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Cover illustration: On the left: Part of a subgroup of rough-toothed dolphins, *Steno bredanensis*, off Kona, Hawai'i. They have very large brain to body size ratios, and sophisticated rapid learning. Photo by Deron S. Verbeck. On the right: Short-finned pilot whales, *Globicephala macrorhynchus*, socialize in the waters off Tenerife, Canary Islands. Photo by Teo Lucas.

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Chapter 5

Maternal Care and Offspring Development in Odontocetes



Janet Mann

Abstract Odontocetes are characterized by slow life histories and extensive maternal care, where offspring nurse for years in some species. Among some of the largest toothed whales, the mother and offspring of one or both sexes stay together for a lifetime, forming the basis of strong matrilineal social units and transmission of culture along maternal lines. Mother and calf face a series of challenges from the moment of birth. The newborn must quickly learn to follow and breathe alongside the mother—and wait for her while she dives for food. Within months the calf transitions to infant position for much of the time, although their swimming ability allows them to associate with others in the mother’s network. Because calves can easily become separated from their mothers, an effective communication system is necessary, and signature whistles and pod-specific dialects appear to serve this function. The mother plays a central role in the development of calf social and foraging tactics. Where this has been studied, calves adopt maternal behaviors, including foraging specializations, and share the mother’s network post-weaning. Although difficult to demonstrate “teaching” per se, dolphins are particularly good candidates given their exquisite learning ability and social tolerance. The role of non-mothers is clearly important in calf development, but whether calf interactions with non-mothers constitute “allomothering” remains unclear for most species. What is clear is that group living by cetaceans affords the calf protection from predators and possibly from infanticidal males. The causes of calf mortality are generally not known, as carcasses are rarely retrieved, but disease, predation, poor maternal condition, and anthropogenic causes (pollutants, provisioning, bycatch, boat strikes), and—rarely—infanticide, are all implicated. Weaning occurs when the calf no longer nurses, evident by cessation of infant position swimming. Interbirth intervals are also used as a proxy for weaning, though the calf frequently nurses during the mother’s subsequent pregnancy. Post-weaning, mothers and daughters continue to have preferential bonds, but in killer whales and pilot whales, sons also continue to have a strong relationship with the mother.

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5.1 Introduction

Outside of humans, no other mammal has such prolonged and intensive maternal investment as members of the dolphin family. Paternal care has not been reported for any wild cetacean species, although data are insufficient for some taxa, especially beaked whales. Among several species of odontocetes, such as sperm whales, killer whales, pilot whales, and false killer whales, at least some offspring remain with their mothers for life, enabling investment that extends well beyond nursing, likely entailing protection, support, food sharing, social learning, and transmission of culture. Strong matrilineal kin bonds are the foundation of most odontocete societies, with such bonds lasting for decades. At its core, there is no greater influence on an individual cetacean's life than his or her mother. It begins with the birth of a relatively large, precocial calf—always one at a time—that follows the mother wherever she goes.

5.2 Birth and the Newborn Period

For most odontocete cetaceans, births are seasonal with peaks during spring or summer. Unlike baleen whales, which have marked periods of breeding and feeding, all odontocetes feed year-round and throughout lactation. Prey availability does not seem to drive birth seasonality. Predation could be a factor, but some of the most common predators (e.g., tiger sharks) also prefer warm waters. Some populations calve during months when predation is less likely (Fearnbach et al. 2012). Reduced energetic costs for mother and calf are plausible factors, since neither mother nor calf would need to maintain thick blubber stores during the early stages of lactation.

All cetacean calves are born tail first and have wobbly dorsal fins, tail flukes, and pectoral fins (flippers) that quickly become more rigid within hours after birth. The distinct fetal lines wrapping their midsection are from being curled up in the womb (Fig. 5.1), and these lines are an excellent visual cue defining the newborn period; in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), they are visible for up to 3 months (Mann and Smuts 1999) but can remain faint for longer if the calf is in poor condition. Parturition, known mostly from bottlenose dolphins and killer whales in aquaria, is relatively quick (20–30 min). The difficult part comes right after birth, when mother and calf face a series of challenges. First, following the mother means swimming and breathing, the latter of which is under conscious



Fig. 5.1 Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, newborn swimming in echelon with her mother. Fetal lines are visible. Calf is doing a “chin up” surfacing characteristic of very young calves as they lift the blowhole out of the water. Photo by Ewa Krzyszczyk, Shark Bay Dolphin Research Project monkeymiadolphins.org

control. Unlike terrestrial mammals, cetaceans sleep with half of their brain at a time, and newborn calves hardly sleep at all (Lyamin et al. 2005, 2007). Similarly, their mothers forgo rest (Lyamin et al. 2005, 2007) and hunt very little in the early days (Mann and Smuts 1999), presumably so that the neonate can tag alongside her in echelon position and not be left alone at the surface (Fig. 5.1). Echelon aids the calf energetically as it can get a hydrodynamic boost in her slipstream (Noren 2008; Noren et al. 2008). Neonate dolphins, although precocious in locomotion relative to most terrestrial mammals, lack aerobic stamina and, as compensation, have relatively more blubber for buoyancy (Dearolf et al. 2000). Presumably, the characteristic of fast swimming at the surface by neonates and their mothers facilitates calf physiological development and following the mother. Behavior during the newborn period is gleaned from a few studies of wild odontocetes. Here, the first few months of life can be characterized as a time mother–calf synchrony and social contact (petting and rubbing) is high (Mann and Smuts 1999; Sakai et al. 2013), but calves also learn to socialize with others, separate from and rejoin with the mother, and experiment in catching fish (Mann and Smuts 1998, 1999; Krasnova et al. 2014). By the end of the newborn period, the calf rarely swims in echelon with his/her mother and can swim well on its own, although diving proficiency takes years (Noren 2008; Noren et al. 2008).

5.3 Infant Position and Nursing

In most species studied, newborn calves transition from predominantly echelon position to infant position by the end of 3 months. Infant position, where the calf swims under the mother's tailstock, by her abdomen, is widespread in toothed dolphins and whales, from narwhals (Charry et al. 2018) to dolphins and porpoises (Mann 2017; Xian 2012). Like echelon, this position provides a hydrodynamic boost to the calf (Noren 2008; Noren et al. 2008; Noren and Edwards 2011), in addition to protection and nursing access. Infant position is akin to "carrying" because of the close contact and energetic cost to the mother. Infant position is also thought to help stimulate milk production, as the calf intermittently bumps the mother's abdomen and mammary glands located on both sides of the genital slit. Calves nurse from infant position by tilting onside and inserting the tongue into the mammary slit. When waters are murky, observers have a difficult time seeing the calf in this position, but it is evident upon surfacing, where the calf is slightly staggered behind the mother and angles in under her after a breath. For example, in *Sotalia guianensis*, this was referred to as the "longitudinal position" (Tardin et al. 2013). Among killer whales in the northwest Pacific, infant position is also called "lateral position" (Karenina et al. 2013). In sperm whales, this has been called "peduncle diving" (Gero et al. 2009), or at the cow's tail or below her tail in beluga whales (Krasnova et al. 2006). In Shark Bay, calves spend about 39% of their time on average in infant position, but this can vary widely from calf to calf (10–80%; Foroughirad and Mann 2013). Under stress, calves stay in infant position more often, such as when the mother is being consorted by males (Watson 2005) or when in poor condition (Mann and Watson-Capps 2005). On rare occasion, calves swim in infant position with a non-mother (typically juvenile females, Mann and Smuts 1998), but this is brief and uncommon. Infant position is a valuable tool for determining lactation length, as calves sometimes continue to associate closely with the mother well after weaning, but not in infant position (e.g., Grellier et al. 2003; Tsai and Mann 2013).

Milk Composition

A critical component of maternal care is nursing, which defines the calf or infancy period in mammals. Compared to baleen whales, odontocetes have lower fat but still very high-energy milk. Lactation strategies have received little attention, in large part because of the difficulty in sampling cetacean milk and knowing the rate, quantity, and composition of milk delivered to offspring. However, based on terrestrial and non-cetacean marine mammals, a pattern emerges that is consistent with theories of maternal investment. Two primary lactational strategies are evident in cetaceans: the baleen whale pattern of very high fat milk (30–60% fat), fast growth, and early weaning versus the odontocete pattern of lower fat (<40%, albeit far higher than terrestrial mammals), slower growth, and late weaning (Oftedal 1997). Consistent with this is the pattern of maternal fasting during most of lactation for baleen whales and minimal or no fasting during lactation for odontocetes. This is also known as capital versus income breeding. At the one extreme, blue whales are estimated to produce and transfer about 500 lbs (220 kg) of milk per day to their

calves (Oftedal 1997). Maternal reserves become substantially depleted for all cetaceans during lactation, but baleen whales dedicate their blubber (capital) to lactation, while odontocete mothers replenish (income) by food intake needs 40–50% higher than normal (Cheal and Gales 1991; Williams et al. 2011). Further, the smaller odontocetes expend more energy per unit of mass than the larger whales, such that they would be incapable of storing enough fat to completely support lactation (Oftedal 2000). A better understanding of odontocete lactation is needed given their prolonged nursing that can extend 8 years or more, with substantial variation within even the same population (Karniski et al. 2018).

5.4 Communication and Coordination

In the marine environment where a calf can quickly swim out of visual contact, communication and spatial coordination prove vital between mother and calf. Calves generally do not stray far from the mother when in groups and can easily or readily associate with others. However, when the mother is foraging and repeatedly diving, the calf cannot always stay with her given its limited diving ability. Options vary depending on species and context. For deep-diving species, mothers might shorten their dives to accommodate calves, but data for most species are lacking. Beluga whale mothers spend more time near the surface than females without calves (Heide-Jørgensen et al. 2001). Observations of a single female narwhal with its newborn indicated that she did not adjust her dive depth or duration compared with other females (Heide-Jørgensen and Dietz 1995). The narwhal pattern is unexpected given that among species that do not dive deeply (<15 m), such as bottlenose dolphins, mothers shorten their dive times when calves are young (Miketa et al. 2018). Similarly, pregnant pantropical spotted dolphins (*Stenella attenuata*) fed mostly on squid, which require deep dives, whereas lactating females ate flying fish, presumably so they could stay near the surface with their calves (Bernard and Hohn 1989).

Acoustic signaling is also critical. As detailed elsewhere (see Chap. 2), signature whistles in some delphinids have emerged as a key mechanism for mother and calf to maintain acoustic contact and navigate separations and reunions (King et al. 2016a; Smolker et al. 1993). We (Mann and Smuts 1998, 1999) proposed the “imprinting hypothesis”—that calves must learn the mothers’ signature whistle in the first week (or two) of life so that there is no confusion on who to follow. This hypothesis was based on the observation that mothers were whistling almost constantly postpartum and that newborns did not venture away from their mothers in the first week of life. Furthermore, mothers were intolerant of others associating closely with calves in the first week and would chase females that attempted to associate with their calves. After the first week, mothers are much more tolerant of mother–calf separations and allow the calf to swim freely with others. The fact that pregnant females and newly parturient females emit signature whistles at very high rates is consistent with the imprinting hypothesis (Fripp and Tyack 2008; King et al. 2016b). Outside of delphinids, a variety of contact calls likely exist, but additional study is needed.

5.5 The Babysitting Debate

The belief that babysitting is a fundamental feature of odontocete societies is so widespread that it persists in popular and scientific literature despite little evidence in support. As the dictum “absence of evidence is not evidence of absence” may well apply, rigorous research on the topic is needed. A few studies have investigated babysitting empirically, most notably in sperm whales (Whitehead 1996; Gero et al. 2009) and bottlenose dolphins (Mann and Smuts 1998) with mixed results. Some studies assume babysitting based on simple association with non-mothers (e.g., Augusto et al. 2017). Clear and rigorous definitions are needed. The theoretical literature on this point is useful and dates back more than 40 years. Hrdy (1976) distinguished between allomaternal behavior, care, and abuse. Allomaternal behavior is when non-mothers interact with offspring, where no costs or benefits to the allomother, offspring, or mother are assumed. Both abuse and care are types of allomaternal behavior. Allomaternal care is when non-mothers nurture, guard, or protect offspring, providing some benefit to the offspring and mother. Babysitting is a special type of allomaternal care that necessitates absence of the mother. The allomother in this case might benefit (e.g., learn to care for offspring, foment a bond with the mother or infant) or incur a cost (e.g., reduced foraging time). Some studies find a fitness cost to breeders, raising the question of whether instances of allomaternal care are adaptive for the mother and offspring (see Gilchrist 2007). Allomaternal abuse is always at a cost to the mother and infant, typically by physically harming the offspring or keeping it away from the mother. Infanticide (see below) is clearly an example of the latter.

In considering cetacean calves, and their precocial ability, calves might readily associate with a wide range of individuals, including other calves, when not with their mothers. Since maternal care is behavior that increases the offspring’s fitness, allomaternal care should do the same. But, maternal care is also defined by its directionality. The mother feeds the offspring, not vice versa. The mother carries the offspring, not vice versa. The mother protects and guards the offspring, not vice versa. Social behaviors and associations of the calf do not in of themselves qualify as they are mutual or reciprocal. Allonursing would obviously qualify but is difficult to demonstrate; spontaneous lactation has been reported in captivity when the “allomother” or foster mother has extensive exposure to the calf (Ridgway et al. 1995). Allomaternal care would also allow the mother to benefit in the proximate sense through resource acquisition (e.g., foraging more or taking longer dives) and, in the ultimate sense, by being able to wean her calf earlier and produce another. Social play, for example, might benefit the calf and the partner, but it is bi-directional and not a form of allomaternal care in of itself. This helps differentiate between instances where two calves are playing at some distance from their mothers. Who is babysitting whom?

Association can qualify as allomaternal care if it entails some form of guarding or protection—i.e., the mother is not nearby. Deep-diving species such as sperm whales and beaked whales appear to fit such criteria. In his original study, Whitehead (1996)

found that sperm whale units were less synchronous in their foraging dives when calves were present, enhancing the chance that at least one whale would accompany the calf at the surface. This is suggestive of “guarding” behavior and where the allomother(s) or “guard(s)” would time dives to minimize the period that the calf is alone at the surface. Subsequent research (Gero et al. 2009) found population differences where either one female or multiple individuals of both sexes were responsible for guarding the calf. Although the trade-off between calf care and deep diving is thought to be a driving force in the matrilineal structure of sperm whale groups, this is not the case for other deep-diving species. Bottlenose whales, *Hyperoodon ampullatus*, have a different fission–fusion social structure and do not show evidence of babysitting (Gowans et al. 2001). Similarly, observations to date on beaked whales do not suggest babysitting, as calves are mostly left alone at the surface during foraging dives (MacLeod and D’Amico 2006). More observations of these elusive subjects are needed.

5.6 Protection from Predators

Habitat use is one way mothers might adjust their behavior to protect their calves. For example, among Risso’s dolphins *Grampus griseus*, females stay closer to shore with young calves, foraging in shallower waters and possibly focusing on different species of squid that do not require such deep dives (Hartman et al. 2014). A number of studies have suggested a preference for shallow, nearshore habitat in several dolphin species (e.g., Pine et al. 2017; Mann et al. 2000; Gibson et al. 2013; Weir et al. 2008; Mann and Watson-Capps 2005), possibly to protect calves from predators, but there are other benefits of shallow habitats, such as more fish for mother and calf, protection from rough seas, or less interaction with conspecific males. Dolphins might generally change their habitat use in response to shark predation pressure (Wells et al. 1987; Heithaus 2001; Heithaus and Dill 2002). Other studies find little evidence for such nearshore preferences among mother–calf groups (e.g., Elwen et al. 2010), but this might be a consequence of large group sizes that mitigate the impact of sharks. Large sharks (tiger shark *Galeocerdo cuvier*), white pointer (*Carcharodon carcharias*), bull sharks (*Carcharhinus leucas*), and killer whales (*Orcinus orca*) are the main predators of odontocetes even if odontocetes are not their major prey source (see Heithaus 2001). Cookiecutter shark scars have been observed on beaked and sperm whales (e.g., McSweeney et al. 2007; Best and Photopoulou 2016), but they are not lethal predators. Killer whales have no known predators except humans.

Grouping is an important way for mothers to reduce calf predation risk, either because of dilution, detection, deterrence, or defense. Dilution just means that by grouping, everyone has a reduced chance of being taken (e.g., 10% chance of being taken in a group of ten as opposed to a 50% chance in a group of two). Detection means that more eyes are available to detect predators. Deterrence refers to the fact that a shark is less likely to attack a group of dolphins than a lone individual. Defense

is characterized by active, even cooperative defense by a group against sharks. There is good evidence that grouping is a common strategy to reduce predation risk. Group sizes tend to be larger when calves, especially newborns, are present (*Tursiops* spp. Mann et al. 2000; Wells et al. 1987; tucuxi, *Sotalia fluviatilis* Azevedo et al. 2005; Indo-Pacific humpback dolphins *Sousa chinensis* Karczmarski 1999). This is also suggested for beaked whales (Chap. 14). Defense by the mother or group against tiger sharks has been observed multiple times in Shark Bay, Australia. Responses include forming a tight ball and facing the shark, mobbing the shark (getting on top of it until it leaves the area), chasing the shark, attacking the shark, and fleeing—depending on how startled they are (Mann and Barnett 1999; Mann and Watson-Capps 2005; personal observation). Even calves (but not neonates) become involved in mobbing and chasing—alongside their mothers.

5.7 Protection from Conspecifics

Conspecific aggression toward calves is rare in cetaceans. One exception is infanticide, which has been reported in at least four odontocete species including bottlenose dolphins (*Tursiops truncatus*; Patterson et al. 1998; Dunn et al. 2002; Kaplan et al. 2009; Robinson 2014), Indo-Pacific humpback dolphins (*Sousa chinensis*; Zheng et al. 2016), guiana dolphins (*Sotalia guianensis*; Nery and Simão 2009), and, most recently, killer whales (*Orcinus orca*; Towers et al. 2018). The classic and mostly supported sexual selection hypothesis (Hrdy 1979) predicts that infanticide by males can enhance their reproductive success (at a cost to the female's) when there is a very low chance the victim is their offspring, the lactation period is long, male tenure or access to the female is short, and there is a high chance of achieving mating success following the infanticide. Additionally, female counterstrategies are expected, such as mating multiply to confuse paternity and “faking” estrous—also to confuse paternity. In some species, females fight back.

Recently, a killer whale estimated to be at least 46 years old assisted her adult son (32 years old) in killing a young calf of another pod (Towers et al. 2018). This was the first report of its kind and is notable because a prominent hypothesis of post-reproductive lifespans in killer whales is that the mother enhances the fitness of their adult offspring, particularly sons. Although one dramatic case, this was the only observation in a marine mammal of a mother assisting her son in killing a conspecific (and likely unrelated) infant. This instance is consistent with Hrdy's (1979) sexual selection hypothesis, but the mother's role as a co-perpetrator in the infanticide is what stands out. It is also notable how vigorously the mother of the calf fought back, with assistance from kin. Although the defense was ultimately unsuccessful, the case highlights why the behavior has rarely been seen in killer whales. Killer whales are typically with their maternal group, and that might act as a deterrent.

Among bottlenose dolphins, evidence for infanticide varies by site. In areas with a considerable influx of males during the breeding season (births and conceptions given a 12-month pregnancy), infanticide has been reported, although the

perpetrators, victims, and relatedness are rarely known (*T. truncatus*: Patterson et al. 1998; Dunn et al. 2002; Kaplan et al. 2009; Robinson 2014; Perrtree et al. 2016). In wild Indo-Pacific bottlenose dolphins (*T. aduncus*), there is good evidence that pregnancy is detected early, evidenced by a marked reduction in male–female association post-conception (Wallen et al. 2017). This suggests that female dolphins could not benefit from counterstrategies widely seen in the mammalian literature (see Hrdy 1979). In addition, some of the most intensively studied research sites, such as Shark Bay, Australia, and Sarasota, Florida, USA, have *not* reported aggression by adult males toward young infants (Wallen et al. 2017; Wells 2014). Paternity data suggest that females in these residential populations mate with local males, those that they have associated with throughout their lives (Krützen et al. 2004; unpublished). Consequently, infanticide might be absent or rare. Albeit difficult to observe, male–female bonds might be maintained, indirectly, which favor paternities within a subcommunity and protection by local males. Although sex segregation is a common feature of bottlenose dolphin societies (Galezo et al. 2018), males and females do associate, and this familiarity might both benefit males in terms of mating success and benefit females in reducing infanticide risk. That said, in locations with periodic influx of unfamiliar males, extra-community *and* local males might gain an advantage with infanticide if it occurs soon after calf birth, the perpetrator is not the father, and the male has a chance of fathering the next offspring. Once the calf has grown (>3 months) and maternal investment is considerable, the chances of a male fathering subsequent offspring declines as the female is unlikely to resume cycling until the next breeding season (Mann et al. 2000).

5.8 Calf Mortality

Both the rate and causes of calf mortality are difficult to identify in cetaceans as perinatal mortality is likely to be missed and mortality rates are surely higher than those reported. Causes are rarely known, other than extreme events such as morbillivirus, when carcasses are retrieved (e.g., Fauquier et al. 2017), or reasonably inferred based on fishing practices (e.g., Noren and Edwards 2007). It is notable that poor maternal care has *rarely* been identified as cause of calf mortality, although human provisioning is linked to maternal neglect (Foroughirad and Mann 2013; Mann et al. 2018).

Bottlenose Dolphins and Other Delphinids

As bottlenose dolphins (common, *T. truncatus* and Indo-Pacific *T. aduncus*) are the best-studied species, the variation in calf mortality and its causes between sites is informative. In Shark Bay, Australia, with 35 years of longitudinal data on Indo-Pacific bottlenose dolphins, the calf mortality rate, defined as survival to age 3, is consistently ~34% ($N = 676$ calves), lower than originally reported in 2000 (Mann et al. 2000). We use age 3 because over 91% of calves are weaned after age 3 ($N = 410$ calves), no calf has been weaned before age 2, and only one (blind)

nursing calf died after age 3 but possibly before weaning. Causes range from human impacts such as provisioning, bycatch, and boat strikes (Foroughirad and Mann 2013; Moore and Read 2008; Stone and Yoshinaga 2000) to shark attack (Mann and Barnett 1999), to maternal condition, which is linked to habitat such as prey-rich seagrass beds (Mann et al. 2000; Mann and Watson-Capps 2005; Miketa et al. in review).

A comparison between Shark Bay and Bunbury, Western Australia, showed that Shark Bay has much higher reproductive and vital rates (Manlik et al. 2016), which is not surprising given that the Bunbury dolphins are exposed to much higher human impact. In the Bay of Islands, New Zealand, bottlenose dolphin (*T. truncatus*) calf mortality is at least 50% by age 2 (>34% before age 1 and an additional 15–59% died by age 2; Tezanos-Pinto et al. 2015). As this population is declining, the high mortality rate and low calving rate are of concern. Although tourism is implicated, the precise causes are not known. In the Moray Firth, Scotland, common bottlenose dolphins appear to have lower calf mortality than all other sites, losing only 17% of their calves before age 2 (Robinson et al. 2017). Predation is virtually absent in the Moray Firth, but there are other environmental stressors, including contaminants (Wilson et al. 1999; Wells et al. 2005). Unobserved mortality (perinatal mortality especially) is also possible and might explain some of the differences between sites, depending on the intensity of monitoring. Outside of *Tursiops*, there are few reports of calf mortality rates. Herzog (1997) reports 24% mortality for Atlantic spotted dolphins (*Stenella frontalis*) in the first year of life. Killer whale calf mortality was originally estimated as between 30 and 50% in the first 6 months of life, but later estimates were that 39.2% of juveniles did not survive to adulthood (Olesiuk et al. 2005).

Most mammals with extensive maternal care, including humans, have a parabolic pattern of high mortality with firstborn offspring, lower mortality with middle born, and then high mortality again with last or later born (Bérubé et al. 1999; Sharp and Clutton-Brock 2010; Nussey et al. 2009; Mar et al. 2012). Firstborn mortality is generally attributed to smaller body size and/or poorer condition and lactational ability of young mothers combined with a lack of experience (Lang et al. 2011; but see Nuñez et al. 2015). Later-born mortality is generally attributed to reproductive senescence, which includes both fertility senescence and maternal effect senescence, declining physiological condition, and ability to nurture offspring (Karniski et al. 2018).

Patterns of firstborn mortality in wild populations are not well-documented for most species, but among three of the longest running bottlenose dolphin study sites, the pattern differs. In Sarasota, Florida, high mortality of firstborn common bottlenose dolphin offspring appears to be linked to maternal depuration of perfluoroalkyl compounds (PFCs) through milk. Later-born offspring receive fewer PFCs from their mothers (Houde et al. 2006; Wells et al. 2005). Moray Firth common bottlenose dolphins also show higher firstborn mortality at 45% (Robinson et al. 2017), but the causes are not identified. In Shark Bay, Indo-Pacific bottlenose dolphins do not show a firstborn effect. In fact there is a strong linear decline in calf survivorship with maternal age where calves born early in a mother's reproductive career have the best chance of survival (Karniski et al. 2018). Shark Bay is a relatively pristine environment, and the lack of contaminants could be a factor. Also, females have their first calf later in Shark

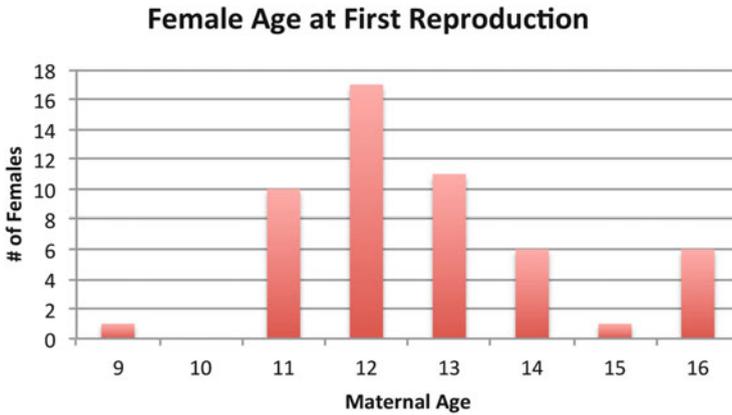


Fig. 5.2 $N = 52$ Indo-Pacific bottlenose dolphin, *Tursiops truncatus*, females in Shark Bay, Australia, with known age of first birth (see also Karniski et al. 2018). These data are conservative and biased toward births at early maternal ages because we excluded any female where we could have missed a late pregnancy (>6 months) or had perinatal mortality. Average is 12.8 years ($SD = 1.6$); 79% of females have their first calf at 12 years of age or later

Bay than the other sites, with 85% of females having their first calf between the ages of 11 and 14 (Fig. 5.2). With a prolonged juvenile period, typically lasting 10 years, immature females have ample opportunity to associate with calves in their network, and appear to be quite interested in doing so (Mann and Smuts 1998; Gibson and Mann 2008). At other sites, females produce their first calves between 6 and 13 years of age, with a mean age of 8 (Moray Firth, Robinson et al. 2017). At Sarasota, Florida, females produced their first calves between 6 and 8 years of age (Wells and Scott 1999; Wells 2003). Patterns of calf mortality might be attributed to maternal experience given that both sites with higher firstborn mortality also have shorter juvenile periods, but the anthropogenic stressors are also greater at Moray Firth and Sarasota than Shark Bay. We are also comparing different species. Herzing (1997) reports first parturition between 9 and 11 years of age for Atlantic spotted dolphins. Killer whale age at first reproduction is also around 11–14 for females (Matkin et al. 2014; Olesiuk et al. 2005). Better demographic data across populations and species will help us better understand how reproductive maturity and calf survival are linked.

Maternal Reactions to Calf Death

Another line of evidence in support of the intensity of the mother–offspring bond is based on responses to calf death, where the mother (or presumed mother) continues to provide care postmortem. Supportive behavior and postmortem attending have been observed with stillborn or dead calves among many toothed whale species—including bottlenose dolphins (*Tursiops* spp.) (Tayler and Saayman 1972; Cockcroft and Sauer 1990; Wells 1991; Mann and Barnett 1999; Fertl and Schiro 1994; Connor and Smolker 1989), sperm whales (*Physeter macrocephalus*) (Reggente et al. 2016), spinner dolphins (*Stenella longirostris*), beluga whale (*Delphinapterus leucas*)

(Smith and Sleno 1986; Krasnova et al. 2014), killer whales (*Orcinus orca*), Australian humpback dolphins (*Sousa sahulensis*), Risso's dolphins (*Grampus griseus*) (Reggente et al. 2016), Hector's dolphin (*Cephalorhynchus hectori*) (Stone and Yoshinaga 2000), short-finned pilot whales (*Globicephala macrorhynchus*) (Reggente et al. 2016), Atlantic spotted dolphin (Alves et al. 2015), rough-toothed dolphins (*Steno bredanensis*) (Ritter 2007), and tucuxi (*Sotalia fluviatilis*) (Santos et al. 2000). Almost all cases involve an adult female with a neonate or calf, although similar behaviors are reported between adults. A recent (August 2018) case, extensively covered by the press, where a killer whale mother in Puget Sound carried her dead calf for 17 days was widely considered intense "grief." Although difficult to interpret, postmortem attending is most characteristic of larger-brained mammals where maternal investment is intense, and it is comparably rare in balaenids compared to toothed whales (Bearzi et al. 2018).

5.9 Weaning

Even though weaning marks the end of infancy and is a critical transition for the calf, determination of weaning in odontocetes remains a methodological challenge. Actual nursing is difficult to observe, and although nursing from the same individual likely involves milk transfer, the amount of milk does not correlate well with nursing frequency, even for terrestrial mammals (Cameron 1998). In Shark Bay bottlenose dolphins, infant position is perfectly correlated with nursing, as all nursing occurs from this position. That, with observations of swollen mammarys, has enabled us to determine fairly precise weaning ages (to the week or month) for a large number of calves (Karniski et al. 2018). Cessation of infant position swimming is also well-timed with precipitous decline in mother–calf association, dropping well below 50%. Of over 450 weaned calves we have tracked, only one resumed nursing after being weaned, when her mother lost her next newborn. Interestingly, this calf was weaned before age 3 and was quite small but visibly caught up in size by nursing for another 1.5 years after her sibling died. Her second weaning occurred a few months after her fourth birthday. Sarasota reports weaning ages occasionally under 2 years and up to 7 years, with interbirth intervals typically 3–6 years (Wells and Scott 1999; Wells 2003). Among killer whales, the average calving interval was 4.88 years between viable calves, although there are some 2-year intervals (Olesiuk et al. 2005).

Herzing (1997) was able to observe both nursing and swollen mammarys of Atlantic spotted dolphins and found that most calves nursed for 3 or more years and up to 5 years. In contrast, average weaning age for pantropical spotted dolphins was estimated at just under 2 years (Myrick et al. 1986). This might be due to pressures from the tuna purse seine fishery (see Noren and Edwards 2007) or methodological differences. Based on longitudinal study, Amazon River dolphins (*Inia geoffrensis*) nurse for 1.5–5.8 years (Martin and Da Silva 2018). Beaked whales likely nurse their calves for 2 or more years (MacLeod and D'Amico 2006; New et al. 2013). Weaning

ages are grossly underestimated for most toothed whales given the paucity of longitudinal observations on mother–calf pairs.

Most sites do not collect infant position data and use a marked reduction mother–calf association or the birth of the next calf as a proxy (e.g., Wells 2014). Another method is using isotope profiles of dentin growth layer groups (GLGs) in teeth (Matthews and Ferguson 2015), but this involves collection of teeth, and one downside is that low rates of nursing might not be captured by this method. Finding milk in the stomachs of calves either stranded or captured during whaling has also been used, but this method is not particularly reliable as the calf would have to have nursed within the last couple of hours for milk to be detected (Ofstedal 1997).

Weaning ages in odontocetes can range from under a year for porpoises and river dolphins (e.g., Franciscana dolphin, *Pontoporia blainvillei*, Denuncio et al. 2013) to >8 years in bottlenose dolphins *Tursiops aduncus* (Mann et al. 2000; Kamiski et al. 2018) and possibly 15 years in short-finned pilot whales, *Globicephala macrorhynchus*, based on harvested pods (Kasuya and Marsh 1984). Stable isotope profiles in tooth layers suggest that Canadian Arctic belugas wean their offspring typically by the end of the second year (Matthews and Ferguson 2015). As is likely for other species, calves were consuming fish well before weaning. Weaning is sometimes inferred from calving intervals or modeling. The tucuxi (*Sotalia fluviatilis*) has calving intervals of 2–3 years, so presumably they nurse for close to 2 years (if they wean just before the next calf; de Oliveira Santos et al. 2001). This species is particularly interesting because of its large brain relative to body size. Consistent with life history theory that amply applies to terrestrial systems, one would expect larger-brained species to have later weaning than smaller-brained, due to the energetic investment in offspring brain growth—in addition to body growth, by the mother—but also because of the extensive learning period (Barton and Capellini 2011; Street et al. 2017).

What is clear is that odontocete calves nurse for very long periods of time, especially when contrasted with the much larger baleen whales, where weaning takes place within the year under most circumstances. Only primates and elephants have such late weaning ages, testimony to the substantial investment that mothers have in each offspring.

5.10 Post-Weaning

There is little research on the juvenile period (Krzyszczuk et al. 2017; McHugh et al. 2011) and mother–offspring associations post-weaning, in part because the decline in mother–offspring associations is used to define weaning. In bottlenose dolphins, mother–daughter associations remain stronger post-weaning than mother–son (e.g., Tsai and Mann 2013; Krzyszczuk et al. 2017), and home ranges continue to overlap extensively with the mother for both sexes (McHugh et al. 2011; Tsai and Mann 2013). With the exception of killer whales and possibly long-finned pilot whales—where both sexes remain with the mother’s group (*Globicephala melas*, Amos et al. 1993; Ottensmeyer and Whitehead 2003; *Orcinus orca*, Baird 2000)—the

relationship between mother and daughter persists post-weaning more than between mother and son, either in a stable group (sperm whales, Engelhaupt et al. 2009) or in dynamic fission–fusion systems (McHugh et al. 2011; Tsai and Mann 2013).

5.11 Maternal and Calf Hunting, Food-Sharing and Cultural Transmission

Unlike baleen whales that fast during much of the calf’s development, odontocete mothers have the challenge of hunting while looking after their calves, a problem compounded by the energetic demands of lactation. Diving presents particular challenges (detailed above).

Prey sharing has been observed in some odontocetes (notably killer whales, Hoelzel 1991; Ford and Ellis 2006), which might mitigate or reduce lactation demands, potentially explaining the shorter than expected weaning times seen in tucuxi dolphins (*Sotalia fluviatilis*) and killer whales (Spinelli et al. 2008; Olesiuk et al. 2005). Notably, despite over 30 years of intensive observation of wild bottlenose dolphins in Shark Bay, prey sharing has only been observed once between a mother and calf—and it may have been incidental, as the dolphins often toss their fish, this one just happened to be tossed into the mouth of her offspring (personal obs.). Through prey sharing and extensive observation of their mothers, calves undoubtedly learn what to eat and what not to eat. Some fish are poisonous, difficult to swallow or digest, spiny or tough, or downright dangerous. Fish have a variety of defensive strategies that make them difficult to catch.

The calf period is undoubtedly a critical learning stage where the offspring can begin to master finding, capturing, and processing prey and navigate a complex environment (e.g., follow migration pathways, avoid stranding, maintain contact with conspecifics, know about seasonal changes in habitat and prey). Calves tend to adopt maternal foraging strategies (Sargeant and Mann 2009; Mann and Sargeant 2003; Mann et al. 2008). Calves learn about their network, and maintaining position in that network can be critical for survival (Stanton and Mann 2012). They might learn displays and a range of social behaviors (dusky dolphins, *Lagenorhynchus obscurus*, Deutsch et al. 2014). In addition to the changing relationship with the mother, the calf develops his or her own social bonds that are critical for survival after independence. Although the calf learns from others besides the mother (e.g., what fish to eat, Mann et al. 2007), it is the mother who provides the foundation for these social contacts. As such, the distinction between vertical transmission (from the parent) and lateral transmission (from non-parents) becomes muddled.

Social transmission and the importance of culture have received a great deal of attention in the field of animal behavior and for cetaceans specifically (Rendell and Whitehead 2001; Whitehead 2017). The most prominent examples of cultural transmission are primarily vertical from mother to calf or from the maternal lineage. Killer whales adopt the maternal pod-specific dialect (e.g., Yurk et al. 2002); sperm

whales also communicate with codas of matrilineal origin (Rendell and Whitehead 2003); bottlenose dolphins adopt maternal foraging tactics and home range of their mother (Tsai and Mann 2013; Mann et al. 2008).

Teaching

In a seminal paper, Tim Caro and Marc Hauser (1992) argued for a rigorous definition of “teaching” as distinct from other forms of social learning, specifically where the “teacher” modifies his/her behavior in ways that costs the “teacher” and expressly benefit naïve individual(s) such that they can learn the behavior. Demonstration that the behavior benefits the learner is also needed. Only a handful of nonhuman studies have met these criteria (e.g., Thornton and McAuliffe 2006), in large part because the last part can rarely be shown in wild animals. That is, the improved skill of the learner must be tied to the teaching experience, not just a product of practice or maturation. Bender et al. (2009) were able to show that Atlantic spotted dolphin mothers modified their hunting behavior in the presence of calves, suggestive of teaching, but it is unclear whether calves improved their hunting skills as a result. Calves might also hinder maternal foraging as they follow the mother in pursuit of prey, but the fact that mothers occasionally “toyed” with prey in the presence of calves is more convincing. Killer whales at times assist calves in beaching to catch pinniped prey in the Crozet Islands (Guinet and Bouvier 1995). Zefferman (2016) argues that sponge dolphins are a good candidate for teaching. In fact, our data suggest that mothers modify their sponging behavior with sons, who are far less likely to become spongers. That is, mothers sponge less when with sons than daughters, and the result is that those sons with less exposure are less likely to sponge. With daughters, mothers do not modify their sponging behavior (unpublished). Similarly, we found (Miketa et al. 2018) that mothers adjusted their diving behavior to accommodate daughters more than sons, as they altered their diving only when daughters were close by. We suggest that mothers were affording their daughters learning opportunities with respect to foraging as daughters are more likely to adopt maternal foraging tactics than sons (e.g., Mann et al. 2008; Sargeant et al. 2005). Although experimental challenges in the field would make it exceedingly difficult to meet Caro and Hauser’s criteria for cetaceans, evidence demonstrating social transmission, learning, and innovative ability (Patterson and Mann 2015) is abundant.

Regardless, the mother plays the central role in calf learning the intricacies of the social and physical environment. By following their mothers for many months, or even decades, the calf acquires the necessary physiological, social, and ecological skills to survive and reproduce. Among most odontocetes, this entails detailed knowledge of their network, kin and non-kin, allies, acquaintances, and even whom to avoid. Like other long-lived mammals, the mother provides essential guidance in the dynamic, intricate, and captivating world of cetaceans.

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