spin out of water and twist screw-like in midair, jointly somersaulting, while surrounded by 5–6 dolphins. Lal Mohan and Kelkar (2015) suggested a "lek-like" mating system in *Platanista*, but perhaps only at high dolphin densities (Haque et al. 1977; Lal Mohan and Kelkar 2015).

Gestation of *Platanista* is about 8–10 months (Kasuya 1972), with calving peaks in February–March in the Ganges River (Sinha and Kannan 2014; Lal Mohan and Kelkar 2015), and May–December in the Indus (Pilleri 1970, 1972) and Brahmaputra Rivers (Haque et al. 1977). Apparently, a female can mate even when her suckling calf has not yet been weaned (Pilleri 1972). The mating season and calving periods are likely tuned to hydrological dynamics and prey availability peaks (rising floods in June–July and receding floods in October) in the Indus-Ganges-Brahmaputra basins. These rivers have peak flow (flooding) from June to September, despite the variable contributions of glacial melt and monsoon precipitation (Zhang et al. 2013a) in a lean period from November to April. Observations from the Ganges (Dey, S.; pers. comm.) suggest that adults might monopolize rich foraging spots such as river

confluences and supplant subadults or juveniles. Mother-calf pairs were seen in shallow river pools in the Gandak River (Choudhary et al. 2012), and Lal Mohan and Kelkar (2015) suggested that they were there to capture concentrated prey and perhaps to avoid male harassment. Strong site fidelity in *Platanista* for stable channels (e.g., near towns/embankments) is noted at multiple sites over many years (Lal Mohan and Kelkar 2015; Smith and Reeves 2012).

Acoustic frequencies and sound source levels of Ganges River dolphins from the Ganges in Bhagalpur (Bihar, India; Kelkar et al. 2018) differed significantly from the Bangladesh Sundarbans (Jensen et al. 2013) and from captive Indus dolphins (Pilleri et al. 1977). These differences could result from varying ambient underwater noise levels in artificial, nontidal, or tidal environments or the overlapping ranges of *Platanista* and Irrawaddy dolphins, *Orcaella*, in Bangladesh, unlike elsewhere, as frequencies may have diverged to avoid interference (Morisaka, T.; pers. comm.).

As for all dolphins, *Platanista* clicks have dual function for communication and echolocation during navigation/foraging (Zbinden et al. 1978), but variation in modulation of click trains has not been studied. *Platanista* emit "burst-pulses" or rapidly repeated click trains (Pilleri et al. 1971b, 1977) that could serve communication functions. Burst-pulses were recorded in May 2014 (mating season) in the Ganges at Bhagalpur (Morisaka, T., pers. comm.). Though burst-pulses are at times used by other dolphin species to indicate aggression (Overstrom 1983), their function in *Platanista* is not understood. Peculiar click trains were recorded near mother-calf pairs, but whether they were contact calls needs further study. Jaw-snapping sounds (Andersen and Pilleri 1970) were perhaps related to social signaling.

19.1.2 **Pontoporia blainvillei**

Toninha or franciscana (also termed La Plata River dolphin), *Pontoporia blainvillei*, dwell in coastal shallow waters from southeastern Brazil to Uruguay close to riverine discharges and riverine systems in Argentina (Cremer and Simões-Lopes 2005; Santos et al. 2009; Bordino et al. 1999). Occurring in usually murky water up to 30 m deep (Pinedo et al. 1989; Praderi et al. 1989), their distribution strongly overlaps with important human fishery areas in Brazil, Uruguay, and Argentina, which exposes them to a high risk of incidental capture (Ott et al. 2002).

Franciscana are sexually dimorphic, with females larger than males (Kasuya and Brownell 1979). They exhibit apparent cooperative foraging of up to 30 dolphins (Bordino et al. 1999) with fish and cephalopod prey associated with the bottom of the water column (Danilewicz et al. 2002). Franciscana tend to associate in small groups of two to three individuals (Bordino et al. 1999; Wells et al. 2013), but records of larger groups exist (Secchi et al. 2001; Di Beneditto and Ramos 2001; Santos et al. 2009). Mating behavior occurs in spring and summer. Franciscana are prey of several shark species, based on stomach content analyses (e.g., Brownell 1975; Praderi 1985; Di Beneditto 2004), as well as of killer whales (*Orcinus orca*, Ott

and Danilewicz 1998; Santos and Ferreira Neto 2005), and grouping may be related to predation risk in coastal populations.

Although their social organization remains poorly known, satellite-tracking data of two separate pairs of female-male adults showed that they moved in close proximity for several weeks along the coast of Argentina, possibly supporting the hypothesis of a single-male mating system (Wells et al. 2013), which is rare among marine mammals (Connor et al. 2000; Wells et al. 2013). A relatively small testis size suggests that sperm competition does not occur in this species (Danilewicz et al. 2002). There are no detailed observations on social behavior of franciscana.

19.1.3   *Inia geoffrensis*

The boto (or Amazon River dolphin), *Inia geoffrensis*, is distributed across six countries (Brazil, Bolivia, Colombia, Ecuador, Peru, Venezuela) and three major river basins (Amazon, Orinoco, Araguaia-Tocantins) (Best and Da Silva 1993). Solitary animals and pairs comprise the majority of sightings throughout their range, although larger group sizes (up to 40 individuals) foraging or socializing may occur, in river confluences, lakes, and river margins (e.g., Vidal et al. 1997; McGuire and Winemiller 1998; Aliaga-Rossel 2002; Martin et al. 2004; Araújo and da Silva 2014; Gómez-Salazár et al. 2012). Groups are predominantly small (up to five individuals) and can vary with water levels across dry-wet seasons (Aliaga-Rossel 2002; da Silva et al. 2010; Gómez-Salazár et al. 2012). In the Central Amazon (Brazil), males and females differ in habitat use, males tend to occupy the main rivers and channels, and females, with their calves, are more commonly found in lakes or low-current habitats such as flooded forest (*várzea*) (Martin and da Silva 2004). The high occurrence of mother-calf pairs and immature botos in floodplain habitats is likely due to prey availability, lower current, and protection from potential aggression by adult males (McGuire and Winemiller 1998; Martin and da Silva 2004; Mintzer et al. 2016). This spatial sexual segregation contributes to differences in home range sizes for both sexes, with males dispersing more than females. In concordance with sexual segregation in habitat use, a high degree of female philopatry has been described by genetic studies of mtDNA of animals from the Amazon, with males being more dispersive (Hollatz et al. 2011). However, in at least one area of the Amazon (Mamirauá Reserve), some animals show a high degree of residency, remaining in one area year-round (Martin and da Silva 2004).

Botos are sexually dimorphic, with males pinker in colour, 16% larger and 55% heavier than females, suggesting a polygynous mating system where males compete for females, so aggressiveness among males and occassionally towards females is expected (Martin et al. 2008). This is supported by the large amounts of scarring found on males due to male-male interactions. During aggressive behavior, botos may produce low-frequency sounds as a possible indication of competitive advantage compared with high-frequency sounds emitted during play and other behavioral contexts (Nunes 2015). Males may also compete for females by displaying

Fig. 19.1 A group of botos, *Inia geoffrensis*, socializing in the Tocantins River, Brazil. Photo by Claryana Araujo-Wang

various objects in a sociosexual context—this was first observed in the Amazon (Martin et al. 2008) and then later reported for botos in the Tocantins River (Araújo and Wang 2012; Santos et al. 2012). During object-carrying behavior, botos raise their heads out of the water while holding or throwing various objects (e.g., branches, stones, leaves, sticks) with their mouths. Botos may also drag the objects as they swim with their heads raised above the surface of the water. Because object-carrying is usually performed by adult males with other females and young males present, it is possible that such behavior is similar to lek-like mating and important for mating success. The mode of transmission of this behavior among individuals is unclear, but due to the presence of younger males in groups of object-carrying males and the social interactions among them, horizontal transmission (i.e., young males learning from interactions with older males) is possible (Fig. 19.1 of socializing botos). Santos et al. (2014) observed a group of six dolphins in the lower Tocantis River displaying sexual behaviours by rubbing against each other and one individual frequently breaching and exposing its penis to the group.

Botos are not known to form long-term social groups. Except during socializing and courtship situations, females do not commonly interact with males and are

usually associated only with their offspring (Araújo-Wang, unpublished data). Play-like behaviours such as body rubbing, tail-slap, rolling, and spy-hoping, tossing inanimate objects such as leaves and playing with fish (e.g., small puffer fish) that are not consumed have been observed (e.g., Araújo-Wang 2017; Santos et al. 2014). Females often become pregnant while still lactating, and older calves may remain associated with their mother (although to a lower degree) until they become independent (Martin and da Silva 2018). In the central Brazilian Amazon, a female performed apparent epimeletic (nurturant) behavior toward a dead calf (Martin and da Silva 2018), but whether there were other females in the group is unknown as it was not documented.

Frequent 'aggressive' interactions between males and young calves occur, but young calves do not always appear harmed, and their mothers may not react negatively toward the aggressive males in such instances (Araújo-Wang, unpublished data). Such apparent aggression toward calves could indicate play, bonding or some lower-level social interactions. However, an instance of potential infanticide behaviour was described by Bowler et al. (2018) in the Napo River (Peru), during which an adult male (of a group of six individuals including a mother-neonate) seemed to target a neonate. An adult female was observed to try and keep the neonate safe, while the male showed forceful and apparently aggressive swimming around the neonate.

An unusual behavior of aerial urination by males has been described for botos in the Tocantins River (Araújo and Wang 2012), in which sometimes another male actively positions his beak close to or into the stream of the urine splashing on the surface of the water, probably receiving chemical cues from the urinating male. Such behaviours have not been observed in females, and females have also not been recorded in groups of males involved in such behavior (Araújo-Wang 2017).

Competition for resources in feeding aggregations (for provisioned and unprovisioned botos) is seen mainly between males, where males show aggressive behaviour and even supplant behaviour in order to monopolize food resources (Santos et al. 2014; Alves et al. 2013; Araújo-Wang, unpublished data). Such all-male groups appear to be structured by social dominance hierarchy (Alves et al. 2013). Larger males in a provisioned feeding aggregation at four human-provisioned locations in Amazons State, central Amazon (Brazil) competed, bit, pushed and rammed into others to supplant them. In unprovisioned botos of the Tocantins River, large males have frequently been observed "stealing" fish from smaller male botos (Araújo-Wang, unpublished data). In this situation, the behaviour of "stealing" fish is not necessarily accompanied by the highly aggressive behaviours such as biting, as seen in provisioned dolphin groups. Usually the larger male "waits" in the periphery for other males to catch fish and then swims quickly towards them and steals the fish in mouth. These types of dominant, aggressive and supplanting behaviours have not been reported in wild female groups, or in cases of provisioned dolphins where females are present (Santos et al. 2014). With high degrees of sexual dimorphism, aggression by males for food and the possibility of infanticide to monopolise mating opportunities, and diverse socio-sexual object-carrying displays, botos seem to be the most socio-sexual of the seven species reviewed here.

19.1.4 **Lipotes vexillifer**

The baiji (forming the monotypic family Lipotidae) once occurred over a great length of the Yangtze River and its large floodplain oxbow lakes such as Dongting (Tung Ting) and Boyang, from the mouth of the river at Shanghai almost up to the far-inland Three Gorges area (Hoy 1923; Yang et al. 2000). But, it has not been reported since 2006 (Turvey et al. 2007) and is considered the first cetacean species to become extinct from anthropogenic impacts (Turvey et al. 2007; Zhou 2009). Due to this sad fact, we rely substantially only on published captive direct and photo/ videographed observations of *Lipotes* maintained at the Institute of Hydrobiology in Wuhan, China, 1980–2003. Of six captive *Lipotes*, one male, "Qi Qi," was the last survivor and lived for over 22 years in captivity, and a female, "Zhen Zhen," lived for >2 years (Curry et al. 2013); the rest died within 1 year of being brought in from nature. Wild observations are extremely few but are also summarized here (Zhou et al. 1979, 1998; Liu et al. 1986; Zhou and Li 1989; Chen 1989; Chen et al. 1997; Zhou 2009).

Adaptation for life in dynamic, sediment-rich, glacial-melt, and monsoon-flooding rivers might have triggered similarities in social behaviors in *Lipotes* and *Platanista*, despite their phylogenetic distance, i.e., being "unrelated" taxa. *Lipotes* appeared to be much more dependent on visual cues unlike blind *Platanista*. Liu et al. (1986, 1994) noted "standing behaviors" in captive *Lipotes*, and Zhou et al. (1998) saw "spy-hopping"-like behaviors in captive and wild *Lipotes*, possibly to detect and evade threats at the surface. Interestingly, Yang et al. (2001) observed *Lipotes* resting without much vocal activity in shaded areas of the tank at night (1800–0600 h), possibly to avoid light (resting = long periods of immobility near the water surface).

Group sizes of wild *Lipotes* typically ranged from 2 to 12 dolphins and displayed consistent group cohesion. Some photo-identified baiji individuals made movements ranging from 200 to 350 km within 1 year, indicating that they (when wild population size went below 50) were highly mobile, possibly moving all the time in response to heavy boat traffic (and constant underwater noise) and destructive fishing practices (rolling hooks, nets, etc.). One baiji travelled almost 100 km in 3 days, based on successive photo-ID locations (Zhou et al. 1998), and one moved 200 km downstream from 14 May 1989 to 24 April 1990. *Lipotes* also swam with foraging groups of Yangtze finless porpoises *Neophocaena asiaeorientalis asiaeorientalis* (Würsig et al. 2000; Zhang et al. 2003).

Unlike *Platanista*, the acoustic repertoire of *Lipotes* was comprised of clicks, cries, creaks, and whistles (Akamatsu et al. 1998; Wang et al. 1999). Hoy (1923) reported a peculiar "rearing noise" heard at night, audible to the human ear, which was apparently from baiji in Dongting Lake. Peak click frequencies were similar in range to *Platanista*, and whistle patterns resembled *Inia* whistles, but differed from marine delphinid whistles. Whistles also showed variable durations and inflection points that could convey specific "messages," which might be a critical need in the very noisy habitats in which the baiji lived out its final years. The absence of

ultrahigh-frequency hearing only in *Lipotes* among all river dolphins (Costeur et al. 2018) might have ostensibly been a factor behind their higher susceptibility to vessel noise, as compared to the sympatric Yangtze River finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*).

Gao and Zhou (1992) confirmed sexual dimorphism with females larger than males, at 2.5 m and males at 2.16 m (based on Chen et al. 1984). Sexual behaviors occurred during spring and autumn (Liu 1988), i.e., during the low flow or dry season, similar to *Platanista*. Frequent erection, rubbing of penis on tank fixtures, and touching the female Zhen Zhen with it were observed in the captive male Qi Qi in these seasons (Liu et al. 1994). The gestation period is 10–11 months, with one calf born per female in February–March, about every second year (Chen et al. 1984). Captive studies recorded *Lipotes* to play with rings, balls, tubes, and brushes. Rarely, side swimming, tumbling, rolling, and leaping/surface-gliding behaviors were described by Kejie et al. (1985) and Liu et al. (1994). *Inia* dolphins were more playful than *Lipotes* in captivity (Pilleri et al. 1980; Liu et al. 1994). Baiji were generally slow and lethargic swimmers, except when alarmed (Liu et al. 1994). From activity patterns of captive *Lipotes*, and constant evasive movements due to disturbances to wild individuals, inferring much about social behavior will remain difficult (Zhou et al. 1980, 1998; Chen et al. 1997; Turvey et al. 2007).

19.1.5 Neophocaena asiaeorientalis asiaeorientalis

The taxon *Neophocaena* includes the Indo-Pacific finless porpoise, *N. phocaenoides*, and the narrow-ridged finless porpoise, *N. asiaeorientalis*, both inhabiting lower reaches of estuaries and coastal waters up to about 50 m depth. *N. asiaeorientalis* has a subspecies *N. a. asiaeorientalis* (the focus of this section), limited to the middle and lower reaches of the Yangtze River of China (from Yichang to Shanghai) and its adjoining lakes (Poyang and Dongting lakes). It is endangered (Wang and Reeves 2017), with fewer than 1000 individuals left in the wild, and is isolated from coastal and estuarine populations (*N. a. sunameri*). Zhou et al. (2018) reconstructed the demographic history of finless porpoises—they identified genes associated with renal water homeostasis and the urea cycle, likely evolutionary adaptations associated with surviving in freshwater versus saline conditions. Their results suggest that Yangtze finless porpoises are reproductively isolated from coastal and marine porpoise populations and diverged between 50,000 and 100,000 years ago.

In the wild, Yangtze porpoises occur alone or in groups of 2–20 individuals, with most common group size of 2–3. Groups >20 individuals are rare. Genetic analysis of relatedness (Chen et al. 2017) using microsatellite markers proved the presence of matrilineal grouping in these porpoises, with a sign of inbreeding only in the Tian'e'Zhou ex situ reserve population, which is environmentally compromised. Surveys in Dongting Lake showed that socializing was not a predominant behavior (only 1% of 419 sightings were of socializing groups (Zhang et al. 2013b), with this low level of social behavior likely attributable to extreme environmental alterations

leading to food resource depletion. In captive situations and ex situ reserves, socializing and resting behaviors were more frequently observed (Jiang 2000; Xian et al. 2010a, b; Zhang et al. 2013b) compared to the extremely altered wild conditions. Predation on Yangtze finless porpoises has not been documented and is probably absent (Wang et al. 2014).

Three Yangtze finless porpoises had been kept in an aquarium for 3–6 years since 2001 (Wei et al. 2004), and 120 observation sessions of these individuals suggested that sociosexual behavior was common. Sexual behavior displays peaked between April–May and September–October. In another captive study of three male porpoises (two adults and one juvenile) with one adult female (Wu et al. 2010), sociosexual behavior peaked in March–July. The monthly mean frequency of sexual behavior of the three males varied, with the youngest male showing highest sexual behavior frequency every month. When the female was absent, these sexual overtures occurred in male-male pairs. The subordinate adult male showed a different behavior—his sexual peak happened from November to January, unlike the dominant adult male, but when the juvenile male porpoise was still intensely social with him. This difference in sexual peaks may have been due to the effects of social factors on hierarchical rank in the male porpoises. In other captive studies, Xian et al. (2010a, b) observed sociosexual behavior in a porpoise calf.

19.1.6   Orcaella brevirostris

Irrawaddy dolphins *Orcaella brevirostris* inhabit rivers, brackish-water lagoons, and coastal waters in South and Southeastern Asia (Beasley 2008). These populations either moved or settled in rivers and lagoons over time given the volume of available prey and reduction of competitive pressure from other coastal dolphin species such as humpback dolphins (Sutaria 2009); or they inhabited these water bodies during the last glacial maximum and got separated from coastal populations as sea levels fell. We compare sociality in a freshwater population of the Mahakam River in Indonesia with one from Chilika Lagoon in India.

Chilika is a bean-shaped, semi-enclosed, muddy, and shallow water body, where the average water depth is 3 m and the connection to the sea is a narrow channel 12–17 km long. The dolphin population in Chilika is less than 150, with socializing the second-most dominant behavior, after foraging. Apparent cooperative foraging for schooling fish is a common strategy. Social structure analyses of the dolphins in Chilika found five primary clusters of associating individuals with association index ≥0.5. Of the 48 individuals sighted more than four times, 14 individuals showed strong associations with one or more other individuals. Group size estimates ranged from 1 to 19, with an average group size of 5 while socializing. Behavioral events in intensely socializing groups included touching in some manner, rubbing, apparent mating attempts and diving on top of and underneath other dolphins, chasing, flipper and fluke slaps, somersaults, and back flips. At times, dolphins moving or feeding together touched, rolled over, and swam on the sides of

Fig. 19.2 Series of photos of Irrawaddy dolphins, *Orcaella brevirostris*, of events and group structure in a mating chase. A group of dolphins in a tight structure chased one dolphin who eventually turned ventrum up and was mated with by one or more individuals. After a mating bout, the group would often come together head to head as seen in the bottom right picture. Photos by Dipani Sutaria

another individual, or one of the animals leaped out of the water or spy-hopped (often when a calf or juvenile was present in the group). Sutaria (2009) observed that aggressive behavior between conspecifics was rare, unless it was an intensely socializing group, involving mating chases (Fig. 19.2). Mating chases occurred during morning hours from February to May, just before the onset of the monsoons, by 3–7 animals, chasing 1–2 other individuals (probably female with young). A mating chase lasted until a boat disturbed the group or the chases stopped naturally in 25–30 min. It often included a behavioral event lasting 0:35–0.50 min of one dolphin upside down and several individuals on top of and around it, indicating attempts to mate by more than one male. The chasing group often showed synchronized movements with 3 or more animals in front and 2–3 animals behind, with 1–2 satellite individuals moving with this fast-moving mating group. Between mating bouts, chasing males slowed down, logged on the surface, and then converged in a circular formation with their heads facing inward, either preparing for another chase or showing head-to-head aggression (Fig. 19.2). Dolphins in groups of two regularly displayed sideways, lateral swimming positions with pectoral fins on the surface held perpendicular to the body, facing another individual in ventral to ventral position, by the water's edge (Fig. 19.3).

Fig. 19.3 Social behavior between an adult and juvenile Irrawaddy dolphin, *Orcaella brevirostris*, in Chilika, where sideways swimming along with pectoral flipper touching occurs. Photos by Dipani Sutaria

In the Mahakam River and Delta (Kreb 2004), average group size was 5–6 dolphins with socializing groups of larger pod sizes. Home ranges calculated for 53 photo-identified river dolphins sighted 12 times on average showed that dolphins moved freely along a 61 km stretch (individual ranges $= 4–181$ km^2) and used an average of 10 km^2 of river area (individual home ranges $= 0.3–35.5$ km^2). Similar to the population in Chilika, female dolphins in the Mahakam had overall smaller home ranges than male home ranges and two center areas of high dolphin density occurred in the river. Site fidelity was high, with residence indices for females significantly higher than for males in Chilika and in Mahakam. Dolphins showed clear preferences for association with certain individuals and had long-term preferred companionships. In 3.5 years, 30 significant long-term dyads were detected, and the associations between females were stronger than for between males. Associations among sexes were fluid, indicating short- or long-term preferred companionships. Mating events occurred in the Mahakam during July–August, March, and December. Mating events took place between 2 and 3 subgroups with total group sizes ranging between 5 and 12 adult individuals per mating event. These interactions were characterized by vocal and behavioral dominance displays: loud blows, fast swimming, rolling along the axis of the dolphin's body, swimming sideward and with belly up, group swimming in small circles and speeding up (chases), jumps,

many fin and fluke waves and slaps, and intensive body contact. Interestingly, water spitting (or squirting) that was often associated with feeding also had been observed three times during socializing, where a spitting dolphin targeted another dolphin's body.

Acoustic studies in Chilika and Mahakam showed that vocalizations included click trains, whistles, and pulse calls, both buzzes and creaks, as for coastal dolphins in Australia and Indonesia (Van Parijs et al. 2000; Kreb 2004; Sutaria et al. 2017). Fundamental frequencies of whistles and contour types from Mahakam, Chilika, and Balikpapan Bay are also similar (Sutaria et al. 2017) and comparable to those described for coastal Irrawaddy dolphins by Hoffman et al. (2017) in Malaysia and by Van Parijs et al. (2000) for Australian snubfin dolphins (*Orcaella heinsohni*).

19.1.7 Sotalia *spp*.

The genus *Sotalia* is composed of two species: the tucuxi (*S. fluviatilis*) and the Guiana dolphin (*S. guianensis*) (Caballero et al. 2007; Cunha et al. 2005). The Guiana dolphin inhabits coastal waters, and tucuxi occur in the major freshwater tributaries of the Amazon and Orinoco River basins (Borobia et al. 1991; da Silva and Best 1996; Edwards and Schnell 2001; Flores and Bazzalo 2004; Flores and Silva 2009; Cunha et al. 2005; Caballero et al. 2007; da Silva et al. 2010; Rosas et al. 2010).

Sotalia is a relatively modern delphinid with a fair bit of retention of older traits, so one would expect it to have more complex behavioral repertoires than its counterparts in this chapter (e.g., Santos and Rosso 2007, 2008). Group size ranges are 1–26 (Santos and Rosso 2008; Santos et al. 2010a), often higher than *Inia* sympatric with tucuxi in many areas, where mean group size was 6 (Gómez-Salazár et al. 2010). Similar to other riverine species, seasonal changes in water levels influence movement of tucuxi, with an increase in length and area of usage during monsoon and post-monsoons in the Central Amazon (Faustino and da Silva 2006; Flores and Bazzalo 2004; Gómez-Salazár et al. 2010). Gómez-Salazár et al. (2010) and Trujillo et al. (pers. comm.) observed a higher frequency of intense socializing and mating in low-water periods when the availability of fish is high, and high site fidelity is also noted in marine and riverine populations (Santos et al. 2001; Azevedo et al. 2004; Rossi-Santos et al. 2007; Lopes et al. 2012). Sexual displays and intense socializing followed cooperative foraging encounters (Santos and Rosso 2008), sometimes including foraging associations with birds (Santos et al. 2010b). Key areas where such behavior occurs are shallow stretches of river close to islands and sandbanks. Group sizes were higher in confluence areas, probably owing to higher density of prey. Predation risk on Guiana dolphin may be significant for grouping behaviors and responses (Santos and Gadig 2009), but risk might be higher for marine than for riverine populations. In Gandoca-Manzanillo (Costa Rica), marine tucuxis and bottlenose dolphins often displayed sociosexual behaviors, but these behaviors have not yet been documented in the freshwater tucuxi population.

19.2   Summary and Discussion

The major limitations to documenting sociality in wild river dolphins are the usually turbid waters, near-inability to differentiate sex, and elusive, difficult-to-see behaviors at the surface. For South Asian river dolphins, narrow-ridged Yangtze finless porpoises, and baiji, behavioral descriptions in captivity could be regarded as the only systematic descriptions of sociosexual behaviors. The intense sociosexual activity described in aquaria, e.g., in Yangtze finless porpoises, could be a result of their unnatural life in captivity.

Movements and group sizes of river dolphins tend to be closely related to water flow dynamics and local prey distribution. Sociality is observed primarily in occasional and loose/variable aggregations, and feeding rather than mating opportunities appear to drive most grouping behaviors. River dolphins appear to largely form only-male or only-female groups, with mixed groups mainly associated with socializing or courtship chases, or in mother-calf associations.

If we compare riverine species in terms of their evolutionary history and complexity of social behavior, some consistent patterns emerge. In Fig. 19.4, we tentatively map the species along four visual axes, suggesting that more obligate and basal river dolphin lineages (toward the left) may have less highly evolved sociality and none or low predation risk, and feed mostly on non-schooling benthic prey. An exception in the older lineages is *Pontoporia*, which however also lives in the coastal open ocean and in which grouping behaviors may be in response to predation risk from sharks and killer whales. Among more recent and facultative river/lagoon phocoenid and delphinid species (toward the right), predation risk and tendency to feed on schooling prey appear relatively higher, and social communication also seems to be more complex, than the "true" river dolphins. The complexity of social communication signaling, e.g., whistle complexity, is positively correlated to social structure (May-Collado et al. 2007). Such complexity is lower in *Orcaella* compared to other coastal delphinids such as *Sotalia* or *Sousa*, but might be greater than for more-basal riverine odontocetes such as *Platanista*. This could corroborate our hypothesis of sociality being a function of evolutionary history—possibly driven by combined effects of low predation risk (Morisaka and Connor 2007; Connor 2007) and constraints on acoustic signaling in shallow estuarine-coastal environments (Jensen et al. 2013).

In the phylogenetically distinct *Platanista* and *Pontoporia*, many similarities may exist through evolutionary convergence, such as in their brain/body mass ratios (the lowest of extant cetaceans, Ridgway et al. 2017) and morphology. Yet, unlike *Platanista*, *Pontoporia* show regular grouping behavior in response to higher predation risk. Other curious behavioral similarities might exist between the unrelated *Platanista* and *Lipotes* that live(d) in riverine habitats driven by similar hydroclimatic forcing effects (e.g., from Himalayan-Tibetan seasonality and climate).

Inia, a more recent river dolphin species, exhibits an advanced degree of sociality and overt sociosexual signaling behaviors. Given that *Inia* still retain many "plesiomorphic" traits and with no documented predation risk, a high level of
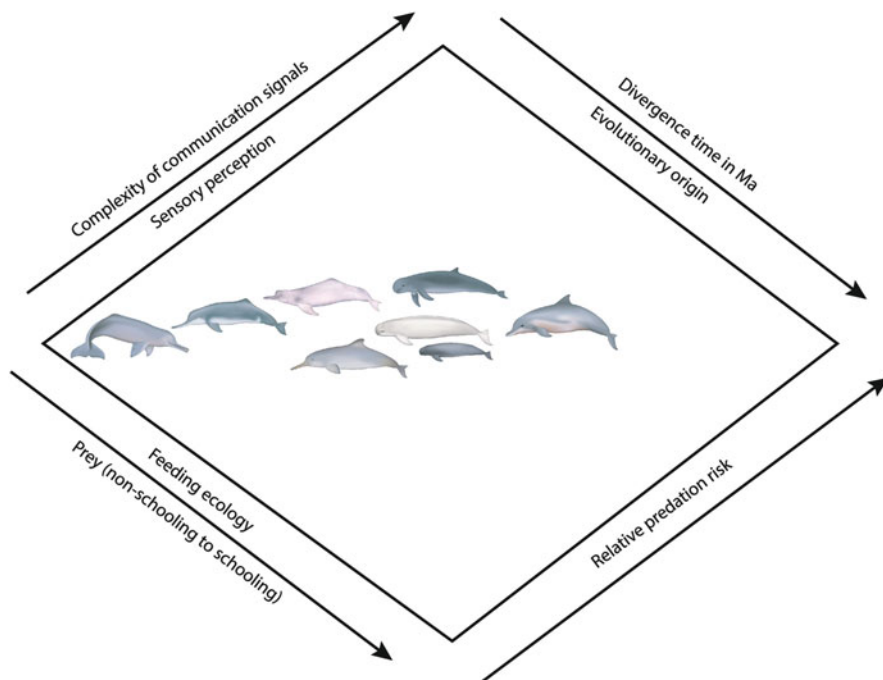
Fig. 19.4 A "map" of the selected species for this chapter, in relation to four axes: (1) evolutionary origin (divergence time: million years), (2) complexity of sensory perception for communication signals, (3) feeding ecology (based on the schooling versus non-schooling prey hypothesis of Connor (2007), and (4) relative predation risk. Species: (from L to R) *Platanista*, *Lipotes*, *Inia*, *Pontoporia*, *Neophocaena adult and calf*, *Orcaella*, *Sotalia*. Illustrations by Uko Gorter, with permission

sociality might be correlated with greater degree of encephalization and habitat-driven selection of visual cue-related behaviors. In contrast, visual limitation in *Platanista* might have constrained the complexity of their social behavior.

In relatively modern species considered as "more recently adapted" to river and lagoon environments than the long-term obligate species, avoidance of resource competition might influence social behaviors, e.g., *Sotalia* sharing habitat with sympatric *Inia* and *Pontoporia*. Such intimate factors, beyond evolutionary effects or selection pressures (Nowak 2003), can translate clear benefits and nontrivial costs of sociality for river and lagoon dolphins. *Orcaella* could be the only dolphin species in some rivers/lagoons (e.g., Chilika, Ayeyarwaddy) that share their range with *Platanista* (in tidal rivers/estuaries, e.g., Hooghly, Sunderbans) or with *Sousa chinensis* and *Neophocaena phocaenoides* (Sunderbans and in coastal habitats, e.g., in Bangladesh, West Bengal, Indonesia, Malaysia, and Thailand). The riverine population of *Orcaella* showed a highly structured society but the population in Chilika showed a more fluid society. This variability in social structure can be explained by differences in productivity, inter-species competition, etc. across habitats. Such

plasticity of sociality and grouping behaviors might underlie the ecological adaptability of *Orcaella* and even explain its long-term persistence in threatened habitats.

Increasing anthropogenic pressures from dams, heavy ship traffic, water pollution, and highly destructive and injurious fishing gears (causing significant bycatch mortality) in riverine, estuarine, lagoon, and coastal environments can strongly impact sociality and related behaviors. Wade et al. (2012) suggested that lack of strong sociality in certain dolphin species might be important for their resilience to direct exploitation and other threats. This might explain the persistence of *Platanista* today, even as it faces significant population declines and unprecedented habitat degradation. In *Lipotes*, with the extreme destruction and abuse of its habitat, disrupted social bonds could have contributed to this river dolphin species becoming overwhelmed by the threats it faced during its last six decades on Earth. How social behaviors will be shaped by rapidly changing environments, anthropogenic impacts, and climate needs to be a key area of enquiry to gain potential insights into saving endangered populations of riverine, estuarine, and coastal odontocetes.

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