

# Chapter 1

## Sex and Behavior



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**Abstract** We provide a conceptual primer for sexual selection and conflict, mating systems, and socio-sexual behaviors and patterns among animals, largely with mammalian and cetacean examples. The important roles of mate choice are discussed (including female choice) and the occasional fluidity of sexual roles. An overview of topics pertinent to sex and behavior is described, including evolutionary drivers (the concept of “why sex after all?”) followed by general mammalian and cetacean mating strategies and tactics. We describe mating systems (monogamy, polygyny, polyandry, polygynandry) with the present understanding that most cetaceans do not have monogamous or polyandrous mating systems. The primer includes brief introductions to historical knowledge and highlights emerging areas of research within the field of sex in cetaceans, with context for other chapters of this book. As part of overall sexual behavior, alloparental care, female reproductive senescence, and non-procreative behaviors including homosexual and necrocoital mating are also introduced.

**Keywords** Female choice · Homosexuality · Mating strategies · Mating systems · Mating tactics · Polygynandry · Polygyny · Reproductive senescence · Sex · Sexual dimorphism · Sexual selection

### 1.1 Why Sex After All?

Sexual reproduction, as proposed by Darwin (1871), has remained somewhat enigmatic due to several resounding disadvantages to sexual intercourse. In the most common case of a stationary gamete (an egg) and a mobile gamete (a sperm), one-half of female and male genetic materials are united to form a new living progeny. Passing on only one-half of ones’ genome is inherently disadvantageous

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if parthenogenesis (one form of asexual reproduction, without sperm) and complete replication of the genome are alternative possibilities (Williams and Mitton 1973). Compared to basal invertebrates and plants, which often have both sexual and asexual reproduction capabilities, it remains unclear why more derived vertebrates generally lack asexual means of reproduction. One hypothesis for this observed pattern is that sexual reproduction has been evolutionarily locked into place for most birds and mammals (Williams 1971). Through sexual reproduction in vertebrates, the possibility exists of passing on at least some autosomal genes that are disadvantageous for the progeny. Additionally, it takes inordinate temporal and energetic investments to find a suitable and reproductively active partner. Once found, there is no assurance that either or both partners are fertile or have compatible gametes. The transmission of diseases from a parent to offspring also looms as a potential detriment of breeding. Thus, why engage in sexual reproduction in spite of all the potential disastrous outcomes?

Sexual reproduction persists due to a number of practical advantages, the most obvious being the production of offspring derived from a female and male that survived to reproduce (Darwin 1871). If the parents survived long enough to breed, then the progeny have inherited genetic materials providing a reasonable chance to also survive to reproduce, given a similar environment, habitat, and ecosystem. Genes may be inherited by offspring that are not immediately needed for survival in the present ecology, but may be useful later on in a different set of habitats or if exposed to particular diseases (Van Valen 1973; Hamilton et al. 1990). Parental genetic material may also provide progeny with an advantage over coevolving species, providing the ability to evolutionarily “outrun” competitors (Van Valen 1973); this hypothesis was expanded by Hamilton (1980) to recognize the advantage sexual reproduction provides to individuals who remain in constant flux with their parasites. Recent evidence on New Zealand snails, *Potamopyrgus antipodarum*, and the crustacean *Daphnia dentifera* illustrate relationships between modes of reproduction and parasite load within two host species and their respective parasites (Gibson et al. 2017, 2018; Gowler et al. 2021).

Due to anisogamy (males produce smaller and less energetically costly gametes than females) and variation in parental investment, the sexes are not reproductively symmetric (Trivers 1972; Maynard Smith 1978; Andersson 1994). In most cases, female reproductive success is limited by resources to invest in parental effort, causing females to distribute themselves relative to resources (Trivers 1972; Emlen and Oring 1977). Unfavorable mate selections have higher fitness costs in females than males; females’ gametic energetic input is much higher than males, and in mammals, females have limited opportunities to produce offspring due to the lengths of gestation and lactation. Accordingly, females generally become the “choosy” sex because they cannot increase their fitness potential through excess matings as males can. Excess matings may have a negative impact on female fitness (Maklakov et al. 2005). Increased progeny numbers may reduce maternal investment per offspring and result in a net decrease in offspring survival to sexual maturity. Therefore, females benefit by selecting a high-quality mate.

The operational sex ratio (instantaneous ratio of sexually active males to sexually receptive females; Emlen and Oring 1977) is often male-biased because sperm are energetically “cheap” to produce and more males are available to mate than females. Males can increase their fitness by mating (potentially indiscriminately) with many fertile females. Strong sexual selection driven by intrasexual variation in the reproductive success of males persists in multiple species. Thus, males generally distribute themselves relative to females and invest heavily in mating effort, especially in species where paternity is uncertain (Daly and Wilson 1983). Males may further increase their fitness through their ability to successfully monopolize a female. Depending on female group size, range, and seasonality of breeding, males vary in their abilities to monopolize females, which influences the mating system (Ralls and Mesnick 2019a).

Evidence that males distribute themselves relative to females can be gleaned by comparing social patterns between the sexes. For an example in cetaceans, dolphins generally live in fission-fusion societies, where groups break apart and join together, often on an hourly basis (an early record provided for dusky dolphins, *Lagenorhynchus obscurus*; Würsig and Würsig 1980) or on an inter-day basis (an early record provided for Hawaiian spinner dolphins, *Stenella longirostris*; Norris and Dohl 1980). Females often occur alone, with their calves, or in short-term associations with females in a similar reproductive state (Gibson and Mann 2008; Elliser and Herzing 2013), whereas males may occur in small groups with stable alliances (Connor and Krützen 2015; Brightwell and Gibson 2023, this book). It has been hypothesized that individuals decrease their group size because of strong competition for resources (i.e., Hoare et al. 2004). Accordingly, male and female association patterns are predicted to be similar if resource competition and predation pressure are the only driving forces (Maynard Smith 1978). However, as natural selection and fitness pressures act on cetaceans, males distribute themselves relative to mating opportunities. When females are clustered in space and time, males may exhibit direct female defense. Whereas when females are dispersed, males may monopolize females through leks or by roving (Ralls and Mesnick 2019a).

## 1.2 Mating Systems

Mating system designations reflect the predominant relationship among individuals in the population. Such relationships can vary seasonally or last throughout an individual’s lifetime and can refer to either social or genetic relationships. Mating systems can be broadly defined as monogamous or polygamous. In a monogamous system, one female and one male mate exclusively within at least one estrous cycle, whereas in a polygamous system, individuals mate with more than one partner. Polygamy can be further divided into polygyny (one male mates with multiple females), polyandry (one female mates with multiple males), and polygynandry (multi-mate; females and males mate with multiple partners). The term

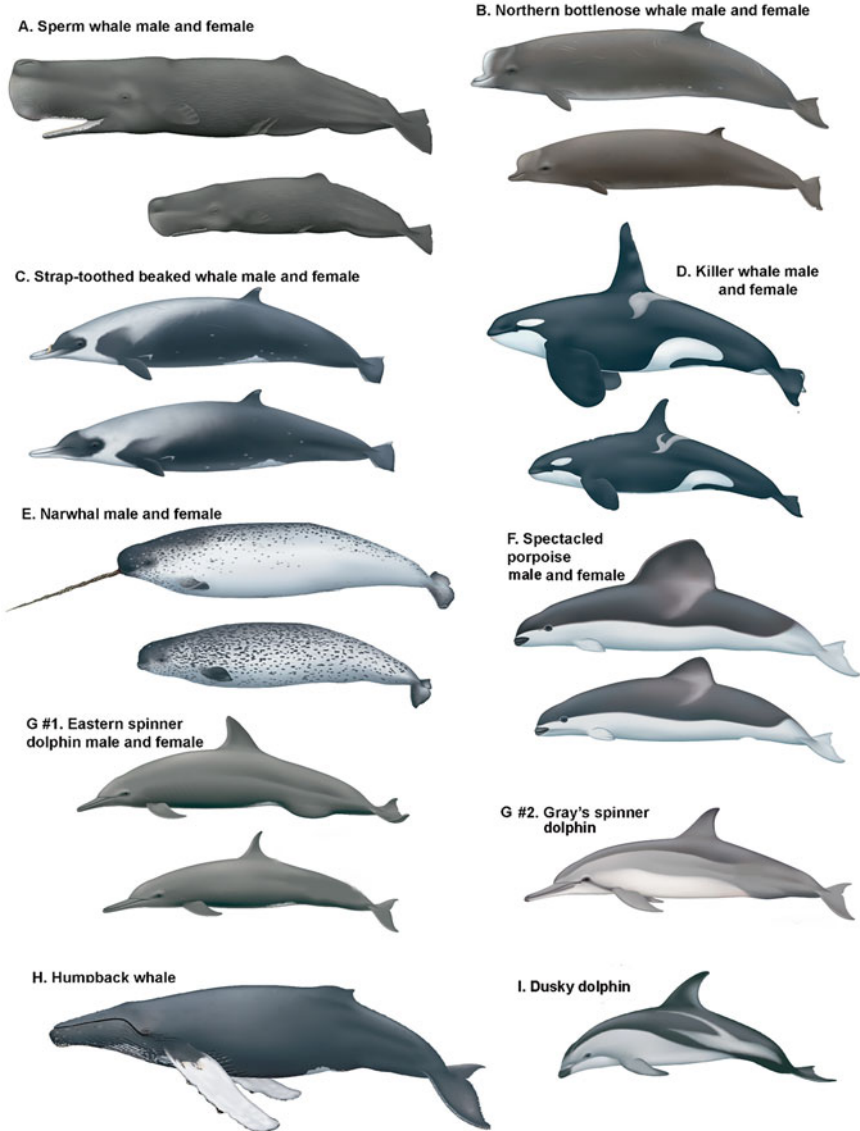
“promiscuity” is discouraged as it suggests a randomness to mate selection and no overt mate choice.

Certain biological and social indicators, such as sexual dimorphism, testes size, and sociality, may be used to predict mating systems among cetaceans where matings cannot be easily observed (Ralls and Mesnick 2019a). However, actual mating success can be best deduced by studying genetically determined offspring (Gerber and Krützen 2023, this book). Sexual dimorphism of skull structures and teeth in ancestral and present-day cetaceans is discussed by Loch et al. (2023, this book), and testes sizes are reviewed by Chivers and Danil (2023, this book), all with implications regarding sexual strategies. In general, characteristics with few differences between sexes tend to broadly indicate either monogamous or multi-mate (polygynandrous) mating systems (Mesnick and Ralls 2018). Many cetaceans are monomorphic (i.e., the sexes do not have greatly disparate body size or shape differences beyond teeth and genitals), and it can be quite difficult to determine the sex of a toothed or baleen whale by external morphology (Jefferson et al. 2015). Figure 1.1 presents images of overt sexually dimorphic external morphologies of males and females for select odontocete species and includes several monomorphic odontocetes as well as one mysticete example (humpback whale, *Megaptera novaeangliae*). In general, adult female baleen whales tend to be larger than similarly aged males, probably because females must be large to effectively produce and nurse large precocial offspring (Mesnick and Ralls 2018).

One obvious potentiality resulting from the general trend of monomorphism among cetaceans is that sight and smell are less important sensory modalities compared to most terrestrial mammals (Tyack 2019). External morphology may not be as important a conveyor of sex and sexual tactics in cetaceans as in many other mammals, although it may be of similar importance especially in dimorphic species. Communication and echolocation (the latter for odontocetes) and other acoustic signals may be of similar importance to cetacean sexual relationships as sight and smell are for most terrestrial mammals (Tyack 2019, for odontocetes). In mysticetes, sexual tactics largely rely on sound (Clark and Garland 2022), although female/male physical adroitness may also be of great importance (Brown and Sironi 2023, this book; Koski et al. 2023, this book; Swartz et al. 2023, this book). The elaborate breeding songs of humpback whales are one such example (Dunlop 2022; Eichenberger et al. 2023, this book).

### 1.2.1 Monogamy

In monogamous mating systems, one female and one male share a reproductive bond. Females and males tend to be physically monomorphic, and both sexes invest heavily in offspring care until offspring can survive independently. In species with biparental care, social and ecological constraints may preclude males from extra-pair mating. However, extra-pair copulations are common among monogamous pairings (i.e., European pied flycatcher, *Ficedula hypoleuca*; Grinkov et al. 2022), supporting



**Fig. 1.1** Several cetaceans with variable dimorphologic features between females and males. (A, B, D, E, F, and G#1) show strong differences in body configurations and size. Drawings are to scale between the sexes, but not to scale across species. (C) of the strap-toothed beaked whale indicates the externally visible large tooth of males, common in beaked whales. (G#2, H, and I) show animals with very muted sexual dimorphism, so only one figure representing both sexes is shown. (G#1) of the eastern spinner dolphin shows strong sexual dimorphism, while most other spinner dolphins of the species *longirostris* are of the “gray-type,” with little difference males vs. females (G#2). (H) of the humpback whale indicates that females and males have similar external morphologies, while females are slightly larger on average than males. (I) of the dusky dolphin also shows only muted sexual dimorphism. Species are (A) sperm whale (*Physeter macrocephalus*), (B) northern bottlenose whale (*Hyperoodon ampullatus*), (C) strap-toothed

sexual selection's fundamental tenet that conflicts exist between the sexes concerning maximizing lifetime reproductive success (Kokko and Jennions 2014).

Among non-mammalian (non-lactating) species with primarily monogamous mating systems, hungry offspring may be fed by either parent. For example, monogamous mating systems are common among birds (although not necessarily mutually exclusive with other mating systems). Biparental care ensures one parent is available to sit on the nest, keep the eggs warm, and protect the offspring, while the other parent forages. If the male does not invest in paternal care, his progeny have a reduced likelihood of survival. Thus, the male has a higher probability of his genes perpetuating if he aids with offspring rearing over abandoning his progeny to inseminate additional mates. In species where males offer parental care, such as in many externally fertilizing fishes, male care of the nest can attract more potential mates, further increasing the male's fitness (Lindström et al. 2006). Monogamy is uncommon among mammals, in which the female gestates the fetus in her body and nurses the offspring with milk, curtailing a male's role in parental care (Lukas and Clutton-Brock 2013). It has been suggested that one species of odontocete, the franciscana (*Pontoporia blainvillei*), may have a monogamous mating system due to their reverse sexual size dimorphism, lack of evidence to support male-male aggression or sperm competition, and prevalence of unrelated male-female pairs caught as bycatch in the same nets (Wells et al. 2013). More research on this and other cetacean species is needed relative to the possibility of monogamy.

### 1.2.2 Polygyny

In polygynous mating systems, males mate with multiple females, and females generally invest extensively in offspring care. In contrast, males invest little if any effort in parental care as paternity is uncertain. Males compete to varying degrees for access to receptive females and then mate with as many females as possible, often resulting in extensive sexual dimorphism. Males may have elaborate morphological features or "displays" that deter rival males, attract females in estrus by demonstrating males' ability to survive despite the handicap induced by their displays (Zahavi and Zahavi 1997), or attract females with desirable traits that may be inherited by their offspring. Male body size and fighting ability are often critical to establish dominant positions associated with access to mates (Andersson 1994).

In highly polygynous societies such as elephant seals (*Mirounga* spp.), only a few males sire the majority of offspring in a colony (Leboeuf 1972; Le Boeuf and Laws

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**Fig. 1.1** (continued) beaked whale (*Mesoplodon layardii*), **(D)** killer whale (*Orcinus orca*), **(E)** narwhal (*Monodon monoceros*), **(F)** spectacled porpoise (*Phocoena dioptrica*), **(G#1 and G#2)** eastern and gray's spinner dolphin (*Stenella longirostris orientalis* and *S. l. longirostris*, respectively), **(H)** humpback whale (*Megaptera novaeangliae*), and **(I)** dusky dolphin (*Lagenorhynchus obscurus*) (figure by Uko Gorter, with permission)

1994). Infanticide (the killing of non-offspring young) occurs in some terrestrial species, potentially to rapidly induce estrus in the mother and gain another opportunity to inseminate her (Hrdy 1977; Clutton-Brock 2016). Among odontocetes, evidence of infanticide is accruing in several species (Barnett et al. 2009; McEntee et al. 2023, this book). Males may also engage in forced copulations (a term preferred over “rape” when referring to animals/wildlife) with sexually mature females, sexually immature individuals of either sex, heterospecifics, dead conspecifics, and inanimate objects (pinnipeds (Rohner et al. 2020) and sea otters, *Enhydra lutris* (Harris et al. 2010)). Recent examples of interspecific necrocoitus between common bottlenose dolphins (*Tursiops truncatus*) and short-beaked common dolphins (*Delphinus delphis*; Methion and Díaz López 2021), intraspecific necrocoitus in common bottlenose dolphins (Kincaid et al. 2022), and masturbatory and homosexual behaviors in captive Yangtze finless porpoises (*Neophocaena asiaeorientalis*; Zhang et al. 2015; see also da Silva and Spinelli 2023, this book; Ham et al. 2023, this book) have been reported.

### 1.2.3 Polyandry

In polyandrous mating systems, one female mates with multiple males, and males generally take care of the young. There are numerous polyandrous species of fishes and birds (e.g., pheasant-tailed jacana, *Hydrophasianus chirurgus*; Fresneau et al. 2021); however, polyandry seems scarce in habitats with ample resources. Polyandrous females can have more striking external markings than their counterpart males. Males in polyandrous species generally have large testes sizes relative to their body size as sperm competition among males is hypothesized to play an important role in paternity determination (Gomendio and Roldan 1993). The uncertain nature of paternity in polyandrous systems decreases the risk of infanticide by male conspecifics, such as in some new world monkeys (e.g., marmosets and tamarins, family Callitrichidae; Pradhan and van Schaik 2008). Polyandrous females have increased fitness within inbred populations, as shown with red flour beetles (*Tribolium castaneum*; Michalczyk et al. 2011).

The challenging nature of studying mating in aquatic mammals makes it difficult to identify polyandry while ruling out polygynandry with certainty in cetaceans. However, several examples of polyandry exist, including the well-studied population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. In this population, multiple males form stable and ongoing alliances and then isolate and consort with a single female. Although paternity is not divisible and males in alliances are not necessarily kin, each male has a higher likelihood of inseminating a female if cooperating within an alliance than attempting to mate with a female on his own (Connor et al. 2000b). Similar to humans and chimpanzees (*Pan troglodytes*), these male alliances among bottlenose dolphins are formed among non-related males with strong social bonds commencing at adolescence (Gerber et al. 2021). Populations of common bottlenose dolphins around Florida and other



areas (Ermak et al. 2017; Brightwell and Gibson 2023, this book) and perhaps Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas (Elliser and Herzing 2013) also exhibit cooperative male alliances. Further long-term studies of cetacean populations may reveal increased prevalence of the alliance formation phenomenon. Little is currently known about post-copulatory mechanisms that female cetaceans may induce to control paternity in polyandrous systems. Further research is needed to determine the degree of female choice and potential additional benefits conferred to females in polyandrous species.

### 1.2.4 Polygynandry

Polygynandry, which incorporates aspects of both polyandry and polygyny, involves both sexes mating with multiple partners during one reproductive period. Polygynandrous females and males tend to be monomorphic in coloration and size, so there can be confusion between monogamy and polygynandry from body structure alone. Females have much at stake if inseminated by a poor choice of sexual partner. By remating subsequently with a different partner, females have the possibility to increase offspring fitness and the genetic diversity of their progeny (Davies et al. 2012). Similar to polygynous mating systems, males in polygynandrous mating systems tend to not invest in parental care; however, male mating tactics in these systems may vary over a male's lifetime (Silk et al. 2020). Male mating tactics to control paternity and increase fitness are well understood in polygynandrous mating systems and include mate-guarding, male-male competition, and sperm competition, as seen in polygynandrous passerines (Briskie 1993). However, mechanisms of cryptic female choice to control paternity are less well understood. Overall, polygynandry can lead to increased care of young and decreased infanticide by males, as their own genetic progeny might be present.

Polygynandry is likely the most common mating system among cetaceans (Tables 1.1 and 1.2). As direct observations of mating are uncommon, large relative testes size is often used to infer a polygynandrous mating system due to the correlation with increased sperm competition (Kelley et al. 2014). Right whales (*Eubalaena* spp.) are presumed to be polygynandrous due to their very large testes size, weighing one metric ton (Brownell Jr and Ralls 1986; Burnell 2001). Other mysticetes such as gray whales (*Eschrichtius robustus*) and bowhead whales (*Balaena mysticetus*) are also hypothesized to have polygynandrous mating systems due to their large relative testes sizes and low aggressive behavior among males (Brownell Jr and Ralls 1986). However, it is difficult to determine whether these mysticete species are polygynandrous or polyandrous due to limited data on female mating patterns (Ralls and Mesnick 2019a). Among odontocetes, polygynandry has been proposed particularly among the Delphinidae family (oceanic dolphins; Caspar and Begall 2022). For example, dusky dolphins, killer whales, long-finned pilot whales (*Globicephala melas*), and harbor porpoises (*Phocoena phocoena*) all have proposed polygynandrous mating systems due to their large relative testes sizes



**Table 1.1** Mating tactics of male odontocetes and potential fitness costs to both sexes (table from Orbach (2019), with permission)

Male mating tactic	Potential costs for males	Potential costs for females	Examples	Species	References
Display competition	<ul style="list-style-type: none"> <li>Increased conspicuousness to predators</li> <li>Time/energy not spent foraging or detecting predators</li> </ul>	<ul style="list-style-type: none"> <li>Time/energy evaluating males</li> <li>“Dishonest” signals</li> <li>Lower offspring survival if inexperienced in evaluating males</li> </ul>	Object carrying and posturing	Humpback dolphins ( <i>Sousa sahulensis</i> )	Allen et al. (2017)
Contest competition	<ul style="list-style-type: none"> <li>High risk of injury</li> <li>Increased conspicuousness to predators</li> <li>Time/energy not spent foraging or detecting predators</li> </ul>	<ul style="list-style-type: none"> <li>Not directly choosing mate</li> <li>Risk of injury if male aggressive to female</li> </ul>	Weaponry—“battle teeth”	Some beaked whale (family: Ziphiidae)	McCann (1974), Heyning (1984), Pitman (2018)
Endurance competition	<ul style="list-style-type: none"> <li>Extensive temporal investment</li> <li>Lost mating opportunities with other females</li> <li>Reduced paternity in alliance</li> </ul>	<ul style="list-style-type: none"> <li>Prevented from mating with preferred mate</li> <li>Reduced socializing opportunity</li> <li>Risk of injury if coerced</li> </ul>	Mate-guarding/consortships	Indo-Pacific bottlenose dolphins ( <i>Tursiops aduncus</i> )	Connor et al. (1996)
Scramble competition	<ul style="list-style-type: none"> <li>Extensive energetic expenditure on challenging chases</li> <li>Conditional on competitive sperm</li> </ul>	<ul style="list-style-type: none"> <li>Time/energy actively evaluating male and avoiding rejected males</li> </ul>	Maneuverability during mating chases	Dusky dolphins ( <i>Lagenorhynchus obscurus</i> )	Markowitz et al. (2010), Orbach et al. (2014)
Sperm competition	<ul style="list-style-type: none"> <li>Tissue costly to maintain</li> <li>Conditional on male copulation success</li> </ul>	<ul style="list-style-type: none"> <li>Limited choice of copulation partners</li> </ul>	Strong seasonal testes mass and cellular activity patterns	Short-beaked common dolphins ( <i>Delphinus delphis</i> )	Murphy et al. (2005)

**Table 1.2** Mating tactics of female odontocetes (table from Orbach (2019), with permission)

Female mating tactic	Example/evidence	Species	References
Signal discrimination	Extended mating chases led by females that may be used to evaluate male maneuverability	Dusky dolphin ( <i>Lagenorhynchus obscurus</i> )	Markowitz et al. (2010)
Mate choice copying	Suggested by patterns of paternal relatedness within matrilineal groups	Sperm whale ( <i>Physeter macrocephalus</i> )	Richard et al. (1996)
Evasive behaviors	Females fled from pursuant males, moved to shallow waters where males could not fit beneath them, rolled ventrum-up, and raised flukes in the air so their genital groove was inaccessible	Dusky dolphin ( <i>Lagenorhynchus obscurus</i> )	Orbach et al. (2015)
Polyestry/multiple matings	Hypothesized mechanism to improve fertility, reduce sexual harassment costs, and obscure paternity	Indo-Pacific bottlenose dolphin ( <i>Tursiops aduncus</i> )	Connor et al. (1996)
Modified genitalia	Complex vaginal folds that occlude penetration of the penis	Harbor porpoise ( <i>Phocoena phocoena</i> )	Orbach et al. (2017)

(Ralls and Mesnick 2019a). Dusky dolphins have a multi-mate system in which males compete and chase females to successfully copulate, a classic example of scramble competition (Orbach et al. 2015). For many cetacean species, particularly among odontocetes, behavioral and anatomical indicators support a polygynandrous mating system.

### 1.2.5 Mating Systems as a Continuum

Although polygamous mating systems are often described as discrete categories (polygynous, polyandrous, or polygynandrous), they are best viewed as a gradient with animals within a population falling along the continuum. Spinner dolphins can be used as a model cetacean species to highlight how mating systems are not defined by phylogenies, but vary according to ecological and social constraints. Although the spinner dolphin is closely related to many polygynandrous species, some populations of spinner dolphins have been hypothesized to have more polygynous than polygynandrous mating systems. Anatomical evidence in support of divergent mating systems includes differences in testes weights. Testes weights are higher among males in the whitebelly spinner dolphin population (an intermediate physical form between eastern and Gray's spinner dolphin (*Stenella longirostris orientalis* and *S. l. longirostris*, respectively, Fig. 1.1g#1 and g#2) than in the eastern spinner dolphin population, indicating a polygynandrous mating system in the whitebelly

spinner dolphin (Perrin and Mesnick 2003). Recent work that examined the genetics of mating system variation among spinner dolphins found single nucleotide polymorphisms in genes which appear to be associated with social behavior, providing further evidence for selection among spinner dolphin ecotypes for different mating systems (Andrews et al. 2021). The costs and benefits of group living vary with ecological conditions and have led to the evolution of different mating strategies and social structures among cetacean species and populations (Acevedo-Gutiérrez 2018). Many species hedge their bets and blur among mating system categories by utilizing a combination of tactics.

Mating systems in cetaceans pose a unique challenge to researchers due to limited opportunistic observations. Consequently, mating systems have not yet been described for many cetacean species, but most cetacean mating systems are hypothesized to be polygynandrous or polygynous (Wells et al. 1999). As resources in the ocean are constantly moving, territoriality is unlikely in cetaceans; thus, females are widely distributed and can seldomly be monopolized by a single male. Additionally, female cetaceans have long interbirth intervals compared to many terrestrial mammals (Whitehead and Mann 2000; Lukas and Clutton-Brock 2012). Gestation is typically 11 months and is timed such that offspring are born during seasons of warm water when thermoregulation demands are reduced. Some cetacean species have even longer gestation periods, such as sperm whales (16 months; Ohsumi 1965) and killer whales (17 months; Duffield et al. 1995). Lactation is brief among baleen whales and often consists of 6 months of nourishing the offspring with very fat-rich milk (up to 40% fat) to facilitate rapid offspring growth, with weaning timed to correspond with seasonal migrations to foraging grounds (Lockyer 1984). In contrast, lactation is prolonged and of comparatively lower fat content among toothed whales, lasting on average 1.5 years and up to 7 years (Reynolds III and Rommel 1999). The lengthy lactation period among odontocetes allows for extensive social bonding between mother and calf and the development of advanced foraging tactics to capture prey and ensures social learning to support offspring survival (Brodie 1969; Tyack 1986). Interbirth intervals in cetaceans range from 1 year, such as in the harbor porpoise, to over 6 years in the short-finned pilot whale (*Globicephala macrorhynchus*; Taylor et al. 2007). Thus, female cetaceans are under strong selection pressures to invest in calf rearing, including ensuring safety and obtaining food. Female cetaceans generally minimize their temporal and energetic expenditures in seeking out mates. Male cetaceans, in contrast, do not incur limitations imposed by parental care and can invest time and energy in searching for receptive mates. However, males face constraints in their abilities to locate, guard, and compete for females, which have led over evolutionary time to many diverse mating strategies and tactics within and among cetaceans.

### 1.3 Sexual Selection

Sexual selection theory has traditionally posited that the evolution of diverse mating strategies at the species and population levels is driven by the selective forces of mate competition (intrasexual competition) and mate selection (epigamic selection; Darwin 1871). A recent proliferation of theoretical and empirical research has expanded the sexual selection framework to recognize an additional significant evolutionary force, sexual conflict, in which the increasing fitness of one sex produces a fitness cost for the other sex (Arnqvist and Rowe 2005). The sexual selective forces of mate competition, mate choice, and sexual conflict are each driven by direct or indirect mechanisms, which are not mutually exclusive.

Direct mechanisms increase or decrease the fitness (survival and reproductive success) of the choosy sex through direct material advantages or disadvantages. Direct benefits may include nuptial gifts, territories, food, defense (i.e., against predators or ardent males), or parental investment. For example, female hangingflies (*Hylobittacus apicalis*) mated for longer with males that provided large insects for her to eat during copulation than those who did not; she is hypothesized to convert this food into nutrients for her offspring (Thornhill 1976). Direct costs involved in sexual selection may include increased risk of predation, expenditure of energy and time, exposure to parasites, sexually transmitted diseases, injury, or death (Jennions and Petrie 2000).

In contrast to direct benefits, indirect mechanisms increase or decrease the genetic fitness of the offspring without providing the choosy sex with material gains or losses. The benefits provided by indirect mechanisms are hypothesized to evolve by two models: (1) Fisher's (1958) "runaway" selection/"sexy sons" model and (2) Zahavi's (1975) "handicap"/"good genes" model. Fisher's (1958) "runaway" model proposes that courtiers possess genetically based traits and choosers possess covarying genetically based preferences for these traits that result in a positive feedback loop. Choosers continue selecting courtiers with exaggerated traits to produce "sexy sons" capable of attracting mates (through their inheritable exaggerated phenotype) to pass their genes on to future generations. In contrast, Zahavi's model (1975) proposes that choosers prefer courtiers with "good genes" that increase the bearer's fitness and increase their offspring's survival and reproduction. The elaborate courtier traits are "handicaps" to their bearer, and the bearer's ability to survive despite the costly trait provides honest evidence of their overall genetic quality. The "sexy sons" hypothesis differs from the "good genes" hypothesis in that "sexy sons" inherit genes purely for attracting mates, whereas "good gene" offspring inherit genes for utilitarian aspects of survival and reproduction.

Two other mechanisms have been hypothesized to drive sexual competition: antagonistic coevolution and sensory bias models. In the antagonistic coevolution or "chase away" model, courtiers and choosers coevolve traits in an evolutionary "arms race" to maintain control of paternity (Holland and Rice 1998). Thus, choosers may not evolve a preference for a courtier's traits, but rather evolve resistance to less elaborate courtier traits (e.g., cetacean genitalia; Orbach et al.

2023, this book). In the sensory bias model, courters capitalize on a chooser's preferences through sensory exploitation, sometimes even before the preferred trait has evolved. The choosy sex typically acquires the trait in a non-mating context, and the chooser has a pre-existing bias before the courter exploits it to increase reproductive success. The courter's signal falls within the chooser's sensory sensitivity such that signals evoke a response and are selected for by reducing costs to the courter (i.e., searching for a mate; Basolo 1990).

Sexual conflict theory highlights conflicting dynamics between the sexes in reproductive encounters in addition to coevolving adaptations and counter-adaptations hypothesized to reduce costs. Sexual conflict can consist of distinct or manifest behavioral, physiological, or anatomical mechanisms that have been hypothesized to increase the fitness of one sex at a fitness cost to the opposite sex (Tregenza et al. 2006). Most research on sexual conflict theory uses insect models (e.g., Eberhard 1985). Theoretical principles and predictions from these models may be limited in their applicability to large-brained, highly social mammals, which experience different ecological constraints and may invest more in parental care than insects (Stumpf et al. 2011). Cetacean genitalia provide a clear example of sexual conflict. Female cetaceans are unique in possessing vaginal folds, protrusions of the vaginal wall into the vaginal lumen. Vaginal folds appear to physically occlude the penis during copulation (Orbach et al. 2017) and may provide females with a mechanism to control paternity by angling her body during copulation to prevent deep penetration of the penis and ejaculation near her ovaries (Orbach et al. 2020). Among harbor porpoises, male sexual behavior has coevolved with the reproductive anatomy of both sexes, and males only approach females on her left-hand side, which appears to bypass the vaginal fold labyrinth (Keener et al. 2018; Orbach et al. 2020; Webber et al. 2023, this book). The evolutionary steps of genital morphology and mating behavior adaptations remain unclear, although the evidence is clear for an evolutionary "arms race" and a possible mating tactic to control paternity during or post-copulation (Tregenza et al. 2006).

## 1.4 Mating Strategies and Tactics

Mating strategies are fixed, conditional, or mixed genetically based mechanisms that are hypothesized to increase reproductive success under certain social and ecological conditions. Mating strategies are essential to find mates and engage in copulations and can include pre-, during-, and post-copulatory mechanisms. Mating strategy evolution is influenced by multiple factors including the distribution of resources, predation pressures, and costs and benefits of group living (Ralls and Mesnick 2019a). Unlike for mammals in many terrestrial ecosystems (Clutton-Brock 2016), territories are not defended by cetaceans in the ocean (Ballance 2018), and males employ mating strategies that are hypothesized to monopolize fertilizations despite potential costs to females. Most male odontocetes use similar strategies to search for receptive females and spend little time with them other than to mate (Connor et al.

2000a; Boness et al. 2002), although there are exceptions (e.g., mate-guarding tactic, Tables 1.1 and 1.2). Intraspecific sexual selection forces are generally strong among cetaceans (Ralls and Mesnick 2019a) and have resulted in the evolution of sexually selected traits among some cetacean species (Loch et al. 2023, this book). Much previous research on cetacean mating strategies has presented males as the actively competing sex and females as the passive choosing sex (Connor et al. 2000b). However, females may have a much more active role than previously considered (e.g., Orbach et al. 2015).

The mechanism underlying female sexual motivation is an understudied area that warrants further research, including the concept that both sexes have a “libido” (sexual drive). Much of the current knowledge of female sexual motivation comes from studies on rats (*Rattus* spp.), which have shown that female sexual motivation is impacted by experience, mate preference, and hormonal control (Guarraci and Frohardt 2019). Research into female sexual motivation in mammals has been limited to small mammals and humans. Current research on sexual motivation in large non-human mammals, such as cetaceans, remains primarily focused on males. The lack of female perspectives on sexual motivation research can be attributed in part to the historical gender bias within reproductive research (Ogden 2021). In recent years, an increasing number of investigators have broadened the field of reproductive research to include a stronger focus on females’ roles in reproduction, and their work has illuminated previously unknown female roles in sexual selection (Orbach 2022). However, further expansion of female perspectives within the field is needed to fully understand the underlying evolutionary and coevolutionary mechanisms of sexual reproduction of both sexes.

While mating strategies have an underlying genetic framework, mating tactics are the phenotypic or behavioral manifestation of the strategy. As sexual maturity and social maturity are not ubiquitous, it can take some males prolonged periods to obtain mating opportunities, resulting in an adoption of alternative mating tactics. Non-mutually exclusive female and male mating tactics have recently been reviewed among cetaceans (Tables 1.1 and 1.2; Orbach 2019). Additional mating tactics observed among marine mammals but not documented among cetaceans include site-guarding, group-guarding, and leks. Site-guarding can occur when females range more widely than the males’ capabilities of sequestering them. A site, or territory, is established by a male through which females roam in search of food and safety. Males do not attempt to herd particular females into that established territory, but instead attempt copulations as females pass through. Sea otters exhibit resource defense polygyny through site-guarding territories and engaging in aggressive copulations with females who enter the territories (Pearson and Davis 2021). Group- or “harem”-guarding occurs when males defend an area occupied by a collection of females for short (seasonal) or long (interseasonal) times. Males actively herd females who attempt to leave the area. Group-guarding is common among some seals and has been described particularly well for northern elephant seals (*Mirounga angustirostris*; Le Boeuf and Reiter 1988). Leks occur when males display and females observe, mating with the male that appears most attractive to them. Leks appear to occur in several pinnipeds such as the New Zealand sea lion

(*Phocarcos hookeri*), California sea lion (*Zalophus californianus*), and some populations of harbor seals (*Phoca vitulina*; Campagna 2018). A type of “floating lek” has also been proposed for Amazon river dolphins or boto (*Inia geoffrensis*; Martin et al. 2008) and humpback whales (Clapham 1996).

The mating tactics of cetaceans are in some cases inherently different from other species, regardless of mating system, because of the constraints of living in the ocean. Females distribute themselves relative to resources essential for foraging opportunities and protection from predators. Resources can be thin and spread over thousands of kilometers in the open ocean, leading to wide female distributions. Subsequently, males are unable to monopolize multiple females simultaneously. Unlike the terrestrial environment, there are few hiding places in the ocean for cetaceans to evade predators or ardent male suitors. Yet cetaceans live in a three-dimensional landscape where costs of locomotion are low, and they can dive to depth or move to shallow waters as a potential escape mechanism. For example, when exposed to killer whale vocalizations, humpback whales exhibit behavioral changes including increased dive times and moving away from the “predator” sound (Curé et al. 2015). While elaborate vocalizations occur on the mating grounds of large baleen whales (Clark and Garland 2022), mating-related sounds/songs are dangerous for small cetaceans in many habitats as they could attract their main predator, killer whales. Because of natural selection pressures associated with aquatic living, cetaceans are also constrained in their development of secondary sexual characteristics to attract a mate. For example, the sleek body design of cetaceans reduces hydrodynamic drag forces, and their low surface-area-to-volume ratio is critical in thermoregulation (Ralls and Mesnick 2019b). Protrusive secondary sexual characteristics, like the elaborate tail feathers of male peafowl (genus *Pavo* and *Afropavo*), would prevent streamlined swimming. Nevertheless, the exaggerated large dorsal fin and pectoral flippers in male killer whales (Wright et al. 2023, this book), large dorsal fin of male spectacled porpoises (*Phocoena dioptrica*, Fig. 1.1), and erupted large tooth of male narwhals (*Monodon monoceros*, Fig. 1.1) indicate that there is female choice of males relative to their (apparently disadvantageous) body morphology (Zahavi 1975, 1993).

## 1.5 Alloparental Care

Alloparental care is a form of cooperation that occurs when an individual performs a behavior that (1) benefits a calf of which it is not the parent, (2) benefits the calf and its mother, and (3) would not be performed if the calf were not present and is therefore costly to the actor (Riedman 1982; Mann and Smuts 1998). The highly social behaviors comprising alloparental care have been reported in a variety of odontocetes, terrestrial mammals (e.g., primates (*Cebus olivaceus*, O’Brien and Robinson 1991; *Cebus nigrinus*, Baldovino and Di Bitetti 2008), buffalo (*Bubalus bubalis*, Murphey et al. 1995), guanacos (*Lama guanicoe*, Zapata et al. 2010), bats (*Pipistrellus pipistrellus*, de Fanis and Jones 1996; *Pteropus rodricensis*, Kunz et al.



1994), fishes (Wisenden 1999), and birds (Riedman 1982)). Alloparental care appears to have evolved convergently across several mammalian taxa, potentially as an adaptation to counter predation pressure or high energetic demands on mothers while rearing offspring.

In some terrestrial birds and mammals, young males (and at times females) may help females partnered with other males to rear neonates, which may seem purely altruistic, but has functions (Trivers 1985). If cooperative neonate rearing occurs in systems where the male helpers have reasonably assured mating opportunities outside their own immediate group, they may stay and help due to being related in some degree to the young they assist. Such kin-selected altruism functions to support the prevalence of ones' genes in the population. Additionally, by staying within the safety of their group, male helpers may survive to perhaps mate within or outside of the group as they further mature. There is limited evidence for males helping to rear young among cetacean species. Resident killer whales of both sexes do not disperse from their natal groups (Baird 2000), and the genetic strategy to treat all young as relatives could increase inclusive fitness in a closed population (e.g., Wright et al. 2023, this book). Male humpback whales "escort" females, both with and without calves. Male humpback whales likely do not offer parental care, and the "escorting" behavior probably serves as mate-guarding of females with whom they have recently mated or with whom they are attempting to mate. While this "escorting" behavior has clear benefits for the males, female humpback whales may benefit from the presence of male "escorts" through reduced risk of predation or harassment from other males (Ransome et al. 2021).

Females may also aid in the care of offspring that are not their own. For example, a sperm whale may guard a calf that is not her offspring from predators, while its mother is foraging on a deep dive (Whitehead 1996; Eguiguren et al. 2023, this book). The kin selection hypothesis for the evolution of social allomaternal care particularly applies to cetaceans that live with relatives in closed matrilineal social groups (Konrad et al. 2019). Allomaternal care is widespread among odontocetes in captivity and in the wild and has been reported in beluga whales (Aubin et al. 2022), bottlenose dolphins, sperm whales, spinner dolphins, killer whales, harbor porpoises, pilot whales, and bottlenose whales (*Hyperoodon ampullatus*; reviewed in Whitehead and Mann 2000). Additional evidence of a female Indian Ocean humpback dolphin (*Sousa plumbea*) providing alloparental care for an Indo-Pacific bottlenose dolphin calf and a common dolphin calf indicates that allomaternal care can be interspecific (Conry et al. 2022).

One form of allomaternal care is allonursing, in which an individual lactates to feed a non-offspring. Although allonursing poses potential costs such as disease transfer and high maternal energetic output (reviewed by Mota-Rojas et al. 2021), allonursing has evolved across multiple taxa in situations where such associated costs are low (reviewed by MacLeod and Lukas 2014). Allonursing has been reported in free-ranging sperm whales (Gordon 1987), captive beluga whales (Leung et al. 2010), and captive bottlenose dolphins (Dudzinski et al. 2022). Evidence of allonursing in sperm whales comes from direct observations of two non-twin calves nursing simultaneously from one female (Gordon 1987), one calf

suckling from different adults (Gordon 1987), and more lactating females than calves found in groups (Best et al. 1984). Older females typically perform the allonursing, and corresponding energetic demands appear to decrease with age (Ekvall 1998). Allonursing can increase nutrient transfer to offspring or alleviate parental care responsibilities such that kin can allocate resources to future offspring. Oblique cultural transmission of communication and navigation skills could potentially be taught to calves during allonursing and sustained interactions (Best et al. 1984). Allomaternal care has been hypothesized as a critical parameter that led to the evolution of sex- and age-class segregation and polygynous mating systems in sperm whales (Gero et al. 2013). Variation in diving capabilities of mothers and calves, combined with high predation pressure on calves, selected for allomaternal care social systems to protect calves while mothers foraged. This biased the operational sex ratio and led to segregations in social schooling by age and sex such that large roving males have an unequal share of matings in a polygynous mating system. While allonursing has not been reported in mysticetes, allonursing has been reported in African elephants (*Loxodonta* spp.; Lee 1989), which share several life history parameters with sperm whales (Weilgart et al. 1996), in African lions (*Panthera leo*), and in other terrestrial species (Karniski 2019).

## 1.6 Reproductive Senescence

Reproductive senescence, when a female continues to live for a prolonged period after she is capable of conceiving and delivering, occurs in mammals, birds, fishes, and invertebrates. However, this phenomenon remains rare. In cetaceans, reproductive senescence has been reported in resident killer whales and short-finned pilot whales (Marsh and Kasuya 1986, overall review by Croft et al. 2015). Lengthy post-reproductive lifespans in beluga whales (*Delphinapterus leucas*) and narwhals suggest that reproductive senescence has evolved independently in multiple odontocete species (Ellis et al. 2018). It is hypothesized that reproductive senescence in cetaceans, particularly those with matrilineal societies, could facilitate cross-generation learning and culture (Whitehead 2015). For example, killer whales exist in matrilineal societies within which the reproductively inactive females (mothers and grandmothers) play an important role in cultural transmission of ecological knowledge that may promote the survival and fitness of their offspring (Brent et al. 2015). Recently, reproductive senescence has been subcategorized as fertility senescence (reproductive physiology aging) and maternal-effect senescence (declining capabilities with age to provision and rear offspring), and Karniski et al. (2018) showed both effects in their long-term study of Indo-Pacific bottlenose dolphins.

## 1.7 Homosexuality

There is much evidence of animal homosexual (same-sex) behavioral interactions. Homosexual pairings may help the young better survive than with heterosexual pairings, as with male black swans (*Cygnus atratus*; Braithwaite 1981), as aggressive males are adept at keeping large territories around their communal nest. Homosexuality also often grades into bisexuality with some same-sex and some opposite-sex behaviors, including tight social unions related at times to age/development of one or both partners. In contrast, several species of sheep (*Ovis* spp.) have a high prevalence of pure homosexuality with the same greeting and courting actions as in heterosexual sheep (Poiani 2010). Apparent homosexual behavior in the form of beak to genital nudging was described for spinner dolphins (Norris and Dohl 1980) and common bottlenose dolphins (Wells et al. 1987). Male common bottlenose dolphins were observed mounting male Atlantic spotted dolphins; however, male spotted dolphins were not observed mounting male common bottlenose dolphins in mixed-species groups (Herzing and Elliser 2013). Additional field studies of homosexual behavior among Indo-Pacific bottlenose dolphins have noted higher levels and longer duration of socio-sexual behavior among male-male pairs of dolphins than among male-female and female-female pairs (Mann 2006). Homosexual behaviors have also been reported among sexually mature bowhead whales (Würsig and Clark 1993) and among sexually mature and immature southern right whales (*Eubalaena australis*; Sironi 2004). More examples of homosexual behaviors among cetaceans are reviewed by Ham et al. (2023, this book).

Homosexual behavior can have variable functions in animals, with interpretations often clouded by human sentiment. Common themes of the function of homosexual mating are to relieve boredom, practice sex, achieve social dominance, play, promote social bonding, and increase the availability of sexual partners (Bagemihl 1999). What has not been adequately explored is that sex may be pleasurable in animals. It was recently shown that the clitoris of female common bottlenose dolphins is highly innervated, suggesting sexual experiences are pleasurable for female dolphins (Brennan et al. 2022). Such information is likely to lead to more advanced understanding of hetero-, homo-, and bisexuality across the animal kingdom.

## 1.8 Summary and Future Directions

This chapter provides a basic review of the evolutionary costs and benefits of sexual reproduction, mating systems, sexual selection, mating strategies and tactics, and several socio-sexual behaviors. Within cetaceans, most species whose mating systems are known are polygynous or polygynandrous. The majority of cetaceans do not have strong sexual dimorphism (pronounced differences in female and male external morphology), although there are exceptions (Ralls and Mesnick 2019a, b).

Mating tactics and strategies can vary within species and among populations according to social and ecological drivers. The evolution of reproductive systems and behaviors in cetaceans is likely driven by traditional models of sexual selection and emerging theories including sexual conflict. Several socio-sexual behaviors have been well-described across cetacean species, including alloparental care, allonursing, and homosexuality. Additional physical sexual associations not explored in detail here include autoeroticism (masturbation), oral and anal sex, potential sex stimulation in odontocetes by sound, interspecies sex (which can be procreative), sex with non-reproductive infants and juveniles, and necrocoitus. Intriguing reports such as sexual stimulation by bubbles need to be further investigated as they indicate potential cooperation in eroticism between females and males and potentially among members of the same sex (Jones et al. 2022). A general review of some of the above behaviors is provided by Balcombe (2006) and Bowyer (2022). Our chapter does not investigate steroid sex hormonal functions, such as the roles of testosterone, estrogens, and androgens (Sapolsky 1997; Ketterson and Nolan Jr 1999). Areas of future research include alternative approaches to explore mating strategies, particularly in deep-diving or pelagic cetacean species, investigation of potential mechanisms of cryptic female choice, and long-term studies of specific cetacean populations to explore the relationship between sexual and social behaviors. Exploration of these areas will further current understanding of sexual reproduction in cetaceans and open potential avenues for comparisons across taxa.

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