

# Chapter 10

## Infanticide and Sexual Conflict in Cetaceans



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**Abstract** Infanticide by adult males is a striking example of sexual conflict; males can increase their reproductive success by killing an unrelated infant and accelerating the mother's return to breeding condition. Reports of infanticide in cetaceans have quadrupled in the past decade, and infanticide has now been documented in six species of toothed whale, including multiple populations of common bottlenose dolphins (*Tursiops truncatus*). Evidence of infanticide in these species is consistent with the sexual selection hypothesis; perpetrators are predominantly adult males and targets are neonates. Toothed whales have long lactation periods that suppress estrus, making infanticide potentially adaptive for adult males. However, it remains unclear if infanticidal males are likely to sire the mother's subsequent offspring. Here, we provide an overview of infanticide in cetaceans, evaluate the evidence for the sexual selection hypothesis, and propose a framework to predict infanticide risk in this clade. Toothed whales do not typically have dominance hierarchies, stable social groups, or monopolizable mating opportunities, all hallmarks of infanticide risk in terrestrial species. Instead, we hypothesize that infanticide risk in toothed whales is modulated by encounter rates with unfamiliar males.

**Keywords** Aggression · Cetacean · Coevolution · Dolphin · Infanticide ·  
Reproduction · Sexual conflict · Sexual selection

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## 10.1 Introduction

Infanticide is broadly defined as any behavior by a conspecific that contributes directly and significantly to the death of an infant and has been described in a diverse array of taxa and a wide range of social contexts (Palombit 2015). No single hypothesis explains the diversity of observed infanticidal behaviors, and drivers of infanticide vary within and among species. For example, male chimpanzees (*Pan troglodytes*) increase their territories after killing extra-community infants (Watts et al. 2002), and some species of male rainbowfish (*Telmatherina sarasinorum*) gain nutritional benefits by cannibalizing their broods when paternity is uncertain (Gray et al. 2007). Dominant female meerkats (*Suricata suricatta*) maximize the alloparental care their offspring receive by killing the offspring of close kin (Clutton-Brock et al. 1998), and elephant seal (*Mirounga angustirostris*) males appear to accidentally trample and kill infants in the course of male-male competition (Le Boeuf and Briggs 1977). Our understanding of the numerous drivers of infanticide has advanced substantially since the adaptive benefits of infanticidal behavior became a subject of study in the 1970s (Sommer 2000). However, due to the logistical challenges of observing marine mammal behavior in the wild, infanticide was not described in cetaceans until the late 1990s. Increases in observational effort have now yielded evidence of infanticide in six species of cetaceans, all toothed whales (Fig. 10.1). Here, we review reports of infanticide in cetaceans to date and bring the cetacean literature into a comparative framework with terrestrial mammals.

Out of numerous hypotheses, infanticide driven by sexual selection has received particular attention in the literature both due to its widespread occurrence and as a notable illustration of sexual conflict. This hypothesis posits that an adult male can increase his reproductive success by killing an unrelated infant and siring the mother's subsequent offspring (Hrdy 1974). Mammalian females often cease estrous cycling during nursing, a phenomenon called lactational amenorrhea; premature death of a nursing infant can end lactational amenorrhea, causing the mother to return to estrus and providing a reproductive opportunity for the infanticidal male (Hrdy 1974; Altmann et al. 1978). Infant death, of course, comes with tremendous costs to the mother, resulting in a coevolutionary arms race between the sexes as females evolve counterstrategies to male infanticidal aggression. Adaptations to counter infanticide risk, and subsequent adaptations to overcome female resistance, can profoundly shape reproductive physiology and social behavior. The discordance between male and female reproductive interests has led sexually selected infanticide by adult males to be considered an "archetype of sexual conflict" (Palombit 2015).

The sexual selection hypothesis makes three basic predictions. First, infanticide is committed by adult males who target infants that are not their own offspring. Second, the mother is likely to return to estrus faster or in better condition than if she had successfully weaned the infant. Third, the infanticidal male has an opportunity to sire the mother's next offspring (Hrdy 1979; Ebensperger 1998). The systems that have generated compelling evidence for sexually selected infanticide



**Fig. 10.1** Infanticidal behaviors appear consistent across multiple species of odontocetes. They include separating the mother from the infant, ramming the infant from below such that the infant is lifted or thrown out of the water, and forced submergence. (a) *Tursiops truncatus*, the Moray Firth, Scotland (Robinson 2014). (b) *T. truncatus*, Turneffe Atoll, Belize (Ramos et al. 2022). (c) *Inia geoffrensis*, Napo River, Peru (Bowler et al. 2018). (d) *Sousa chinensis*, Pearl River Estuary, southeast China (Zheng et al. 2016)

are characterized by high levels of male-male competition and high reproductive skew, in which one or several males obtain a disproportionate number of paternities (Palombit 2015). In langur monkeys (*Presbytis entellus*), an early and foundational study system for infanticide, male leaders of multi-female troops monopolize the majority of matings (Hrdy 1974). Takeovers (the displacement of the resident male by an immigrant male) are associated with infanticidal aggression and high infant mortality (Hrdy 1974), and infanticidal males father the subsequent troop offspring (Borries et al. 1999). Further observations of infanticide in primates, carnivores, and rodents support the hypothesis that male replacement of previous dominant breeders is a key risk factor for infanticide. In groups with female-biased adult sex ratios, in which a male or group of males can take over and displace resident males (e.g., langur monkeys, gelada monkeys (*Theropithecus gelada*), lions (*Panthera leo*)), male takeovers result in high rates of infanticide (Packer 2000; Beehner and Bergman 2008). In multi-male multi-female groups (e.g., Japanese macaques (*Macaca fuscata*) (Soltis et al. 2000), colobus monkeys (*Colobus vellerosus*) (Teichroeb and Sicotte 2008), savannah baboons (*Papio* spp.) (Zippel et al. 2017)), infanticide rates increase after immigrant males rise in the dominance hierarchy, replacing previous dominant males. In two species of deer mice (*Peromyscus* sp.) that nest alone or in male-female pairs, dispersing males kill pups they encounter outside of their home

range (Wolff and Cicirello 1991). These observations are further supported by phylogenetic analyses; infanticide by adult males is most likely to evolve in stable bisexual groups, groups that have female-biased adult sex ratios, and groups with high paternity skew and short male breeding tenures (Lukas and Huchard 2014).

## 10.2 Cetaceans

Cetaceans provide a useful parallel system to terrestrial mammals for examining both interspecific and interpopulation variation in infanticide. Most odontocetes have exceedingly long lactation periods (Whitehead and Mann 2000) that are likely substantially shortened by the death of a nursing offspring. On the other hand, the social factors that we know result in increased infanticide risk in terrestrial mammals do not apply neatly to cetacean social systems. Cetaceans are often wide-ranging and highly migratory with diffuse social networks and community boundaries that are rarely as delineated as they are in primates (Tsai and Mann 2013; Rendell et al. 2019). In primates and lions, short breeding tenures may refer to a period of years; for cetaceans, habitat overlap can be seasonal and associations in fission-fusion groups can last just a few minutes (Galezo et al. 2018). Bottlenose dolphins (*Tursiops* sp.), the most intensively studied genus of cetacean, do not have stable male dominance hierarchies (Samuels and Gifford 1997). The classic examples of male takeovers of multi-female groups or male changes in dominance position do not occur in cetaceans; while there is evidence of intense sexual conflict in multiple species, it remains unclear if and how males monopolize mating opportunities. In the fission-fusion social system of Indo-Pacific bottlenose dolphins (*T. aduncus*), alliances of males cooperate to harass and mate-guard females (Connor et al. 2022); females are consorted by up to 13 males in a breeding season (Connor et al. 1996), suggesting males are not able to completely monopolize mating. In species with modular social structures, such as killer whales (*Orcinus orca*), mating occurs outside the social group during temporary associations (Pilot et al. 2010). While life history factors make toothed whales excellent candidates for sexually selected infanticide, the social factors that stabilize infanticidal behavior could differ substantially from those in terrestrial species.

### 10.2.1 Baleen Whales

No evidence of infanticide has been reported in baleen whales. While this does not preclude the possibility that infanticide occurs and has not been observed yet, the seasonal breeding systems and short lactation periods of baleen whales could explain the lack of infanticide in this clade. Sexually selected infanticide is strongly associated with non-annual breeding (Lukas and Huchard 2014). When lactation lasts less than a full year and seasonal changes cue the commencement of estrus, the death of

dependent offspring will not result in earlier estrous cycling and will therefore not provide an adaptive benefit for infanticidal males. Baleen whale interbirth intervals range from 2 to 3 years, but nearly all baleen whales wean their offspring within a year of birth (Bannister 2009). In a sample of Antarctic humpback whales (*Megaptera novaeangliae*), 55% of females were simultaneously pregnant and lactating (Pallin et al. 2018), suggesting postpartum estrus may have been a common feature of mysticete reproduction in healthy pre-whaling populations. If postpartum estrus was common historically, sexually selected infanticide would be very unlikely to evolve. It has been proposed that male infanticide can be adaptive in annual breeding systems if the death of a dependent offspring results in better maternal condition and higher fecundity in the subsequent breeding season (Hrdy and Hausfater 1984). However, even if infanticide reduced a mysticete mother's interbirth interval or improved her condition, the diffuse social structure, polygynandrous mating system, and spatiotemporal expanse of movements (Rendell et al. 2019) mean that an infanticidal male may be unlikely to encounter the same female, let alone sire her offspring, in the next breeding season. Finally, mysticete females are larger than males and can effectively defend their offspring (Ralls 1976; Pitman et al. 2017). The lack of evidence for infanticide in mysticetes is consistent with the hypothesis that seasonal breeding, postpartum estrus, migratory lifestyle, and polygynandrous mating system all make baleen whales unlikely candidates for the evolution of sexually selected infanticide by adult males.

### 10.2.2 *Toothed Whales*

In contrast to baleen whales, toothed whale reproduction is characterized by slow calf growth and long lactation periods (Mann 2019), life history characteristics that make them prime candidates for the evolution of sexually selected infanticide. Bottlenose dolphins typically wean around age 4, but in exceptional cases, calves can nurse for up to 8 years (Karniski et al. 2018). While simultaneous lactation and gestation occur, interbirth intervals are long and females appear to begin estrous cycling only within a year of weaning (Mann et al. 2000; Karniski et al. 2018). Many odontocetes exhibit seasonal peaks in mating and birthing, but females seem to be able to reproduce throughout the year and long interbirth intervals are likely shortened by the death of a dependent calf (Robeck and O'Brien 2018). While these life history characteristics may predispose toothed whales to the evolution of sexually selected male infanticide, species- and population-specific social structure, mating system, and migratory tendencies likely interact to determine the actual risk of infanticide. Here, we review reported evidence for infanticide by species and date (Table 10.1).

**Table 10.1** Published reports of evidence of infanticide in cetaceans by species and date. The age of victims and identity of attackers are consistent with the sexual selection hypothesis. Individuals are classified as neonates if they are estimated to be under 3 months old, roughly the age at which fetal lines disappear. Female defense reactions suggest both individual defense and social defense are important in these systems

Species	Population	Age and survival status of victim	Aggressor age-sex class and group size	Association history between aggressor and mother	Female defense behaviors	Reference
<i>T. truncatus</i>	The Moray Firth, Scotland	Five out of eight necropsied calves showed evidence of infanticidal attacks; all five were estimated <1 year old. An attack on a freshly dead calf of unknown age was observed.	The aggressor was an adult of unknown sex. No other individuals besides the mother and calf were present.	Unknown	The presumed mother remained close to the calf but did not contact the calf or the aggressor.	Patterson et al. (1998)
<i>T. truncatus</i>	Virginia, USA	Nine out of 20 necropsied calves showed evidence of infanticidal attacks. Nine were estimated <1 year old; five of those were < 2 months old.	N/A	N/A	N/A	Dunn et al. (2002)
<i>T. truncatus</i>	St. Augustine, Florida, USA	An attack on a calf <2/3 the size of the adult animals was observed. Authors state that the injuries the calf sustained were likely fatal, but death was not confirmed.	At least two of the aggressors were male, confirmed by observations of erections. The sexes and total number of other aggressors were unknown. Group size varied from 2 to >18 individuals throughout the event.	Unknown	No dolphins appeared to intervene.	Kaplan et al. (2009)
<i>T. truncatus</i>		An attack on a neonate "several days old" was	One adult male was the aggressor. The event	Both the mother and aggressor were well-	The mother and several female associates	Robinson (2014)

	The Moray Firth, Scotland	observed. The neonate survived the initial attack but developed a spinal deformity that was not previously obvious, likely as the result of injuries sustained during the attack. The calf live stranded and died ~8 months after the attack.	occurred within a subgroup of a large, mixed-sex group of 41 individuals.	known to researchers but were not known associates. They were observed together 2 weeks after the attack.	intervened and recovered the calf from the aggressor several times. The mother positioned herself between the calf and the aggressor and held the calf on her back. Several other males encircled and obstructed the aggressor as the mother and infant escaped with female associates.	Perrtree et al. (2016)
<i>T. truncatus</i>	Savannah, Georgia, USA	A birth and a subsequent attack on the neonate (4 minutes old) were observed. The neonate was sighted alive the following day; long-term survival status is unknown.	Two adult males were the primary aggressors; sex was confirmed by observation of erections. Group size varied from five to ten individuals.	The mother and aggressors were known to researchers, but no previous association between them was reported. The male aggressors were presumed alliance partners. The mother, calf, and aggressors were seen together the day after the attack.	The mother lifted and carried the neonate on her back and head. The mother also engaged in potentially defensive behaviors including “thrashing her flukes through the air, lunging, and a high-arch dive”.	Perrtree et al. (2016)
<i>T. truncatus</i>	Galician coast, Spain	Case 1: an attack on a live neonate was observed; the neonate was killed in the attack. Case 2: an attack on an already dead neonate was observed; the body was recovered, and a necropsy confirmed the neonate was a few days	Case 1: six adults of unknown sex were the aggressors. The group included only the aggressors and mother-calf pair. Case 2: the group included the mother-calf pair and two adult males. One adult male was the	Case 1: no individuals were identified from previous work in the area. Case 2: all individuals were identified from previous work in the area; the adult male aggressor had never been seen with the mother before, while	Case 1: the mother was separated from the calf by the aggressors and later surfaced with the calf, presumed dead, on her head. Case 2: the mother held the dead calf on her head and repeatedly positioned herself between	Díaz López et al. (2018)

(continued)

**Table 10.1** (continued)

Species	Population	Age and survival status of victim	Aggressor age-sex class and group size	Association history between aggressor and mother	Female defense behaviors	Reference
<i>T. truncatus</i>	Sabine Lake, Texas and Louisiana, USA	Old and that the infantile attack was the cause of death. Case 3: the dead body of a neonate was recovered; a necropsy indicated that the neonate was a few days old and died from an infantile attack.	Primary aggressor, while the other adult male remained nearby but did not participate. Case 3: unknown	The bystander male was a known associate of the mother. Case 3: unknown	the dead calf and the aggressive male. Case 3: unknown	Ronje et al. (2020)
<i>T. truncatus</i>	Turneffe Atoll, Belize	An attack on a neonate (< 2 months from fetal lines) was observed; observation ended while aggression was ongoing with the neonate still alive. The calf was not reidentified within the next 2 years.	Three individuals were the primary aggressors: one adult male and two adults of unknown sex. Two more adults of unknown sex participated in the attack, and one adult female performed both aggressive and	The aggressor was known to researchers and had been previously observed in the area; the mother, calf, and one other individual in the group had not been observed in the area before.	The mother intervened in the attack, positioning herself between the calf and the aggressor. The mother and calf continued to travel in same direction as the group but put some distance (~100 m) between themselves and the group.	Ramos et al. (2022)



<i>I. geoffrensis</i>	Napo River, Peru	An attack on a neonate (<1 week old, suspected a few hours old) was observed. The neonate survived the attack but was swimming poorly at the end of the observation.	One adult male was the aggressor. Three additional individuals were in the group but did not participate.	Unknown	The mother repeatedly positioned herself between the calf and the aggressor and made potentially defensive contact with the aggressor.	Bowler et al. (2018)
<i>I. geoffrensis</i>	Japurá River, Brazil	Five attacks on neonates were observed. Case 1: the neonate was dead when the observation began. Case 2: the neonate was dead when the observation began and appeared to have been dead for at least a day. Case 3: the neonate survived the attack, but its long-term survival status is unknown. Cases 4 and 5: the neonates survived the attacks and were observed alive several months later. Additionally, five necropsied neonates showed evidence of infanticidal attacks.	Case 1: three adult males were the primary aggressors; eight more adult males also participated. About 20 individuals were in the area. Case 2: one adult male and one subadult male were among the primary aggressors; the other two to four aggressors were described as males. About 18 dolphins were in the area. Case 3: six adult males were the aggressors. An estimated 37 individuals were in the area. Case 4: one subadult male was the aggressor. About seven additional individuals were in the area. Case 5: five adult males and one juvenile of	Case 1–4: several individuals were known to researchers, but association history was not reported. Case 5: one aggressor was the adult maternal brother of the targeted calf.	Case 1: no dolphins appeared to intervene. Case 2: no dolphins appeared to intervene. Case 3: a group of adult females occasionally swam close to the calf and lifted it to the surface on their heads. Case 4: mother did not intervene. Case 5: mother intervened to protect the calf toward the end of the attack.	da Silva et al. (2021)

(continued)

Table 10.1 (continued)

Species	Population	Age and survival status of victim	Aggressor age-sex class and group size	Association history between aggressor and mother	Female defense behaviors	Reference
<i>S. guianensis</i>	Sepetiba Bay, Brazil	An attack on a neonate was observed; the neonate was presumed to have been killed in the attack.	unknown sex were the aggressors. Up to 25 individuals were in the area. Six adult males were the aggressors. No other individuals besides the mother and calf were present.	Unknown	The mother was separated from the calf by the aggressors and repeatedly aggressed on when she tried to reunite with the calf.	Nery and Simao (2009)
<i>S. chinensis</i>	Pearl River Estuary, China	Three attacks on neonates were observed. Case 1: the neonate was killed in the attack. Case 2: the neonate was alive at the end of observation. Case 3: the neonate was killed in the attack. Additionally, 3 out of 25 calf carcasses that were necropsied showed evidence of infanticidal attacks.	Case 1: 11 adults were the aggressors. Case 2: two adults and one subadult were the aggressors. Case 3: three adults were the aggressors. The aggressors in all cases were presumed males based on their behavior. No other individuals besides the mother, calf, and aggressors were present.	Case 1–3: the authors describe “infrequent and casual” associations between the perpetrators and presumed mothers before and after the attacks. Case 3: two of the aggressors were seen with the mother 2 days before the attack.	Case 1: the presumed mother tried to protect the neonate and charge the aggressors but was repeatedly separated from the neonate by the aggressors. Case 2: the presumed mother used echelon position to successfully block the aggressors from accessing the calf. Case 3: the presumed mother unsuccessfully tried to block the aggressors from accessing the calf.	Zheng et al. (2016)
<i>O. orca</i>		An attack on a neonate (< a few days old) was	One adult male and his postreproductive mother	The mother and male aggressor had been seen	The mother and her female kin apparently	

	Vancouver Island, Canada	observed; the neonate was killed in the attack.	were the aggressors. The mother-calf pair was accompanied by five members of their matriline.	together on two prior occasions.	tried to separate the aggressors from the neonate by forming two groups. The mother rammed the male aggressor, and the male and his postreproductive mother suffered tooth rakes.	Towers et al. (2018)
<i>L. obliquidens</i>	Mutsu Bay, Japan	An attack on a neonate (~2 months old) was observed; the neonate was alive at end of the observation.	The first group of aggressors included two adult males and two individuals of unknown sex. The second group included two adult males, one possible male, and three individuals of unknown sex. About 24 total individuals were present.	Unknown	The presumed mother charged and aggressed on the attackers.	Rosser et al. (2022)

### 10.2.2.1 Bottlenose Dolphins (*T. truncatus*)

The first evidence of infanticide in cetaceans came from a residential population of bottlenose dolphins in the Moray Firth, Scotland, in the mid-1990s (Patterson et al. 1998). Five of eight necropsied bottlenose dolphin calves were found to have significant internal injuries likely caused by intraspecific aggression (Patterson et al. 1998). Additional necropsy evidence from dolphins stranded on the coast of Virginia, USA, supported these findings (Dunn et al. 2002). Internal injuries indicated that attacks came from multiple directions and were concentrated on the head and thorax of the calves (Dunn et al. 2002). One calf had an external bite mark consistent with the tooth placement of an adult bottlenose dolphin, and some calves showed evidence of being subject to multiple traumatic injuries over several weeks (Dunn et al. 2002).

Patterson et al. (1998) observed one interaction in which an adult dolphin repeatedly attacked an already dead calf, lending credence to the hypothesis that intraspecific aggression is a significant cause of infant death in the Moray Firth population. Since then, reports of calf-directed aggression and apparent infanticidal attacks have accelerated. Aerial footage collected off the coast of Florida, USA, captured extensive and likely fatal attacks by multiple adult bottlenose dolphins on a calf over the course of 51 minutes (Kaplan et al. 2009). In the Moray Firth, where long-term research effort means that some of the dolphins' individual histories are known, Robinson (2014) reported an event in which a large adult male was seen repeatedly attacking a calf that was just a few days old. The mother of the calf appeared to try to intervene in the attack, positioning herself between the aggressive male and the calf (Robinson 2014). A female associate accompanied the mother, and other adult males obstructed the aggressive male's access to the calf by encircling him, facilitating the mother and calf's escape (Robinson 2014). The first published observation of a bottlenose dolphin birth, off the coast of Georgia, USA, was accompanied by an observation of an infanticidal attack. Just minutes after the calf was born, two males repeatedly attacked and attempted to submerge the neonate (Perrtree et al. 2016). The two male aggressors were presumed alliance partners and had been seen together several times before; they were seen flanking the pregnant female hours before the birth, indicating that they could have been tracking her impending parturition (Perrtree et al. 2016). Despite the increase in observations of calf-directed aggression, so far there is only one case in bottlenose dolphins in which a complete successful infanticide attack was observed. Off the coast of Galicia, Spain, Díaz López et al. (2018) observed six dolphins coordinating an attack on a neonate that resulted in the infant's death. Additional bouts of intense calf-directed aggression by bottlenose dolphins have been observed in Sabine Lake in the Gulf of Mexico (Ronje et al. 2020) and off the coast of Belize (Ramos et al. 2022). A survey of dolphin researchers working in the Gulf of Mexico revealed extensive records of calf-directed aggression, though no successful infanticidal attacks were observed (Ronje et al. 2020).

Several unpublished incidences of aggression toward calves indicative of infanticidal attempts have been observed in the Potomac River and Chesapeake Bay,

USA, despite only a few years of detailed observation (Ann-Marie Jacoby pers. comm. November 2022; JM pers. obs.). Dolphins inhabiting these waters overlap with the dolphin population(s) observed off the coast of Virginia Beach, USA (Dunn et al. 2002), so observations of infanticide were not unexpected. Two unsuccessful infanticidal attempts on neonates by suspected adult males (based on physical and behavioral features) were observed. One occurred immediately postpartum, similar to the case described by Perrtree et al. (2016). The calf was chased, tossed into the air several times, and held underwater by a suspected male before the mother was able to intervene and flee with the calf. The other case involved a neonate that was estimated to be 5 to 10 days old (Mann and Smuts 1999); the calf was repeatedly charged and chased, and in one incident was tossed out of the water. The mother and a juvenile (possibly her weaned offspring) appeared to defend against the attackers by repeatedly positioning the calf less than one-half meter alongside the research boat, effectively preventing the males from accessing the calf. Every time they separated from the vessel, the males resumed chasing, and the mother, neonate, and juvenile returned to the vessel. Both calves were observed with their mothers at least 1 month later and appeared to be healthy.

#### **10.2.2.2 Amazon River Dolphins (*Inia geoffrensis*)**

Amazon river dolphins are the only species besides bottlenose dolphins in which there are multiple published observations of infanticidal behavior and the only cetacean species outside of the delphinid family in which infanticide has been observed. In Peru, a newborn Amazon river dolphin was attacked by a large adult male, while the mother tried to intervene and keep the male away from the infant (Bowler et al. 2018). Five additional observations of infanticidal aggression were reported in Brazil (da Silva et al. 2021). In one case, one of the male aggressors was the maternal brother of the neonate target, and the authors suggest that this event is not consistent with the sexual selection hypothesis. For several of the attacks, there were large numbers of dolphins in the area, and da Silva et al. (2021) suggest that this behavior could be a form of sociosexual display (discussed further below).

#### **10.2.2.3 Guiana Dolphins (*Sotalia guianensis*)**

One observation of infanticide has been reported in Guiana dolphins in Brazil; a mother and neonate were separated and both repeatedly attacked by a group of six individuals of unknown sex (Nery and Simao 2009). The calf disappeared and seemed to have been killed within 12 minutes of the attack starting (Nery and Simao 2009).

#### **10.2.2.4 Indo-Pacific Humpback Dolphins (*Sousa chinensis*)**

Among Indo-Pacific humpback dolphins in southeast China, three infanticidal attacks have been reported, two of which resulted in the death of the infants

(Zheng et al. 2016). In all three cases, neonates were targeted, and the presumed mothers repeatedly tried to shelter the infant from aggression, even charging and attacking the aggressors. The number of attackers ranged from 3 to 11 dolphins all believed to be male (Zheng et al. 2016). Necropsy data on three additional calves indicate that the cause of death was blunt force trauma, implicating infanticide.

#### **10.2.2.5 Killer Whales (*O. orca*)**

One notable observation of infanticidal behavior occurred in mammal-eating killer whales off British Columbia, Canada (Towers et al. 2018). In 2016, an adult male and his postreproductive mother engaged in a long chase and eventual killing of a neonate. The mother of the neonate and her matrilineal kin apparently tried to separate the attackers from the neonate by forming two groups. When the attackers caught up to their target, the mother of the neonate defended her calf, aggressing on and ramming the infanticidal male. The neonate was killed quickly, and defensive behavior did not persist. While the infanticidal male and neonate's mother had been sighted together twice before (in 2005 and 2007), they were not regular associates. It was not reported if the infanticidal male was seen in association with the mother after the attack, but at the time of publication she had not yet been seen with a new calf, suggesting that a successful pregnancy was not immediate.

#### **10.2.2.6 Pacific White-Sided Dolphins (*Lagenorhynchus obliquidens*)**

Recently, a group of male and unknown-sex Pacific white-sided dolphins were seen repeatedly attacking a neonate in Mutsu Bay, Japan (Rosser et al. 2022). A separate group of dolphins displaced the first aggressive group and continued the attack, a behavior that has not been described in any other accounts. The authors noted that it is unusual to see neonates in this location; this was the first neonate sighting in 5 years (Rosser et al. 2022).

### **10.3 The Sexual Selection Hypothesis in Cetaceans**

#### ***10.3.1 Prediction 1: Infanticide Is Committed by Adult Males Who Target Infants That Are Not Their Own Offspring***

Overall, cases of infanticide in odontocetes are consistent with the sexual selection hypothesis. First, where age and sex are known, the perpetrators are by and large adult males (Table 10.1). However, there are several reports of subadult males participating in infanticide attempts (Zheng et al. 2016; da Silva et al. 2021). Even though subadult males are unlikely to sire a female's next offspring, engaging in

attacks may serve as practice, particularly if these attempts are relatively low cost for males. In one case, a female who could have been the calf's mother was involved in both aggressive and helping behaviors (Ramos et al. 2022), which is unusual but difficult to interpret without confirmation that the female was the mother. In the most conspicuous example of a female participating in an infanticidal attack, in which an adult female killer whale assisted her adult son, the exception may prove the rule (Towers et al. 2018). Postreproductive killer whale females provide fitness benefits to their adult offspring, particularly their sons (Foster et al. 2012; Brent et al. 2015). If a mother's assistance in an infanticidal attack results in her son being more likely to sire offspring, the sexual selection hypothesis applies to both mother and son.

Previous social association between the infanticidal individuals and their victim's mothers is often not known, but when it is reported, infanticidal males appear to be socially unassociated with the female and unlikely sires of the targeted infant (Table 10.1). In several cases, the males were not frequent associates of the mother (Robinson 2014; Zheng et al. 2016; Díaz López et al. 2018; Towers et al. 2018), and in others, the attackers and the mothers seemed to be from different subpopulations (Ronje et al. 2020; Ramos et al. 2022). The conspicuous exception to this is a case in the Amazon river dolphin, in which one attacker was the maternal brother of the targeted calf (da Silva et al. 2021). Given the large number of individuals who were involved in this attack, it seems relatively unlikely that the male would father his mother's next offspring; however, inbreeding rates are high in some dolphin species (Frère et al. 2010; Ford et al. 2018), and it is not impossible. While attacking one's sibling certainly seems detrimental to inclusive fitness, observations of adaptively neutral or maladaptive infanticide events do not necessarily represent evidence against the sexual selection hypothesis (Hrdy 1979). These behaviors are cued by complex circumstances that involve long-term individual recognition and memory, and occasional maladaptive attacks are probable. Overall, the evidence to date suggests that adult male cetaceans target infants that they are unlikely to have sired.

### ***10.3.2 Prediction 2: The Mother Is Likely to Return to Estrus Faster, or in Better Condition, than if She Had Successfully Weaned the Infant***

The second prediction of sexually selected infanticide is also met in all cases reported herein; the odontocete species that engage in infanticidal behavior have long lactation periods and no known postpartum estrus. The death of a dependent offspring is very likely to accelerate the return to conceptive estrus in these species (Robinson et al. 2017; Karniski et al. 2018; Martin and Da Silva 2018; Nattrass et al. 2019; Bezamat et al. 2020). Lactation requires large energetic investments in milk production (Cheal and Gales 1991), and losing a very young calf may be less costly to mothers than losing an older calf. Mothers who lose a neonate appear to conceive rapidly within a few weeks or months, while mothers who lose older calves can

sometimes take over a year to conceive again (Mann et al. 2000). Infanticidal males who kill a very young calf may only have to maintain an association or consortship with the mother for a period of a few weeks to sire her next offspring. An infanticidal male who kills an older calf would have to ensure that he is in contact with the mother after she has recovered sufficient body condition to return to estrus, which may take months or years. The potential benefit of killing a young calf is therefore much higher than killing an older calf, and it is salient that the vast majority of the targets described in the literature are neonates (Table 10.1). In multiple cases, attacks occurred within minutes or days of birth, and in two cases, males may have been tracking the female before she gave birth (Peritree et al. 2016; Ann-Marie Jacoby pers. comm. November 2022). While neonates may be particularly vulnerable and easier to kill than older calves, the size differential and fact that attacks often involve multiple adult aggressors suggest that adult males could kill older calves as well. Given the transitory association patterns in some of these migratory populations, however, targeting neonates may help maximize the likelihood of subsequent conceptive mating. Feticide, male aggression against a pregnant female that induces abortion, could also operate in these systems, given that males seem able to determine a female's reproductive state (Wallen et al. 2017). Whether pregnancy loss results in a rapid return to estrus is not known, although it seems likely. Rates of feticide would be difficult to assess in wild cetaceans, but male aggression toward pregnant females would be telling.

### ***10.3.3 Prediction 3: The Infanticidal Male Has an Opportunity to Sire the Mother's Next Offspring***

The third prediction of the sexual selection hypothesis remains uncertain in all cetacean cases reported herein; no studies reported mating or association during estrus between infanticidal males and the mothers of their victims. In terrestrial systems, the monopolizability of mating and the likelihood that an infanticidal male will sire the next offspring have been highlighted as important modulators of infanticide risk (Lukas and Huchard 2014). In cetaceans, however, most species have polygynandrous mating systems (Würsig et al. 2023, this book), and mating monopolizability is likely relatively low. In cetacean species in which male-female associations are seasonal and unpredictable, the likelihood of a male siring a female's next offspring without committing infanticide could be zero. If costs of infanticidal behavior to males are low, it may be adaptive to commit infanticide for even a small chance of siring the subsequent offspring. In one case in bottlenose dolphins, the mother and calf who survived the initial attack were seen with the aggressor several weeks later (Robinson 2014), demonstrating the plausibility of males maintaining an association with the mother long enough to mate. Still, this key requirement of the sexual selection hypothesis is yet to be demonstrated in cetaceans.



### ***10.3.4 Cooperation During Infanticide***

Infanticidal attacks in toothed whales often involve multiple males launching highly coordinated attacks against a victim (Table 10.1). While early accounts of sexually selected infanticide in langurs and lions note that groups of males can be involved in takeovers and infanticide attempts (Hrdy 1974; Packer and Pusey 1984), to our knowledge the number of males and the level of coordination described in cetaceans represent an extreme of this behavior. Many of the events involved between 3 and 6 attackers, with 1 event involving 11 (Table 10.1), and coordinated behaviors including “sandwiching”, in which the mother or infant was trapped between two attackers, were described by multiple observers (Zheng et al. 2016; Díaz López et al. 2018; Rosser et al. 2022). In two cases, the observers described what seems to be strategic coordination, in which a subgroup of attackers sequestered the mother, preventing her from reaching her calf, while another subgroup focused their aggression on the infant (Díaz López et al. 2018; Rosser et al. 2022). The presence of multiple attackers poses an obvious challenge to the sexual selection hypothesis; if males cooperatively kill infants, not all infanticidal males can benefit by siring the female’s next offspring. At the same time, cooperative attacks may reduce the cost for each individual male. In some cases, males could be cooperating with relatives, as in the killer whale event (Towers et al. 2018). Cooperation between related (Parsons et al. 2003; Diaz-Aguirre et al. 2018) or unrelated (Gerber et al. 2020) males in alliances that compete over access to paternity, an indivisible resource, is a characteristic feature of bottlenose dolphin mating systems (Gerber et al. 2022). While it remains unclear how paternity is divided between alliance partners, strong cooperative bonds appear to provide a reproductive benefit (Gerber et al. 2022). Cooperation during infanticide attempts may be an extension of male-male cooperation to gain access to mating opportunities, and thus consistent with the sexual selection hypothesis.

### ***10.3.5 Alternative Hypothesis for Infanticide***

Numerous other hypotheses for adaptive infanticide are supported in a variety of systems (Ebensperger 1998; Palombit 2015), but so far there is little evidence for them in cetaceans. None of the cases of infanticide described in cetaceans are consistent with the predation hypothesis, as none of the infants were eaten after being killed. Killer whales are one of only a few cetacean species that eat mammals, and even in the killer whale infanticide case, the dead infant was not consumed (Towers et al. 2018). The resource competition hypothesis posits that individuals kill unrelated infants to increase their or their offspring’s access to resources (Ebensperger 1998), but cetacean prey are typically non-monopolizable, and competition over prey or territory is not obvious. The adoption avoidance hypothesis posits that infanticide can prevent individuals from investing alloparental care

into unrelated infants (Ebensperger 1998). While alloparental behavior has been documented in sperm whales (*Physeter macrocephalus*) (Konrad et al. 2019), infanticide has not. All of these hypotheses predict that adult females will be equally or more likely than males to attack infants, which has not been reported in cetaceans.

Nonadaptive hypotheses for infanticide are divided between neutral and pathological explanations. The neutral generalized aggression hypothesis suggests that infants can be killed incidentally in the course of male competition or male aggression on females (Palombit 2015). This does not fit observed patterns in cetaceans as all cases involved extensive, repeated, and highly directed aggression against an infant. While aggression and sexual behaviors against the mother did occur during infanticidal attacks, the infant was always the primary target. Since the 1960s, nonadaptive or pathological explanations for infanticide have been proposed (e.g., Curtin and Dolhinow 1978) and dismissed (Hrdy 1979; Packer 2000). Pathological hypotheses focus on the idea that infanticide can be a maladaptive response to anthropogenic disturbance and stress. While there is no evidence supporting the idea that human disturbance results in aberrant aggressive behavior, there is some suggestion that disturbance can indirectly impact infanticide via demographic variables such as immigration or male turnover rates (Sterck 1999; Swenson et al. 2001). Anthropogenic induced stress in cetaceans is pervasive, but there is little evidence linking human disturbance to infanticidal aggression. The one potential exception is in Amazon river dolphins, where the population is in severe decline. Despite constant research effort since 1998, all five observations of infanticidal aggression described by da Silva et al. (2021) occurred after 2010. It is possible that population decline may have disrupted social structure and resulted in decreased access to females in estrus and increased infanticide rates, but this has not been proven.

One hypothesis in the literature is unique to cetaceans. Da Silva et al. (2021) suggest that infanticide in Amazon river dolphins could be a form of sociosexual display, akin to the object carrying that males perform in this species (Martin et al. 2008). The fact that a maternal relative engaged in an infanticidal attack leads the authors to conclude that sexually selected infanticide is unlikely. Observations of males handling a neonate who had been dead for at least a day, along with the large number of dolphins present during attacks, supports the display hypothesis. Still, it seems equally maladaptive to kill a half-sibling to obtain a display object as it would be to obtain a mating opportunity, and it is possible that sexually selected infanticide and sociosexual display of the dead neonate could occur sequentially in this species.

## 10.4 Interspecific Infanticide

While the sexual conflict literature defines infanticide as a behavior committed by conspecifics (Palombit 2015), interspecific attacks are a prominent feature of reports of cetacean infanticide. Non-predatory interspecific aggression has been reported in a number of odontocetes (e.g., Shane 1995; Weller et al. 1996; Orr and Harwood 1998), with bottlenose dolphins featuring heavily as aggressors (Ross and Wilson 1996; Herzing et al. 2003; Wedekin et al. 2004; Barnett et al. 2009; Puig-Lozano

et al. 2020). At first glance, these attacks are inconsistent with the sexual selection hypothesis and raise the possibility of an alternative underlying driver of both intraspecific and interspecific attacks. Details of some of these aggressive interactions, however, are consistent with sexually selected infanticide. Harbor porpoises are similar in size to dolphin neonates, and porpoise-directed aggression could be a form of object-oriented play that allows males to practice infanticidal behaviors or to reinforce social bonds and improve coordination between male social partners during aggression (Patterson et al. 1998). In “porpicide” events observed off the coast of California, bottlenose dolphin aggressors were confirmed or putative males, supporting the hypothesis that this behavior is linked to sexually selected infanticide (Cotter et al. 2012). One observation of three male Indo-Pacific bottlenose dolphins harassing a dead spinner dolphin (*Stenella longirostris*) neonate and its assumed mother closely resembles accounts of conspecific infanticidal behavior (Estrade and Dulau 2017). While no bottlenose x spinner dolphin hybrids are known, bottlenose dolphins do hybridize with other sometimes less closely related species (Herzing et al. 2003; Crossman et al. 2016; Estrade and Dulau 2017) suggest that the sexual selection hypothesis could apply in this and other interspecific attacks. Alternative hypotheses for interspecific attacks have been raised, including aberrant aggression, sexual frustration, and aggressive tendencies driven by testosterone (Ross and Wilson 1996; Patterson et al. 1998). In practice, it would be difficult to differentiate between males expressing general aggressive tendencies on a low-cost target and males practicing aggressive behavior on a low-cost target, and these explanations represent potentially compatible proximate and ultimate hypotheses. Alternatively, interspecific resource competition may be relevant in some cases and would generate distinct predictions from the sexual selection hypothesis, including the prediction that females would be involved in attacks. Non-predatory interspecific aggression likely has different drivers in different species, and research targeting the social and ecological circumstances of these events will help determine if they are compatible or at odds with sexually selected infanticide.

## 10.5 Female Counterstrategies to Infanticide

Infanticide risk has been hypothesized to influence virtually every aspect of female reproductive biology and social behavior, including physiology, mating strategies, territoriality, group sizes, and social bonds (Agrell et al. 1998; Palombit 2015). Phylogenetic analysis suggests that multi-male mating, measured by relative testes size, has evolved in response to infanticide by adult males in multiple lineages (Lukas and Huchard 2014). Males who have mated with the mother of an infant are less likely to target that infant in attacks, as the cost of potentially killing their own offspring is very high (Palombit 2015). Polyestrous cycling and multi-male matings that confuse or “dilute” paternity occur in many odontocetes and may be important for reducing infanticide risk (Connor et al. 1996). Many odontocetes breed seasonally, likely to ensure calves are born during warm months. Breeding

synchrony between females may also serve to reduce male monopolization of mating opportunities, further confusing paternity. However, polygynandrous mating and synchronous estrus appear insufficient to deter infanticide completely in these species, likely because extra-group males, or males with whom the female has little or no prior association, are still unlikely to have mated with the mother and are therefore more likely to target her infant.

Other types of reproductive and sexual anti-infanticide strategies are less likely to operate in cetaceans. Concealed ovulation, postconception sexual behavior, and pseudoestrus can all confuse paternity and dilute infanticide risk in species where males cannot accurately judge female reproductive state (Ebensperger 1998). However, toothed whales have sophisticated echolocation and appear to readily detect early pregnancy (Wallen et al. 2017). Spontaneous abortion following exposure to an unfamiliar male, the “Bruce effect,” occurs in rodents and primates (Beehner and Lu 2013); females terminate their pregnancies (i.e., “cut their losses”) when the offspring is likely to be killed after birth. Due to stable social grouping, females cannot avoid the newly immigrant infanticidal male, and ending the pregnancy reduces the cost of infanticide. This is an unlikely scenario for cetaceans because novel males rarely establish tenure in a female group.

Deterrence tactics from the mother were prominent in many of the events described in cetaceans. Mothers often tried to place themselves between attackers and their infants, and several mothers aggressed on their attackers. Female cetaceans rarely engage in aggressive behavior compared to males (e.g., Scott et al. 2005), and the few cases of female aggression that have been reported in cetaceans are in defense of their offspring (e.g., Mann and Barnett 1999). In classic infanticidal species, where males take over or rise to dominance in stable social groups, females are unlikely to be able to fully avoid infanticidal males, and their infant may be at risk of infanticide for months. In the fission-fusion social system of odontocetes, females who successfully fend off infanticidal males may be able to avoid those males until their calf is less vulnerable. Limited sexual size dimorphism in some dolphins may also enable females to better defend against males. While in the killer whale event the mother’s attempts to defend her calf failed, both the infanticidal male and his mother suffered injuries in the attack (Towers et al. 2018), suggesting maternal aggression can be costly for infanticidal attackers.

Social strategies likely also play a role in infanticide deterrence in cetaceans. In several descriptions of attacks, mothers were assisted in infant defense by female kin, female associates, or male associates (Robinson 2014; Towers et al. 2018; da Silva et al. 2021). Large group sizes are characteristic of mothers with newborn infants (Mann et al. 2000), and groups of females with calves might deter infanticidal attacks or inflict injury on the perpetrators, as in the killer whale event (Towers et al. 2018). Females might also travel with residential males with whom they commonly associate. Polygynandrous mating could result in multiple potential fathers that could provide infant protection, though this is dependent on fathers remaining in association with mothers when the calf is vulnerable. While there is no known paternal care in cetaceans, it is possible that dyadic male-female relationships could result in fathers or male associates providing infant protection. In one

described case in which a male attacked an already dead calf, a different male who was present at the infanticide attempt but not involved in the aggression was seen with the mother in the weeks following the attack (Díaz López et al. 2018). While the authors hypothesized that the male could have been involved in the attack and benefited by fathering the female's next offspring, it is also possible that as a known associate of the mother, he provided the mother support or intervened in the attack before the calf's death.

## 10.6 Summary and Future Directions

The instances of infanticide described in cetaceans are most clearly consistent with the sexual selection hypothesis. While much remains unknown about the relative costs and benefits of sexually selected infanticide in cetaceans, this group can provide an important comparative system to study the evolutionary drivers of infanticidal behavior and defense. Descriptions of infanticide in these highly mobile, multi-male mating systems challenge previous findings that infanticide occurs in stable bisexual groups in which few males monopolize mating opportunities (Lukas and Huchard 2014). Instead of being associated with male takeovers or changes in dominance status, we hypothesize that infanticide risk in cetaceans is largely determined by contact with unfamiliar males. We expect infanticide to occur when populations experience seasonal influxes of unfamiliar males or when multiple subpopulations interact and males encounter females with whom they have had little to no previous contact.

There is substantial evidence for infanticide in multiple bottlenose dolphin populations. However, several long-term bottlenose dolphin sites have *not* reported infanticide. In residential populations of bottlenose dolphins with bisexual philopatry in Shark Bay, Australia, Doubtful Sound, New Zealand, and Sarasota, Florida, USA, infanticide has not been reported. Calf-directed aggression has been described in Sarasota, but it is unclear if those events meet the standard of intense, highly directed infanticide attempts (Ronje et al. 2020). In Shark Bay, where there has been intensive research effort for over 38 years, there is no evidence of infanticide or calf-directed aggression. Infanticide events are always rare and often relatively brief, and it is possible that unobserved infanticide does occur in these populations. Even in extremely well-studied populations of primates with strong demographic evidence for infanticide, the behavior has never been witnessed (Zipple et al. 2017). However, the lack of observed infanticide could be the result of effective female counterstrategies to male infanticidal aggression. Females in stable, socially integrated, residential groups (Tsai and Mann 2013) with polygynandrous mating systems and polyestrous cycling (Connor et al. 1996) are surrounded by males with whom they have social histories and have likely mated with (Foroughirad et al. 2022), potentially minimizing infanticide risk.

We see several promising areas for future research. First, as research effort and researcher interest in infanticide in cetaceans increase, anecdotal reports of

infanticidal behavior and necropsy evidence will likely continue to accelerate. These anecdotal reports are extremely valuable, and standardization of vocabulary to describe these behaviors will facilitate comparison over different research programs and species. Second, in populations where infanticide has been described, researchers can explicitly investigate the risk of infanticide based on the presence of unfamiliar males who are unlikely to have sired current offspring. Third, continued long-term monitoring of cetacean populations is likely to yield further information about the post-infanticide patterns of association between infanticidal males and females, and increases in the use of high throughput sequencing technologies will improve our understanding of male reproductive success. Determining the realized benefit of infanticide (i.e., the likelihood of an infanticidal male fathering the mother's next offspring) is a key component for advancing our understanding of the evolution of infanticide in these systems. Fourth, researchers can examine mating and association patterns that may reduce infanticide risk, both in sites where infanticide has been observed and where it has not been. Increased attention to low-level calf-directed aggression and maternal protective behaviors will further our understanding of infanticide, even in the absence of conspicuous attacks. Cetaceans provide an exciting opportunity to investigate the drivers of infanticide in mating and social systems that differ substantially from their terrestrial counterparts. Continued research effort will elucidate how infanticide evolved in species without dominance hierarchies or stable social groups, providing insight into the evolution of infanticide overall.

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