Chapter 16
The Indo-Pacific Bottlenose Dolphin (*Tursiops aduncus*)

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Abstract The behavioral ecology of *Tursiops aduncus* (Indo-Pacific bottlenose dolphin) is usually reviewed alongside the much more widely studied *T. truncatus* (common bottlenose dolphin). However, the smaller, typically shallow water *T. aduncus* has been closely scrutinized in Australian and Japanese waters. As a result, there now exists a robust body of information spanning all three of Hinde's levels of social analysis—interactions, relationships, and social structure—that may be unmatched in any other cetacean. Research on *T. aduncus* has contributed significantly to the social complexity hypothesis of large brain evolution and our understanding of delphinid mating systems, communication, and individual differences in foraging tactics within populations. Here, we focus on behavioral research at two primary sites, Shark Bay in Australia and Mikura Island in Japan, with additional observations of importance from other locales in each region.

Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) typically occur near shore in shallow tropical and temperate waters of the Indian and western Pacific Oceans. They are smaller than *T. truncatus*, at less than 2.7 m in length, and are generally

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smaller in the tropics (Fig. 16.1a). Where abundant, *T. aduncus* are prominent in coastal waterways, often surfing waves along beaches (Fig. 16.1b) and foraging around estuaries, seagrass beds, and rocky reefs. Most populations consist primarily of resident animals (e.g., Möller et al. 2002; Shirakihara et al. 2002; Tsai and Mann 2013), but some individuals have been documented across sites separated by several hundred kilometers (e.g., Brown et al. 2016; Tsuji et al. 2018). *T. aduncus* eat small fish and cephalopods primarily, although some may target larger fish and occasionally sharks, rays, and crustaceans. After spending several years with their mothers, *T. aduncus* achieve sexual maturity at 10–15 years of age and may live 40–50 years (Karniski et al. 2018).

The earliest studies of *T. aduncus*, indeed, some of the earliest studies of any odontocete, are those of Tayler and Saayman in wild and captive settings in South Africa (Tayler and Saayman 1972; Saayman and Tayler 1973). Observations on wild populations were limited to grouping patterns, but Tayler and Saayman's (1973) descriptions of a captive dolphin infant retrieving milk from its mother and then spitting it out to imitate a human viewer exhaling cigarette smoke, and using
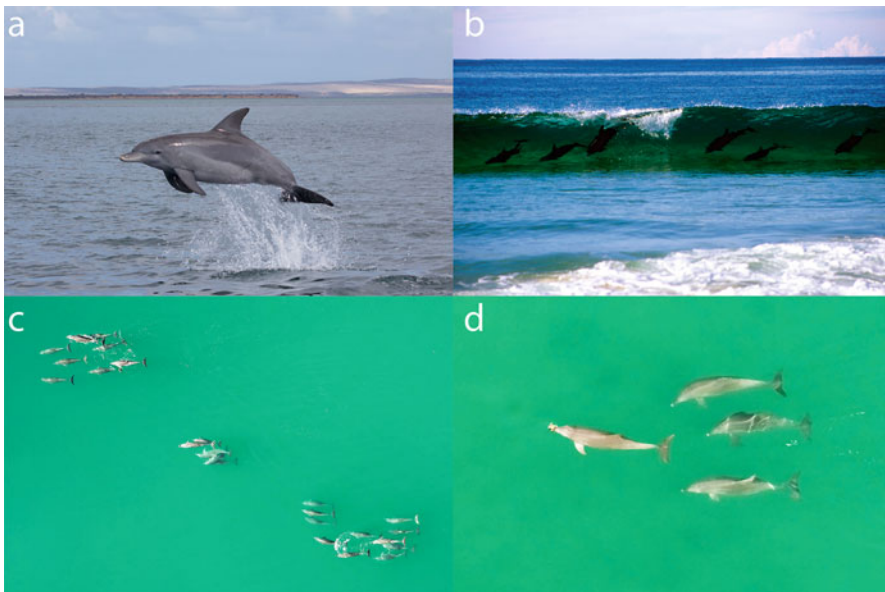

Fig. 16.1 (**a**) Adult Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, from Shark Bay, Western Australia. Note the robust body, medium-length rostrum/beak, large fins relative to body size and ventral speckling characteristic of *T. aduncus* bottlenose dolphins in warmer climes. (**b**) *T. aduncus* surfing the beaches of southern New South Wales. (**c**) Alliances of alliances, Shark Bay: a second-order alliance comprising two trios (first-order alliances) of adult males following two female consorts (top left of frame); a first-order alliance and female consort with calf of weaning age (center); and a second-order alliance of three trios and two consorts (bottom right). (**d**) A first-order alliance following their female consort who is between bouts of foraging with the aid of a sponge tool (photos: S. Allen)

objects and blowing bubbles to imitate scuba divers cleaning their tank, are among the most widely cited examples of dolphin imitation.

The most detailed behavioral work on wild *T. aduncus* has been conducted in Australia and Japan. We review the long-term research in Shark Bay, Western Australia, and then survey notable observations from other Australian locations and Japan, where key studies based on subsurface observations have been conducted.

16.1   Australia

16.1.1   *Shark Bay, Western Australia*

The >35-year Shark Bay *T. aduncus* study is the longest running and most in-depth for the species, spanning Hinde's (1976) three levels of social analysis: interactions, relationships, and structure. Using a range of approaches and tools, studies of social and other behaviors have been integrated increasingly with demographic, life history, genetic, and ecological analyses. The original study off the east side of Peron Peninsula, which bisects Shark Bay, was joined in 2007 by a comparative study in the western gulf, and the two sites have proven highly complementary (e.g., Krützen et al. 2014).

16.1.1.1   Social Structure and Mating System

The Shark Bay dolphins have a social and mating system within a dynamic fission-fusion grouping pattern in which both sexes exhibit natal philopatry (Connor et al. 2000a; Tsai and Mann 2013). Females may first conceive at 10 or 11 years of age and give birth 1 year later (Karniski et al. 2018). Weaning age ranges from 2.6 to 8.6 years (mean = 4.0) and increases with maternal age (Karniski et al. 2018). In the transition to independence, young juvenile dolphins increase their same sex associations (Krzysczyk et al. 2017), anticipating differences in associations among adults (Smolker et al. 1992). A female's reproductive success is enhanced if she has successful female relatives or if she associates with successful females; interestingly, this second factor is actually enhanced for female associates that are less closely related (Frère et al. 2010). Females typically become attractive to males when their infants are about 2.5 years of age (Connor et al. 1996). Thereafter, for varying periods of time over months, possibly extending for a time after they conceive, females become involved in the males' complex system of nested alliances (Connor et al. 1996; Connor and Krützen 2015; Galezo et al. 2018).

Males cooperate in pairs and, more often, trios (= first-order alliances) to consort individual females for periods of minutes to weeks (Connor et al. 1992a, b, 1996, 2011; Fig. 16.1c, d). Many consortships are established and maintained by aggressive herding (Connor et al. 1992a). While males are coercing females to remain with them, we have no evidence that males are physically forcing copulation; indeed,

females may role away from mounting males. On the other hand, in a manner similar to chimpanzees, males may use intimidation to coerce females into copulating (Connor and Vollmer 2009).

During the year they conceive, females typically occur in consortships with a number of alliances over months. The costs from male aggression, and possibly reduced foraging efficiency of females being herded away from their core ranges, led Connor et al. (1996) to predict infanticide in bottlenose dolphins (*Tursiops* spp.). Subsequently, evidence for infanticide was reported in a number of locations (e.g., Patterson et al. 1998; Dunn et al. 2002; Robinson 2014). Females can reduce infanticide risk by mating with many males to confuse paternity. Escaping from her male consorts after mating with them, having multiple attractive periods and increasing range size during cycling may help females mate with more males (Connor et al. 1996; Wallen et al. 2016). Male associations with females decline post-conception (Wallen et al. 2017), but at a rate that is consistent with females continuing to be attractive and confusing paternity (contra Wallen et al. 2017), particularly if such behavior is more likely among a subset of females that have failed to mate with many males prior to conception.

Most males belong to groups of 4–14 (= second-order alliances), where they find their first-order alliance partners (herding by males from different second-order alliances occurs infrequently, Connor et al. 2011). Males in second-order alliances cooperate in contests for females against other groups. One first-order alliance may even recruit another within the same second-order alliance to attack another alliance to steal their female (Connor et al. 1992b). These second-order alliances also serve a defensive function, especially during the mating season, when most males in a second-order alliance may be consorting females. Connor and Vollmer (2009) suggested that the importance of such defensive associations has increased the need for aggressive herding in Shark Bay compared to other locations without second-order alliances. If males simply followed their female consorts rather than herding them, they would often be led away from second-order alliance partners as their females traveled to different favored foraging areas, rendering the males more vulnerable to attack from other alliances.

The stability of first-order alliances within second-order alliances varies and is not strongly related to second-order alliance size (Connor et al. 2011). Further, the rate that males consort females correlates with the stability of their first-order alliances (Connor et al. 2001; Connor and Krützen 2015), a possible indication of dominance relationships, which otherwise are only known from one study of captive *T. truncatus* (Samuels and Gifford 1997). The most stable pairs and trios can persist for decades, as can second-order alliances (with the expected attrition as males die)—considered the "core" unit of male social structure (Connor and Krützen 2015; Fig. 16.1c).

Relatedness is a significant factor in subadult male associations but not among adults (Gerber et al. 2019). As males mature and consolidate their second-order alliance membership, they associate with a larger number of age-mates. The relatedness signal that shows up in subadults may be a by-product of the bisexual philopatry, as immature male associates may often be the offspring of related females (Gerber et al. 2019).

A third level of alliance is indicated by preferential association between second-order alliances and, sometimes, second-order alliances and "lone trios" (typically the

aged remnants of previously larger second-order alliances), as well as cooperation in conflicts with other groups over females. The functional redundancy of third-order alliances may reflect a kind of "insurance," given the disparity in second-order alliance sizes and the fact that second-order alliance partners are not always present to provide aid in conflicts (Connor et al. 2011). Third-order alliance fights can involve over 30 male dolphins.

16.1.1.2   Social Interactions

Shark Bay dolphins conduct interactions and relationships with a wide range of motor and vocal behaviors. Affiliative interactions often include gentle contact behaviors, such as use of the pectoral fin to "pet" another dolphin and rubbing their body against another dolphin's fins or body. Such behaviors are analogous to primate grooming.

One kind of gentle contact behavior, "contact swimming," is rare in males but occurs often between females being harassed by males (Connor et al. 2006a). In contact swimming, one female places her pectoral fin against the side of another, swimming close to, but slightly behind her. Such episodes are often brief but can last for up to 20 min. Contact swimming can occur when one, both, or neither of the females are being herded by males in the group. Bouts of contact swimming may include partner and role switching between more than two females. Interestingly, contact swimming occurs between familiar females and those rarely observed together (and are only together because both are being herded by males in the same second-order alliance). Given the similarity in appearance to calves swimming in infant position, Connor et al. (2006a) suggested that contact swimming may reflect support from the lead female to the trailing female, who is responsible for maintaining contact.

The benefits of primate grooming include parasite removal and stress reduction (e.g., Aureli et al. 1999; Zamma 2002). Dolphin affiliative contact behaviors are unlikely to involve parasite removal, although removal of dead skin may be beneficial (dolphins shed skin cells much faster than humans, Hicks et al. 1985). However, as illustrated by the typical context of contact swimming, stress reduction seems an obvious plausible benefit, and role switching during and across bouts of petting or contact swimming might represent a kind of reciprocity.

Sexual behavior is used as a social tool in dolphins and is found in many non-conceptive contexts and, to varying degrees, between all age and sex classes (Connor et al. 2000a; Mann 2006). The two most common and obvious sexual behaviors are mounting and "goosing", where one dolphin probes the genital area of another with its rostrum. The same behavior, e.g., goosing, may be performed gently, accompanied by petting and rubbing, or roughly, accompanied by threats and direct aggression, indicating that sex is used in both affiliative and agonistic interactions. Connor and Vollmer (2009) showed that males tended to mount other males but goose females more, suggesting that the origins of goosing might lie in stimulating female receptivity.

Consortship initiation may include long chases and direct aggression in the form of biting and hitting with peduncles and flukes. Females sometimes attempt to escape from males by "bolting" (accelerating rapidly away from the males). Males use a vocalization, "pops," to keep a consorted female close (Connor and Smolker 1996; Vollmer et al. 2015). Pops are low-frequency, low repetition rate click trains (Connor and Smolker 1996) that are reinforced by other vocal and physical threats (burst-pulsed vocalizations, head-jerks, and charging at the female), as well as direct aggression. Cycling females have significantly more new tooth rake marks than non-cycling females (Scott et al. 2005).

Males in the Shark Bay nested alliance system maintain individually distinctive "signature" whistles for communication (King et al. 2018). Synchronous movement also plays an important role in male alliance behavior. Males often surface synchronously side-by-side with first-order alliance partners. In trios, the pair that is found together most often synchronizes more when all three are present (Connor et al. 2006b). Sometimes two males from different first-order alliances within a second-order alliance surface side-by-side synchronously, especially when they are excited around a consorted female, suggesting a reduced tension function. The side-by-side synchronous surfacing by male dolphins in alliance contexts is similar to human synchrony and raises the question of why such a potent visual signal is so rarely observed in other primates that form coalitions (see Connor et al. 2006b; Connor 2007).

Males also perform synchronous displays around females, often in consorting context. This suggests that, while males are coercing a female's proximity and possibly intimidating her into copulating, they may still need to impress a female to achieve a reasonable chance of fertilizing her egg (females may have internal mechanisms to choose among males, e.g., Firman et al. 2017; see also Chap. 4). Some synchronous displays are observed repeatedly, while at the other extreme, some have been observed only once. Simple side-by-side synchrony might be produced by mutual entrainment (Wilson and Cook 2016), but it is difficult to explain some of the more elaborate displays this way. Connor and Krützen (2015) suggested that some male displays might be creative, with one dolphin closely following the movements of another. Herman (2002) showed that captive *Tursiops* are capable of creating synchronous displays. Links to captioned videos of the behaviors and vocalizations described here may be found at www.dapinc.org.

16.1.1.3 Ecology

Shark Bay dolphins feed on a wide range of schooling and solitary fish, and occasionally cephalopods and crustaceans, throughout the water column, sometimes catching jumping and skittering fish in the air and probing for partially buried prey in the substrate (Connor et al. 2000a, b; Fig. 16.2a, b). The incidence of shark bite scars is unusually high (74%, Heithaus 2001) compared to other dolphin populations (eclipsed only by the recently reported 89% of snubfin dolphins in Cygnet Bay, Western Australia, Smith et al. 2018), indicating significant predation risk. The

Fig. 16.2 (**a**) Shark Bay *T. aduncus* captures a fleeing garfish (*Hyporhamphus* sp.) amidst its final leap. (**b**) This *T. aduncus* (bottom left of frame subsurface) would be feeding on the tiger prawn (*Penaeus* sp.) it had flushed from the substrate and pursued to the surface if not for the untimely theft from the crested tern (*Thalasseus* sp.) above. (**c**) An adult *T. aduncus* intentionally beaches itself in pursuit of a mullet (*Mugil* sp.), while her calf looks on, Peron Peninsula. Beaching, where individuals chase fish through the shallows and even onto a beach to capture them (Sargeant et al. 2005), is a specialized foraging technique developed by calves of beaching mothers (photos: S. Allen). (**d**) Another specialized foraging technique is shelling, where dolphins lift large trumpet (*Syrinx aruanus*) or baler (*Melo amphora*) shells out of the water to dislodge prey that are hiding inside (Allen et al. 2011; photo: A. Pierini, Dolphin Innovation Project)

dynamic fission-fusion grouping pattern in Shark Bay (2.4 events/hour in one study, Connor and Krützen 2015) reflects a continually shifting balance between the benefits of grouping (socializing, reducing predation risk, and feeding on schooling fish) and reducing competition for food, a balance that tips easily either way given the low cost of locomotion in dolphins, relative to many terrestrial mammals (Connor 2000).

Some behavioral variation among dolphins in Shark Bay, both across a larger spatial scale and within a given area, has an ecological component. Adult females within a given area differ in the number of their same sex associates and activity budgets, and their home ranges vary by an order of magnitude (Watson-Capps 2005), variation likely linked to individual differences in learned foraging techniques (Connor et al. 2000a, b; Mann and Sargeant 2003). One specialized foraging technique that is especially time consuming is "sponging," where a dolphin carries a marine sponge on its rostrum to probe for prey in the substrate (Krützen et al. 2005, 2014; Mann et al. 2008, 2012; Smolker et al. 1997; Fig. 16.1d). Sponging females conduct their limited social lives preferentially with other "sponger" females (Mann

et al. 2012; Kopps et al. 2014). At the other end of the spectrum, it seems likely that highly sociable females with large home ranges and a large number of associates might feed to a greater degree on schooling fishes (Connor et al. 2000a), but this has not been tested.

The homophily observed in female spongers may also play an important role in the development of alliances. As mentioned, age similarity trumps relatedness in alliance affiliation as males mature and, as in the case of female spongers, male spongers also associate preferentially (Bizzozzero et al. 2019).

Second-order alliances that have extensively overlapping ranges often differ in foraging habitat use; for example, one forages more over shallow seagrass beds, while another favors an adjacent channel (O'Brien et al. in review). While essentially random demographic variation may impact the size of second-order alliances (e.g., number of male age-mates maturing together in an area), foraging differences, to the extent that they impact the costs of grouping, might also play a role. This possibility is of broad interest because it would require an extension of the standard behavioral ecology paradigm, where resources and shelter impact female distribution, which, in turn, determines male strategies. In Shark Bay, some of the variation we see in male alliance size may be influenced directly by variation in resource use. However, given the importance of being in an alliance for male reproductive success, we would expect to see males shift foraging style or habitat for the chance to join an alliance (O'Brien et al. in review). Males clearly strive to join alliances in Shark Bay, and solitary males have lower reproductive success (Krützen et al. 2004; Connor and Krützen 2015). The greater proportion of female calves born to sponging mothers that become spongers themselves indicates that the conflict between optimizing their social lives and foraging preferences is reduced relative to males, but it is not entirely absent. Complete freedom in foraging behavior may be limited not only by predation risk but by males herding females away from favored foraging areas where their specialized learned techniques are useless. We have observed sponging females foraging without sponges on shallow seagrass banks while males were herding them there.

Along with complex social lives, the array of specialized foraging techniques and links to different habitats has been another exciting area of discovery in Shark Bay. In addition to the well-studied sponge carrying, foraging techniques (see Figs. 16.1d and 16.2a–d, for example) include swimming into shallows to be fed by people (Connor and Smolker 1985; Foroughirad and Mann 2013) and kerplunking, where a percussive, bubble-forming tail slap may prompt a startle reaction by prey that was otherwise concealed (Connor et al. 2000a, b). Several of these techniques are linked to specific habitats. For instance, while spongers are more likely to forage in deeper channels (Sargeant et al. 2007; Tyne et al. 2012), kerplunking occurs over shallow seagrass beds (Connor et al. 2000b).

Sponging and beaching behaviors (Figs. 16.1d and 16.2c), both typically transmitted from the mother to offspring, are observed more often in females, and none of the techniques appear to have a male bias (Kopps et al. 2014; Mann et al. 2008; Sargeant et al. 2005). The demonstration, via fatty acid signature analysis, that sponging dolphins have a different diet than non-sponging individuals foraging in the same

habitat (Krützen et al. 2014) remains the only empirical demonstration that one of the specialized foraging techniques in Shark Bay is a resource specialization.

Variation is also found on a broader spatial scale. From south to north along the eastern shore of Peron Peninsula, males form more trios (relative to pairs) to consort females, consort females at a higher rate, have a greater coverage of new tooth rake marks on their dorsal fins, and make greater seasonal movements (Connor et al. 2017; Hamilton et al. 2019). Shallow seagrass-covered banks subdivided by deeper channels characterize the southern part of the study area, while the north is mostly open embayment plain. Presently, the weight of evidence favors the "rate of interaction" model over food or predator distribution (discussed in Connor et al. 2017), in which males form larger alliances when they encounter each other more often in competition for estrus females (Whitehead and Connor 2005; Connor and Whitehead 2005). More than one environmental factor may influence the rate that males encounter each other. For example, the southern area may be marginal habitat with a lower density of dolphins that encounter each other less often, while the open northern waters may conduct sound further, effectively increasing encounter rate (see Connor et al. 2017).

16.1.1.4   Cognition

Humans and some species of dolphins have the largest relative brain sizes among mammals and are the only mammals with multilevel male alliances within social groups. This convergence led Connor and co-authors (Connor et al. 1992b; Connor 2007; Connor and Mann 2006; Randic et al. 2012) to explore the cognitive implications of a multilevel alliance system in an unbounded social network where individuals show strong preferences and avoidances within second-order alliances, recruit alliance members for attacks on others, rush to a conflict to aid second- or third-order alliance members; and where allies are often separated from each other and may have only partial information about the relationships and strength of rival groups. We identify three major insights that have emerged from considerations of the Shark Bay dolphin society:

1. Negotiating multilevel alliances should be more cognitively demanding than a single level because decisions at one level may significantly impact other levels. If, for example, a trio evicts a member to form a pair, so each member enjoys a greater probability of fathering a consorted female's calf, the drop in their second-order alliance size from six to five males may weaken their ability to defend their females from thefts by other groups. Biological anthropologists, focusing on the cognitive challenges of relationships within one level of nonhuman primate alliances or resulting from conflict between human groups (warfare), largely overlooked the challenges of a nested alliance structure (see Connor et al. 1992b; Connor 2007).
2. Societies of terrestrial mammals are "bounded"; individuals are members or they are not (think of a baboon troop, a wolf pack, or a chimpanzee community).

Primatologists especially, evaluating the cognitive challenges of social living, focused on the number of group members (as equal to the number of social relationships) and whether individuals had knowledge of "third-party" relationships (it would be obviously unwise to attack a subordinate individual when her larger, dominant friend is close by). In the dolphins' unbounded society, range overlap varies tremendously and, thus, so will individuals' knowledge of third-party relationships. Connor (2007) turned the primatologist logic on its head and emphasized third-party knowledge uncertainty. Your own allies may be strengthening their bonds at your expense while they are out of sight and sound, and the small, weak alliance that you easily defeated at the edge of your range 2 years ago may have doubled in size.

3. In the context of adaptations to the environment, Randic et al. (2012) pointed out a previously unrecognized convergence in the "big three" in mammalian brain evolution: dolphins, humans, and elephants all have adaptations to reduce the cost of locomotion. Elephants have the lowest cost of locomotion of any terrestrial mammal, humans have clear adaptations that reduced locomotion costs relative to our nearest relatives, and dolphins have much lower costs of locomotion than terrestrial mammals (see Connor 2000 and discussion in Randic et al. 2012). In all three mammals, low costs of locomotion allowed larger ranges, resulting in contact with a larger number of individuals (for a given population density) and, hence, greater cognitive challenges in the social domain.

16.1.2   Other Australian Study Sites

Outside of Shark Bay, the most detailed description of social structure and mating behavior comes from a relatively small population (ca. 120–140 individuals) in Port Stephens, a ca. 160 km^2 embayment on the mid-north coast of New South Wales. A larger "eastern community" of at least 90 dolphins inhabits a marine sand and seagrass habitat and is socially segregated from a smaller western community of about 30 individuals that forage in an estuarine mud and mangrove habitat (Möller et al. 2002, 2006; Wiszniewski et al. 2009). Learned foraging tactics in the different habitats may have driven this division (Wiszniewski et al. 2009). At a finer scale, relatedness plays a role in associations within several clusters of females, as well as their male associates (the latter likely owing to bisexual philopatry, Wiszniewski et al. 2011).

Möller et al. (2001) describe consortships between single females and pairs, trios, and one quadruplet of strongly associating but mostly unrelated males (Fig. 16.3a). Some consortships in Port Stephens are coerced, as indicated by observations of captures and escape attempts by the female (Möller et al. 2001). Males in larger groups (3–4) enjoyed greater reproductive success (Wiszniewski et al. 2012). The males of Port Stephens may also have second-order alliances, but this is presently uncertain.

An unusual case of object manipulation/play coincided with an influx of large blubber jellies (*Catostylus mosaicus*) to western Port Stephens. Individuals were
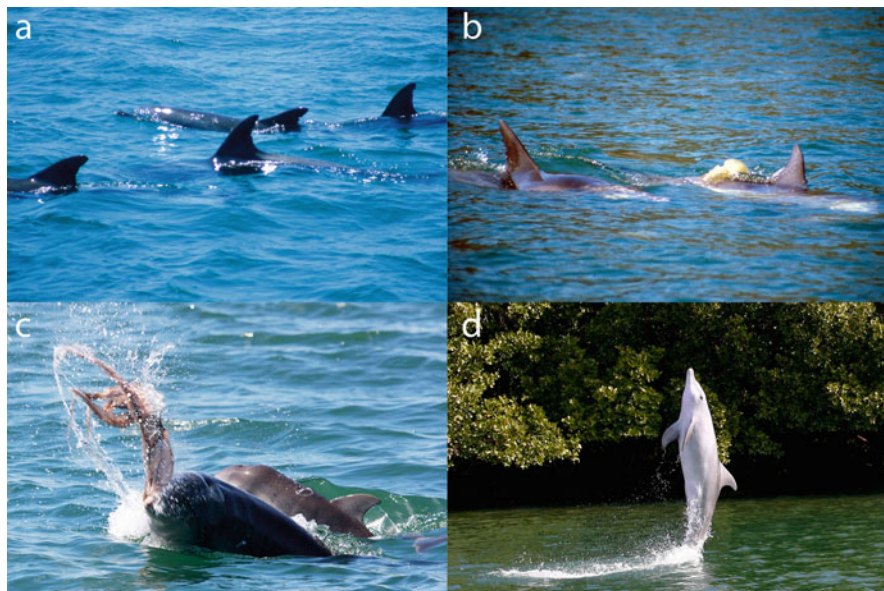
Fig. 16.3 (**a**) All four members of the allied quadruplet of adult male *T. aduncus* in Port Stephens, New South Wales. From left to right of frame are George, Paul, John, and Ringo Starr. (**b**) A pair of allied male *T. aduncus* pushing jelly blubbers (*Catostylus mosaicus*) to the surface on their rostra/ melons in western Port Stephens. Note the individual on the right of the frame, Kenny (Norris), already has a jelly rolling down his caudal peduncle. (**c**) An adult female *T. aduncus*, newborn beside her, incapacitates an octopus with a specific prey-handling technique off Bunbury in southwestern Australia (photos: S. Allen). (**d**) A tail-walking dolphin in the Port River Estuary of Adelaide, South Australia (photo: M. Bossley, WDC)

observed pushing the jellies to the surface on their rostra/melons and then rolling the jellies down their backs and over their peduncles, sometimes raising their peduncles/ tails above the surface as the jelly slid off (Allen pers. obs., Fig. 16.3b). We speculate that the dolphins engaged in this behavior for the sensation of the jelly and/or the "tingle" of the nematocysts (stinging cells) on their skin.

Foraging driven social segregation within a *T. aduncus* population can change rapidly. Despite considerable home-range overlap, dolphins foraging in association with prawn trawlers in Moreton Bay, Queensland, were socially segregated from those that did not (Chilvers and Corkeron 2001), but when trawler presence diminished, the social partition disappeared (Ansmann et al. 2012). Prawn trawler association fits the "producer-scrounger" model (Barnard and Sibly 1981), but there is an historical record of a cooperative fishing association between *T. aduncus* and aboriginal Australians (Hall 1985), similar to that which still occurs between fishers and *T. truncatus* in southern Brazil (e.g., Daura-Jorge et al. 2012).

Finn et al. (2009) detailed the stepwise process used by *T. aduncus* in Spencer Gulf, South Australia, for removing the ink and calcareous cuttlebone from giant cuttlefish (*Sepia apama*) before consumption. In southwestern Australia, Sprogis

et al. (2017) outlined two methods, "shaking" and "tossing," by which *T. aduncus* incapacitate captured octopus (Fig. 16.3c). Dolphins who fail to disable octopus prey have died of suffocation (Stephens et al. 2017).

A remarkable case of the rise and fall of an arbitrary cultural fad was reported recently from the Port River estuary in South Australia (Bossley et al. 2018). A young dolphin that became trapped in a harbor was held for 1 month in a dolphinarium for rehabilitation, where it received no training but was able to observe the show dolphins perform their routines, which included tail walking. The dolphin was first observed tail walking 7 years after its release, but another dolphin performed the vast majority of tail walking, which was observed in 11 individuals, including 6 adult females and 5 juveniles. The occurrence of tail walking peaked 23–24 years after the original dolphin's stint in captivity and 15–16 years after tail walking was first observed in the wild. Thereafter the behavior declined. The authors argue that the temporary spread of tail walking in this population was most likely a case of social learning, given that tail walking is virtually unheard of in wild dolphins and is energetically costly and of no obvious adaptive value (Bossley et al. 2018; Fig. 16.3d).

16.2   Japan

Photo-identification studies on Indo-Pacific bottlenose dolphins have been conducted in seven distinct locations in Japan (e.g., Shirakihara et al. 2002; Kogi et al. 2004; Morisaka et al. 2013; Funasaka et al. 2016). Genetic differentiation suggests strong site fidelity and limited gene flow among populations, including possible multiple founding events from large, genetically diverse southern populations (Hayano 2013; Chen et al. 2017). Significant differences in the characteristics of whistles were found among Amakusa-Shimoshima, Mikura, and Ogasawara Islands (Morisaka et al. 2005a). In keeping with the behavioral ecology theme, we focus on underwater observations around Mikura Island and boat-based studies around the Amakusa-Shimoshima Islands.

16.2.1   Mikura Island

Mikura is a small (ca. 20 km^2), volcanic island located about 220 km south of Tokyo and thus represents a markedly different habitat from those of the Australian populations. Underwater video-identification studies have been conducted since 1994 on an estimated 160 *T. aduncus* within 300 m of the island's coastline, at water depths 2–45 m, during spring to early autumn (Kogi et al. 2004). Ad lib observations have been supplemented recently by fecal sampling to examine genetic information (Sakai et al. 2016; Kita et al. 2017).

16.2.1.1 Ecology and Social Structure

Mikura *T. aduncus* sometimes forage during the day for cephalopods (particularly octopus), flying fish (Exocoetidae) and other teleosts, but the timing of defecation suggests that nocturnal feeding predominates (Suzuki 2005). Morisaka et al. (2015) recorded continuous nocturnal vocalizations in shallower water, where dolphins are common during the day, which included burst-pulsed sounds with continuously decreasing inter-pulse intervals indicative of foraging activity.

Female Mikura dolphins first give birth at ~10 years of age (mean = 10.3, range = 7–13 years), calves are typically weaned after ~3.5 years (mean = 3.4, range = 2–5 years). The population is quite closed, with no immigration of unidentified adults for more than 20 years (Kogi et al. 2004; Kogi 2013). Tsuji et al. (2018) report 41 (25 male and 16 female) emigration events from Mikura to adjacent islands as far as 390 km distant. No sex difference was found in emigrants, but adults tend to emigrate more than younger animals. Population density around Mikura Island is high (6.5 individuals/km^2), which may be driving this emigration, and would thereby appear to be a source for neighboring populations (cf. Manlik et al. 2018).

Underwater observations dictated a different group definition than typical of boat-based studies (e.g., Smolker et al. 1992; Allen et al. 2012). A group was defined as all video-recorded dolphins from the time a videographer entered the water to when he/she returned to the boat. Nagata (2006) documented relatively low association indices between female and male pairs, although some male pairs associated for at least 9 years. During underwater interactions, several dolphins typically swam line abreast; with subgroups of several such lines—pairs of more closely positioned animals were identifiable within lines (Miyazaki 2009). Ueda (2013) analyzed female relationships based on associations in lines and found that females without calves tended to associate, as did those with calves, similar to findings that shared reproductive state enhanced female associations in Port Stephens *T. aduncus* (Möller and Harcourt 2008).

16.2.1.2 Social Interactions

Underwater observations have revealed detailed characteristics of many social interactions at this study site. Affiliative petting or "flipper rubbing," for example, involves one dolphin (the "rubber") rubbing its pectoral fin over various parts of a partner's (the "rubbee") body (Sakai et al. 2006b; Fig. 16.4a). The rubbee tends to be more active than the rubber, and individuals often switch roles during bouts. Flipper rubbing occurs most often between individuals of the same sex and age class and is also common in mother–calf dyads. The left pectoral fin is used more frequently and for longer periods, and configurations during flipper rubbing events revealed that this asymmetry owed not to the laterality of the rubber but by a preference for use of the left eye by both dolphins during bouts (Sakai et al. 2006a), possibly reflecting a left-eye advantage in conspecific recognition. Significant left-side bias was also observed
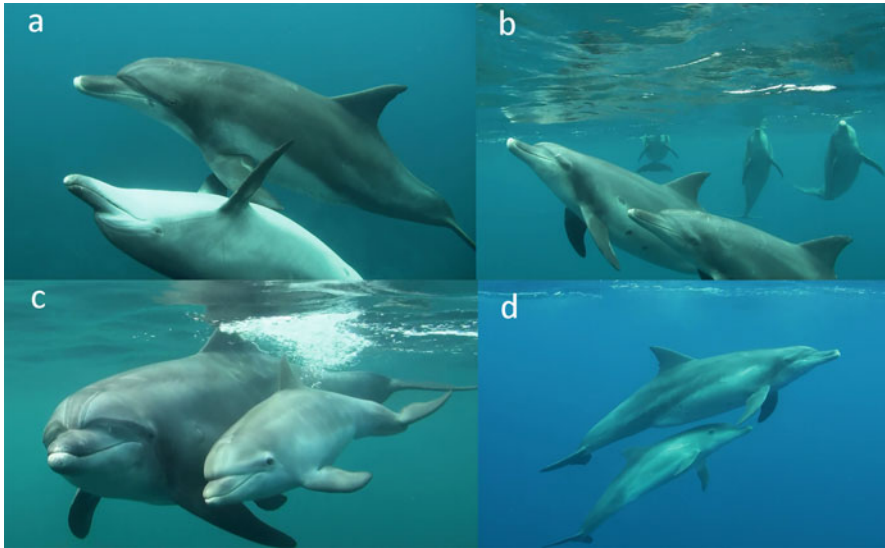
Fig. 16.4 (**a**) Flipper-to-body rubbing behavior of *T. aduncus* around Mikura Island. (**b**) Synchronous breathing between Mikura *T. aduncus*; three dolphins yonder breathe synchronously, while two synchronous dolphins are in the foreground. (**c**) A *T. aduncus* calf in echelon position next to its mother near Mikura Island. (**d**) A *T. aduncus* calf in infant position below its mother (photos: M. Sakai & T. Morisaka)

in flipper rubbing events initiated by the rubbee, determining its position during rubbing and thus enhancing the behavioral asymmetry by choosing the left side of the rubber, perhaps ensuring longer affiliative contact.

Dyadic synchronous breathing was common among individuals of the same age and sex class, as well as in mother–calf and escort–calf pairs (Sakai et al. 2010; Fig. 16.4b). The interindividual distance during synchronous breathing was less for mother–calf pairs than for other pairs and for female compared to male pairs. The size of a dolphin's "personal space" (Hall 1966; the region surrounding each person or that area which a person considers their domain or territory) may vary with age and sex. Personal space for female–female pairs is smaller than for male–male pairs in adults and subadults. Interestingly, the time differences between breaths for synchronous surfacing (0.63 ± 0.48 s) were intermediate between those reported for Shark Bay males as "social synch" (0.14 ± 0.11 s) and "nonsocial synch" (0.87 ± 0.56 s). However, the subjects in Connor et al. (2006b) were exclusively alliance members, while the Sakai et al. (2010) study included all male pairs. Allied males may engage in more precise synchrony than those not as tightly bonded.

Contact swimming (as per Shark Bay) was recorded more often between females than males (Chaturaphatranon 2011). Contact swimming appears similar to the echelon position (Fig. 16.4c) of mother–calf pairs, in which the calf gains a hydrodynamic benefit. Indeed, the fluke stroke frequency of the actor (0.45/s) was significantly lower than that of the receiver (1.11/s).

As might be expected, neonates tended to swim closer to their mothers than 1–3-year-old calves, and they utilize the echelon position (Fig. 16.4c) before gradually transitioning to the infant position (Fig. 16.4d; Masaki 2003). Primiparous mothers engaged in rubbing and synchronous breathing with their calves less than parous mothers. The distance between parous mothers and their calves always increased during development, but not in primiparous mother–calf pairs, suggesting a role for maternal experience (Kimura 2009). "Escorting," or "babysitting"/alloparental care, where dolphins other than the mother swam with dependent calves, was observed frequently. Young nulliparous females babysat more than other sex-age classes. Calves used echelon position significantly more than infant position during babysitting, and a preliminary genetic study found no role for kin selection in babysitting (Haraguchi 2005).

Sakai et al. (2016) documented the adoption of a calf following the death of its mother, by a subadult female. On 3 of 18 observation days post-adoption, the calf was observed swimming in the suckling position, and milk was seen leaking from the female's mammary slit. A 5-year dataset revealed no significant social or kin relationships between the biological mother and allomother (Sakai et al. 2016). Ridgway et al. (1995) reported that orphans in captivity immediately tried to nurse from allomothers, and dry adult dolphin females were brought into lactation by repeated nursing attempts. Thus, nursing attempts by the calf may have been critical in the adoption process. Several kinds of epimeletic or helping behaviors have been reported in dolphins (reviewed in Sakai et al. 2016). These behaviors suggest that dolphins have the capacity for empathic perspective taking (de Waal 2008), but the precise nature of these cognitive abilities remains unknown. The cognitive characteristics that evoke adoption behaviors in dolphins need additional study to determine the extent to which they reflect social cognition or more proximate responses.

Groups of between 2 and 14 Mikura Island *T. aduncus* have been recorded engaging in sociosexual behavior (Fig. 16.5a). Such bouts included mounting, in which one dolphin attempts to insert its penis into the genital slit of another dolphin, rubbing the genital area of another dolphin, and contact between the rostrum or melon and genital area and rostrum-to-genital propulsion (recall "goosing" in Shark Bay above for these latter two). Sociosexual behavior was observed among males, sometimes among subadult females, and between mothers and their male calves (Shimomaki 2001; Jiroumaru 2008).

Play behaviors including object carrying were also observed, using seaweed, plastic bags, and, on occasion, octopus (Morisaka, Sakai pers. obs.; Fig. 16.5b). Object carrying as a component of play has been documented across many delphinids in both wild and captive settings (Greene et al. 2011). A rare spontaneous ejaculation event was also filmed in this population (Morisaka et al. 2013; Fig. 16.5c). Dudzinski et al. (2003) documented two cases of apparently inquisitive behavior toward a dead conspecific. Repeated investigative behaviors such as echolocation and scanning toward the genital and chest area occurred first, followed by male erections. The carrying of dead calves has also been observed frequently, primarily by adult females, followed by other, mostly male, dolphins (Sakai, Morisaka pers. obs.).
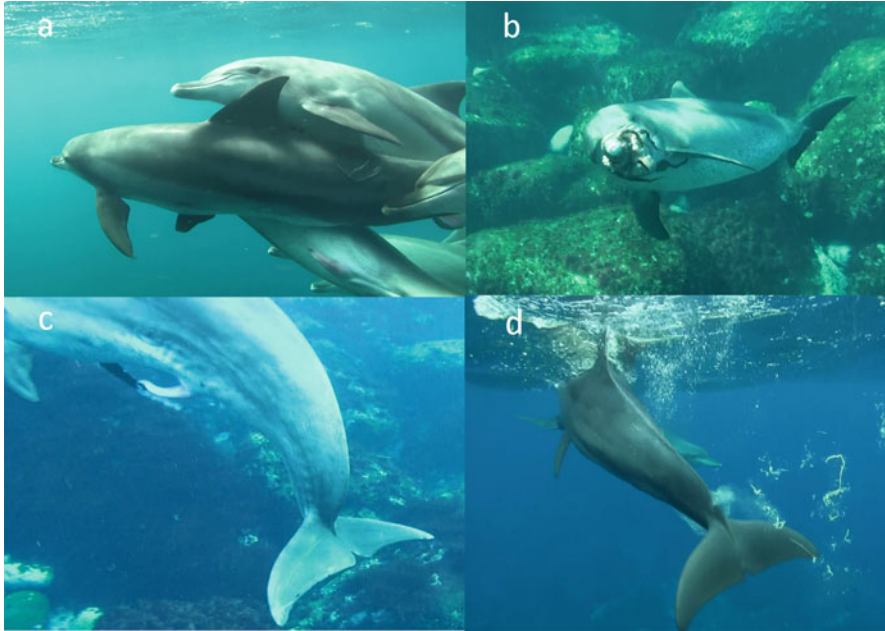
Fig. 16.5 (**a**) Sociosexual behavior of male *T. aduncus* near Mikura Island. (**b**) A female Mikura *T. aduncus* holds (or is held by?) an octopus for play and as food. (**c**) Spontaneous ejaculation by a 16-year-old male Mikura *T. aduncus*. (**d**) Defecation toward a swimmer by *T. aduncus*, Mikura Island (photos: M. Sakai & T. Morisaka)

Suzuki (2005) observed defecation by Mikura dolphins immediately in front of other dolphins and human swimmers (Fig. 16.5d). All defecating dolphins changed direction just after defecation; in most events, the dolphin first engaged in "inquiring" behaviors (echolocation and/or circle swim around the human swimmer) followed by defecation just in front of the swimmer, implying that defecation by Mikura dolphins may function as a mild threat behavior.

16.2.2 Amakusa-Shimoshima Island

At Amakusa-Shimoshima Island, western Kyushu, boat-based photo-identification studies have been conducted since 1994 (Shirakihara et al. 2002). A resident population of *T. aduncus* occurs along the northern coast of the island, where there are estuarine features. Similar to recently reported large group sizes of South African *T. aduncus* (Bouveroux et al. 2018), group size commonly exceeded 100 individuals (Shirakihara et al. 2002). In contrast to Bouveroux et al. (2018), who invoked predation risk from large white sharks (*Carcharodon carcharias*) as a driver of larger aggregations, Shirakihara et al. (2002) suggested that large groups are likely

formed in response to rich food sources. Even the usually solitary finless porpoises (*Neophocaena phocaenoides*) occurring in this area sometimes form groups of more than 100 individuals (Yoshida et al. 1997).

Ambient ocean noise levels around Amakusa-Shimoshima Island are much higher than those around Mikura Island and Ogasawara Island, because of rich biotic sounds produced by crustaceans, especially snapping shrimp (Alpheidae; Morisaka et al. 2005b). The resident *T. aduncus* tend to produce lower, less frequency-modulated, high amplitude whistles, probably to overcome these noisy conditions (Morisaka et al. 2005b). The range over which dolphins can recognize each other's whistles around this island was estimated to be comparable to the diameter of the majority of groups. Thus, the Amakusa-Shimoshima Island dolphins should be able to hear the whistles produced by most group members even in large but cohesive groups (Morisaka 2009; Morisaka et al. unpub. data).

In the year 2000, most individuals moved 60 km to the southern part of the island, and then all but 20 returned the following year. Nishita et al. (2015) found that male–male pairs in the new, southern community had higher associations before splitting, indicating long-term relationships, but that was not the case for male–female and female–female pairs. Nishita et al. (2017b) documented ten male pairs that associated across multiple years and which sometimes flanked single females, suggesting consortship behavior, while Nishita et al. (2017a) found associations among females were based on shared reproductive status, similar to Ueda (2013) for Mikura Island. Females that lost infants within 1 year of birth changed their associations accordingly. These features, also of other populations, are maintained even when ecological factors favor much larger group sizes.

16.3 Discussion

The Indo-Pacific bottlenose dolphin *Tursiops aduncus* is usually compared with its congener, *T. truncatus* (e.g., Connor et al. 2000a). The two longest running *Tursiops* studies in the world are in Sarasota Bay, Florida (see Wells, this volume), and Shark Bay, Australia. The most distinctive difference between the two species and populations is the markedly more complex male alliance formation in Shark Bay. The Sarasota males form first-order alliances of two males only, whereas the Shark Bay males form three alliance levels, with trios predominating at the first-order level (Owen et al. 2002; Connor et al. 2011; Connor and Krützen 2015).

The leading model to explain differences in alliance formation between populations is the rate of interaction model (Connor and Whitehead 2005; Whitehead and Connor 2005). This model posits that selection for alliance formation is greater when individuals encounter each other more often in competition for resources (estrus females, in this case). The encounter rate should increase with population density. Given that population density decreases with body size (Cotgreave 1993; White et al. 2007) and that *T. aduncus* are smaller than *T. truncatus* (Hale et al. 2000), we could expect that, if other factors were equal, *T. aduncus* populations exhibit

higher densities and more complex alliance formation than *T. truncatus*. However, other factors may impact encounter rates, including detection distance, as well as day and home range (Connor and Whitehead 2005), and these factors will likely vary among habitats. Further, population densities of both *Tursiops* species vary between locations, and possibly even within study sites (Connor et al. 2017), impacting selection for alliance formation. The single report of second-order alliances in *T. truncatus* is instructive; Ermak et al. (2017) report second-order alliances (based on associations between male pairs) in an unusually high-density population in the St. Johns River, Florida. They further suggest that their discovery was evidence against the habitat structure hypothesis (Connor et al. 2000a), where males would form alliances more in open habitats versus subdivided habitats, in which males could hide with female consorts. This conclusion depends on the movements of dolphins in the habitat; if dolphins seeking prey must travel along a narrow river, their encounter rates with others might be unusually high.

The differences in alliance structure may also impact the dolphins' communication systems. The complex alliances in Shark Bay, where males often switch first-order alliance partners and interact with a larger number of second- and third-order allies, may favor the retention of individual identity signals compared to Sarasota, where an alliance "badge" may be more practical in the strongly bonded stable pairs (King et al. 2018).

Learned foraging behaviors that vary within and between habitats can lead to social segregation (e.g., Moreton Bay, Chilvers and Corkeron 2001; Port Stephens, Wiszniewski et al. 2009; Shark Bay, Mann et al. 2012). Specialized foraging tactics like those described in Shark Bay are also reported in populations of *T. truncatus* (Wells, this volume). A case of social segregation based on association with human fisheries was recently reported in *T. truncatus* (Kovacs et al. 2017). More broadly, the phenomenon may be widespread in delphinids and could, for example, account for the culturally and often genetically distinct ecotypes in killer whales (Riesch et al. 2012) and even the remarkable speciation of delphinids (Connor and Krützen 2015).

As a result of recent advances in technology, including hydrophone arrays for localizing sound production to individuals and drones for observing behavior, the future of *T. aduncus* research is bright. One of the broader questions to address is whether *T. aduncus* in other populations also lead apparently more complex social lives than found in *T. truncatus*. If so, such differences may be represented in measures of the size of the brain or brain components and in cognitive abilities. As noted by Connor (2007), inshore delphinids are ecological outliers in the Delphinidae; and some offshore species living in large, fast-moving groups may be even more complex socially, but we are fortunate to have a species like *T. aduncus* that combines astonishing social complexity with ease of observation by humans.

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