Chapter 6
Interspecific Comparison of Reproductive Strategies

Susan J. Chivers and Kerri Danil

Abstract Knowledge of cetacean life history, morphology, and social behavior provides clues to the niche-specific adaptations that have evolved to maximize reproductive fitness. An essential component of a species' life history is mating, particularly the sex-specific mating strategies that have evolved. Mating strategies vary within and among species reflecting phylogenetic constraints and the interplay of selective forces molding each species' adaptations. The suite of cetacean mating strategies that have evolved ultimately determines how a species' mating system operates. Thus, mating systems provide a unifying framework to compare and contrast cetacean strategies for reproduction and mating. Theory predicts that the degree of sexual size dimorphism (SSD) and the relative testes size of mammalian species will be good indicators of their mating system. However, interspecific and intraspecific variability in SSD and relative testes size reveal unique tradeoffs made in response to evolutionary pressures and ecological processes that result in exceptions to the theoretical predictions. In this chapter, we review current knowledge of cetacean reproductive biology and how that information furthers our understanding of their mating systems.

Keywords Behavior · Cetaceans · Growth · Mating strategies · Mating systems · Mysticetes · Odontocetes · Reproduction · Sexual dimorphism · Testis size

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6.1 Introduction

Mammalian mating systems have long interested scientists seeking to understand how species maximize reproductive fitness, and those of cetaceans are no exception. Mating systems describe the mating dynamics between the sexes, often in terms of the number of mates. Operationally, a suite of mating strategies has evolved to control the number of mates while maximizing an individual's reproductive fitness. The evolutionary constraint of internal gestation and subsequent lactation among mammals means that the parental investment by females is greater than that of males. This inherent disparity in contributing to the production of offspring means that the evolutionary pressures on females and males differ, with females maximizing reproductive fitness by ensuring survival of offspring, while males seek multiple mates. Thus, all mammals are predisposed to polygamous mating systems (Trivers 1972; Clutton-Brock et al. 1989; Clutton-Brock and Parker 1992).

Cetacean mating systems, like those of other mammals, are expected to be polygamous with multiple partners among reproductive individuals. The two cetacean suborders, the baleen (mysticetes) and toothed whales (odontocetes), are predicted to be predominantly polygynous, a form of polygamy in which individual males mate with multiple females. Additionally, the polygamous systems of polyandry in which individual females mate with multiple males, and of polygynandry (multi-male multi-female) in which both females and males have multiple mates, are predicted to play a role. Observations consistent with these predictions suggest that all three mating systems occur in cetaceans (Mesnick and Ralls 2018a; Gerber and Krützen 2023, this book; Würsig et al. 2023, this book).

Mating systems provide a framework for discussing sex-specific mating strategies, because they represent the synthesis of evolutionary pressures on a species' life history characteristics, including attributes of their reproduction (e.g., interbirth interval, age at attainment of sexual maturity (ASM) and longevity), morphology (e.g., body size and shape), and behavior (e.g., group dynamics, mating) that maximize reproductive fitness (Fig. 6.1). Most of what we know about cetacean reproduction and morphology has come from cross-sectional studies using biological material collected from dead animals sampled from direct or indirect takes or found stranded on beaches (e.g., Lockyer 1984; Perrin and Reilly 1984). However, longitudinal studies have provided unique and valuable insights about the sociobiology of species, including the life history and social strategies associated with mating and reproduction (Mann and Karniski 2017; Trillmich and Cantor 2018). The multi-decadal longitudinal studies of the bottlenose dolphin (*Tursiops* spp.; Connor et al. 2000b; Wells 2019), humpback whale (*Megaptera novaeangliae*) (Cartwright et al. 2019), killer whale (*Orcinus orca*) (Baird 2000; Ford 2019), and sperm whale (*Physeter macrocephalus*; Whitehead and Weilgart 2000; Cantor et al. 2019) together with the longer, but not multi-decade, studies of the dusky dolphin (*Lagenorhynchus obscurus*; Würsig and Würsig 2010) and Hawaiian (or gray's) spinner dolphin (*Stenella longirostris longirostris*; Norris et al. 1994; Lammers 2019) have contributed greatly to understanding the complexities of cetacean social

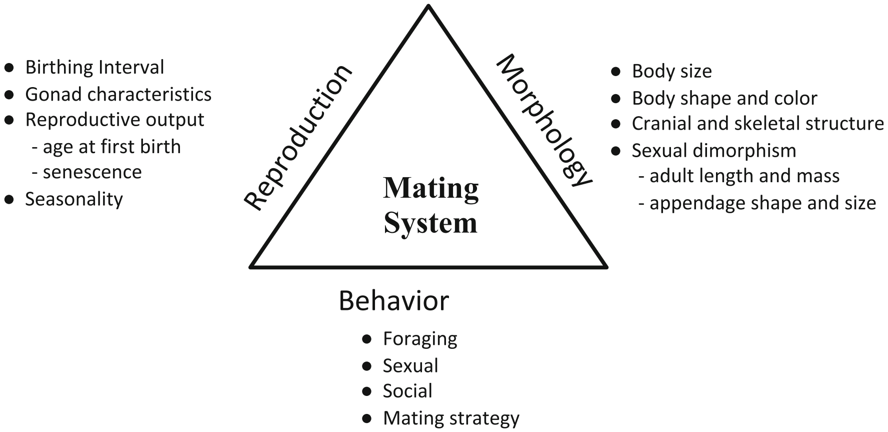

Fig. 6.1 Comparing and contrasting attributes of cetacean reproduction, morphology, and behavior provide insight about their mating systems and the role of sexual selection in the evolutionary process forming species-specific adaptations

systems and the variability in lifetime reproductive output among individuals. This is knowledge that cannot be obtained from cross-sectional studies and is particularly valuable to interpreting life history characteristics, especially parameter estimates, that differ between cross-sectional and longitudinal studies (Mann and Karniski 2017).

In this chapter, we present an overview of cetacean life history characteristics focusing on the reproductive and morphological characters associated with mating. We use the term mating strategies to refer to mate selection within a mating system, which is defined by the number of mates per individual. This terminology is consistent with the published literature, which also uses the term “reproductive strategies” in this context (e.g., Connor et al. 2000a; Whitehead and Mann 2000; Boness et al. 2002). We consider the term mating strategies to be a general term that encompasses the tactics, or operational mechanisms of mating, about which we know little for most cetacean species. We focus on providing as broad a comparison of species as possible to complement the other chapters in this book presenting updated information about the sexual strategies of bottlenose dolphin, Risso’s dolphin (*Grampus griseus*), killer whale, sperm whale, gray whale (*Eschrichtius robustus*), bowhead whale (*Balaena mysticetus*), and right whale (*Eubalaena* spp.). As our knowledge of cetacean mating strategies improves, so too will our understanding of their mating systems. The inherent difficulties of studying most cetacean species means that reviewing what we know about mating will facilitate revising proxies to infer the mating strategies of the least known and most difficult-to-study species and identifying the knowledge gaps limiting our understanding of their mating systems and the evolutionary forces molding them.

6.2 Reproduction

All cetaceans are large and long-lived mammals. Females produce few offspring during their reproductive years and bear the energetic costs of gestation and lactation to rear calves with little or no contribution from males. Studies of cetacean reproductive biology have primarily focused on females to facilitate the development of conservation and management plans, because females are the limiting sex and define the inherently low population growth rates of all species. Consequently, less is known about male life history strategies. However, biological studies of male reproduction have contributed to understanding some of the variability in cetacean mating systems.

6.2.1 Females

The morphology and histology of cetacean ovaries and reproductive tracts have been quite well studied for a number of toothed and baleen whale species. Much early research focused on understanding the female reproductive system, which contributed to later studies of cetacean life history strategies (e.g., Harrison et al. 1969, 1972; Slijper 1979; Lockyer 1984; Perrin and Reilly 1984). The maturation and ovulation processes of female cetaceans, including delayed sexual maturity, are similar to those of other large, long-lived mammals. In cross-sectional studies, sexually mature female cetaceans are typically identified by the presence of a fetus or milk in the mammary glands or by detecting evidence of an ovulation. The latter is indicated by the presence of a corpus luteum (CL) or corpus albicans (CA) on the ovary (Fig. 6.2). The CL is an endocrine gland that forms to produce the hormones necessary to maintain pregnancy and degenerates to a CA after an infertile ovulation

Fig. 6.2 Stages of delphinid ovary development from immature (left) to mature (center) and to mature and pregnant (right). The mature ovary (center) shows multiple corpora albicantia, which are the scars of regressed corpora lutea that remain after ovulation and pregnancy. The mature and pregnant ovary (right) shows the corpus luteum (smooth round structure on top of the ovary) that forms when ovulation occurs and remains throughout pregnancy (Credit: M. Lynn, NOAA, NMFS, Southwest Fisheries Science Center, La Jolla, CA)

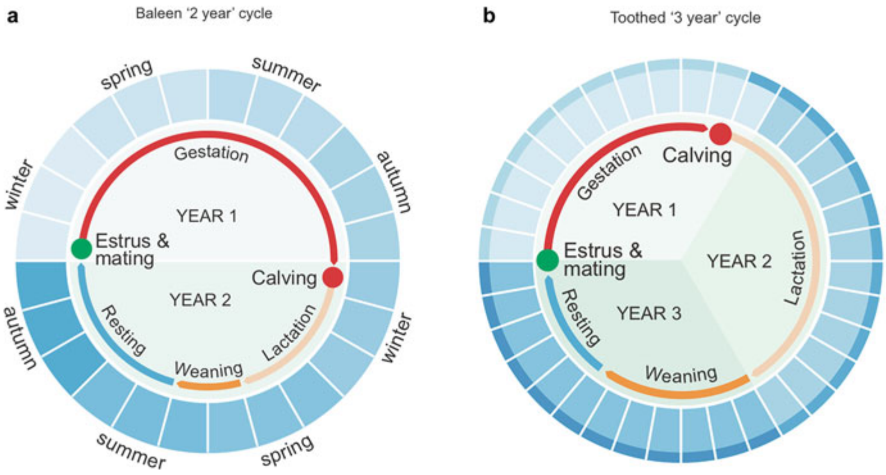

Fig. 6.3 The reproductive cycle of (**a**) baleen whales is typically 2 years and is correlated with their annual migration between winter breeding and summer feeding grounds, while that of (**b**) toothed whales is a minimum of 3 years in most species with the lactation period lasting 2 or more years in some species (Credit: Reproduced from Berta (2015) with permission from Ivy Press, UK)

or following birth if pregnancy occurs. CAs are thought to persist indefinitely in cetaceans and provide a record of past ovulations (Perrin and Donovan 1984), but there is some evidence that they do not persist and that CAs resulting from ovulation and pregnancy have different characteristics (Takahashi et al. 2006; Dabin et al. 2008). Age-specific CA accumulation rates differ within species. The hypotheses for this pattern include underlying differences in pregnancy rates reflecting variability in the health of adult females, mating success, resource availability, or anthropogenic stressors (Perrin and Henderson 1984; Perrin and Mesnick 2003; Ferreira et al. 2014).

Cetaceans give birth to single, large and precocial young after a gestation period of approximately 1 year. The lengthy gestation in part balances the cost of producing a large neonate capable of swimming and diving with its mother when born. The reproductive cycle is typically 2 years in baleen whales and 3 years in many toothed whale species (Fig. 6.3). Baleen whale breeding and calving are more synchronous and less variable than those of toothed whales. Among toothed whales, the small delphinids tend to have fairly diffuse calving peaks that may include spring and fall peaks, while nearly all species have extended (i.e., >1 year) lactation periods (Perrin and Reilly 1984; Connor et al. 2000b; Whitehead and Mann 2000; Chivers et al. 2016; Chivers 2018).

Reproductive success varies throughout the life of large and long-lived mammals. The lower reproductive success associated with older age at attainment of sexual maturity is thought to be due in part to the physiological tradeoffs between reproduction and growth that occurs as individuals continue to grow to physical maturity after becoming sexually mature (Stearns 1977; Clutton-Brock 1984; Segura et al.

2021). Like other mammals, adult female cetaceans exhibit stage-specific changes in reproductive rates with evidence of lower reproductive success among newly mature females equated to fewer successfully weaned calves. This pattern has been documented in the well-studied common bottlenose dolphin (*Tursiops truncatus*) (Wells and Scott 1990) and in several baleen whales, including the fin whale (*Balaenoptera physalus*) (Lockyer 1987), North Atlantic right whale (*E. glacialis*), and southern right whale (*E. australis*) (Browning et al. 2010; Miller et al. 2011). Lower reproductive rates among older adult female common bottlenose dolphin have also been documented as longer interbirth intervals with an extended (i.e., 3- to 8-year) lactation period (Wells and Scott 1990). Similarly, ovulation rates, and thus presumably reproductive rates, have been found to be lower for older individuals in other delphinid species. These include the pantropical spotted dolphins (*Stenella attenuata attenuata*) and spinner (*S. longirostris*) dolphins, false killer whale (*Pseudorca crassidens*), and long- and short-finned pilot whales (*Globicephala melas* and *G. macrorhynchus*, respectively), in which post-reproductive females have been identified by atrophic ovaries (Perrin et al. 1976, 1977; Marsh and Kasuya 1984; Perrin and Reilly 1984; Martin and Rothery 1993; Photopoulou et al. 2017). Post-reproductive females have also been identified in Baird's beaked whale (*Berardius bairdii*), beluga whale (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), northern right whale dolphin (*Lissodelphis borealis*), and sperm whale, which suggests this trait has evolved independently several times within the toothed whales (Ellis et al. 2018). The percentage of post-reproductive, or senescent, females differs markedly among toothed whale species, but to date, there is no evidence of post-reproductive females in baleen whales. The adaptive significance of this life history characteristic is not yet understood. However, the hypothesis that post-reproductive females may increase the reproductive success of related individuals is supported by evidence that species with the greatest proportion of post-reproductive females are those with fairly complex and often matrilineal social structures. For example, post-reproductive females care for young that are not their own but may be those of related individuals in sperm whale, short-finned pilot whale, and killer whale populations (Christal et al. 1998; Whitehead 1998; Ottensmeyer and Whitehead 2003; Ward et al. 2009).

Annual variability in reproduction in cetaceans may be linked to resource availability influencing the body condition of females. Cross-sectional studies have provided data to link body condition and fertility (e.g., fin whales; Lockyer 1986), while longitudinal studies have provided valuable insight into how reproductive output varies among individuals and is influenced by environmental conditions. For example, annual monitoring of gray whale calf production since 1994 revealed a positive correlation between seasonal access to Arctic feeding grounds and calf production; more forage for pregnant adult females results in higher calf production. This linkage contributes to interpreting how Arctic ecosystem changes impact gray whales (Perryman et al. 2020; Moore et al. 2022). The influence of the environment on reproductive output is as important to understand for the conservation and management of cetacean species as are the selection pressures molding their life histories to maximize lifetime reproductive fitness.

6.2.2 Males

The life history characteristics of males are less well known than those of females. This largely reflects that knowledge of males is less critical to understanding cetacean population dynamics than that of females. However, male life history characteristics provide a more complete picture of a species' reproductive potential and insights about mating strategies.

Male reproductive tracts were also well studied early on in cetacean biology (e.g., Harrison et al. 1972; Slijper 1979) and found to be similar to those of other mammals. One obvious difference between terrestrial and aquatic mammals is that the reproductive organs of aquatic mammals are inside the abdominal cavity. This adaptation evolved with other traits associated with streamlining cetaceans for aquatic life. For example, the internalization of the male reproductive tract was accompanied by the evolution of a countercurrent heat exchanger to thermoregulate the testes to ensure spermatogenesis (Rommel et al. 1992, 2007).

Histological examination of the testis tissue has documented the sexual maturation process of cetaceans, which is typically mammalian (Perrin and Reilly 1984; Plön and Bernard 2007). Identifying sexually mature males from histological sections (Fig. 6.4) provides the ability to describe sexually mature males from proxies, including testis weight, total body length (TL), and age (e.g., Chivers et al. 1997). TL is often the most readily available information for cetaceans and correlates well with body mass and testes weight to provide a valuable proxy for identifying sexually mature individuals (for baleen whales, see Lockyer 1976; for toothed whales, see Perrin et al. 2005; for monodontids, see Kelley et al. 2014b). The ability to use proxies of male sexual maturity facilitates estimating age and TL at attainment of sexual maturity from larger data sets than might otherwise be available for cross-sectional life history studies (Lockyer 1984; Perrin and Reilly 1984).

6.3 Sexual Dimorphism

Sexual dimorphism refers to differences in external and internal features (e.g., TL, color patterns, cranial morphology) between the sexes. Sexually dimorphic traits are the result of evolutionary pressures acting differently on the sexes, with sexual selection playing a key role. For example, growth patterns differ between the sexes in most cetacean species, resulting in some degree of sexual dimorphism (Boness et al. 2002). Both sexes have high growth rates from birth through weaning that then become progressively slower until reaching full adult size. However, the sex that grows to be the largest typically sustains higher growth rates after weaning. In cetaceans, this is generally the male (Ralls and Mesnick 2009; Mesnick and Ralls 2018b).

Differential growth patterns result in males having an older ASM than females. The largest difference in ASM is in species with the greatest degree of male-biased

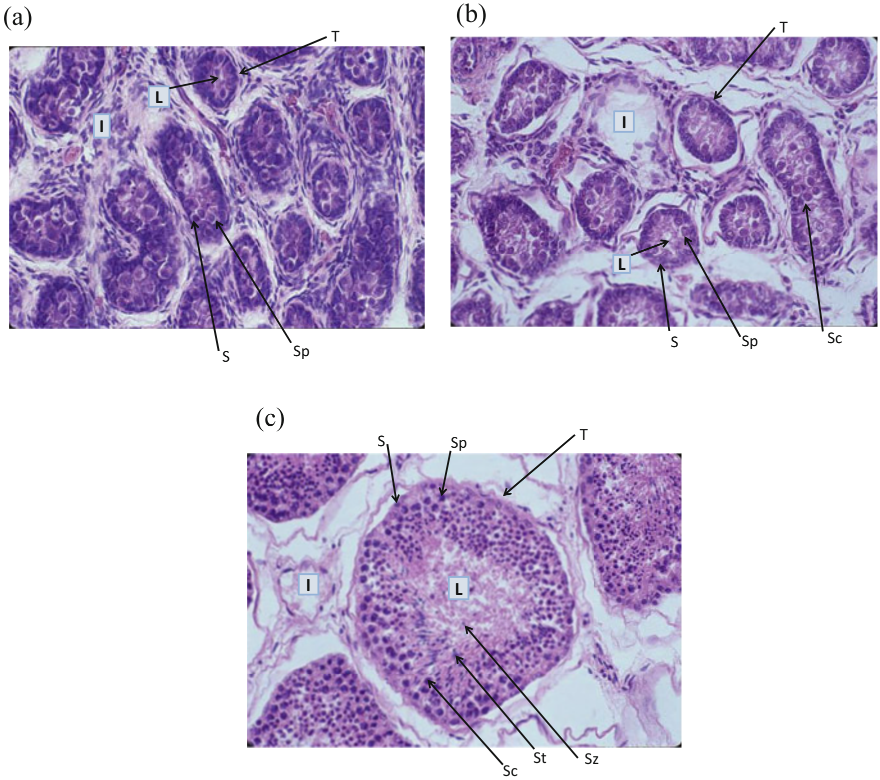

Fig. 6.4 Histological sections of (a) immature, (b) maturing (or pubertal), and (c) mature testes collected from pantropical spotted dolphin (*Stenella attenuata attenuata*) specimens provide an example of testes maturation in male cetaceans. Components of the testes visible at 40x magnification for each stage are labeled: T = seminiferous tubule, I = interstitial tissue, L = lumen, S = Sertoli cells, Sp = spermatogonia, Sc = spermatocytes, St = spermatids, and Sz = spermatozoa. The maturity stages can be identified by increasing seminiferous tubule diameter (T), decreasing interstitial tissue (I), and evidence of active spermatogenesis as males mature (Credit: S. Chivers, NOAA, NMFS, Southwest Fisheries Science Center, La Jolla, CA)

sexual size dimorphism (SSD). For example, adult male sperm whales are more than 60% bigger than females and reach sexual maturity at approximately 20 years of age compared to 9 years in females (Whitehead 2018). The difference is similar in killer whales and the long- and short-finned pilot whales, reflecting the additional time required to grow to about 85% of their asymptotic length, which is the approximate size at which all mammals become sexually mature (Laws 1956). On the other hand, the small delphinids with little SSD reach sexual maturity at more similar ages. For example, male common bottlenose dolphins and pantropical spotted dolphins reach sexual maturity only about 3 years later than females (Perrin and Reilly 1984).

SSD in cetaceans is typically expressed as the ratio of male-to-female adult TL. Among baleen whales, females are generally 5% larger than males. This female-biased SSD provides females more blubber storage capacity to meet energetic demands of migration and reproduction, especially lactation. Similarly, female-biased SSDs occur among the smallest toothed whales, which are the porpoises and river dolphins, and these females are as small as they can be to produce a precocial calf that is large enough to survive (Ralls 1976). Among the other toothed whales, SSD is male-biased and, while variable, is relatively moderate (i.e., ~5–10%) in most species (Mesnick and Ralls 2018b; Cantor et al. 2019).

Within the toothed whales, males of many of the delphinids (family Delphinidae) are more robust (e.g., heavier) than females but differ little in TL. Additionally, differences in the external morphology of the sexes are evident in comparisons of the size and shape of the head, dorsal fin and peduncle (e.g., anal hump), dentition, and uro-gentital color patterns. Notable examples include the head shape of sperm whales, the dorsal fins of killer whales and members of the Globicephalinae family, the dorsal fin and post-anal hump of eastern spinner dolphins (*S. l. orientalis*), the uro-genital color patterns of Dall's porpoise (*Phocoenoides dalli*), the tusk of narwhals, and the dentition of beaked whales. If sexual selection is an evolutionary driver of sexually dimorphic traits, then such traits can allow for inferences about mating systems (Mesnick and Ralls 2018b).

6.4 Mating Systems

Mating strategies maximize an individual's reproductive success. Thus, cetacean males may spend time searching for receptive females to sire as many offspring as possible, while females may invest heavily in rearing calves. Interspecific variability and intraspecific variability in mating strategies revealed by longitudinal studies suggest that a population's social behavior and ecological niche influence the evolution of mating tactics and strategies. Thus, mating tactics operating within a given strategy are expected to reflect the tradeoffs made by individuals to maximize their reproductive success (Mesnick and Ralls 2018a; Boness et al. 2002). However, the mating strategies of most cetacean species have been inferred from SSD and relative testes size, which is the ratio of testes size to body size, and actual mating tactics remain poorly known.

6.4.1 Female Mating Strategies

Like other large long-lived mammals, adult female cetaceans invest heavily in each calf reared. Females need to meet demands of gestation and lactation and to protect their young from predators; their fitness is enhanced by choosing a mate that can provide valuable resources or good genes (Trivers 1972; Stearns 1977; Clutton-Brock 1989; Clutton-Brock et al. 1989).

Cetacean female mating strategies remain poorly understood (Orbach 2019). The inherent difficulties studying cetaceans that live in oceanic habitats contribute to this and further exacerbate conducting studies to evaluate the role of sexual selection in molding mating strategies. The role of female choice has been considered less important than the largely more obvious behaviors of males competing with each other for mates or resource guarding. However, there is mounting evidence that female choice shapes behavioral and physiological adaptations that ultimately define mammalian mating systems (Birkhead and Møller 1993; Gomendio and Roldan 1993a, b; Gomendio et al. 1998). Among cetaceans, evidence of female choice has been revealed by long-term studies of humpback whales, right whales, common bottlenose dolphins, and dusky dolphins documenting that females avoid or repel males attempting to mate (Brownell and Ralls 1986; Palsbøll et al. 1992; Clapham 1996, 2000; Connor et al. 2000b; Whitehead and Mann 2000; Boness et al. 2002; Orbach et al. 2015).

Two categories of female choice tactics have been proposed from observations made in longitudinal studies of the dusky dolphin, Indo-Pacific bottlenose dolphin, and sperm whale. The tactics are either behavioral (signal discrimination, mate choice copying, and evasive behaviors) or physiological (polyestry/multiple matings and modified genitalia) (Orbach et al. 2023, this book). The behavioral tactics focus on mate choice by evaluating cues from male secondary sexual characters (discussed in the next section) or copying the choices of other females and avoiding mating with undesirable males. In contrast, the physiological tactics focus on avoiding conceptions from poor quality males by repeated estrus cycling or mating or excluding sperm from the uteri. Cross-sectional studies of vaginal morphology contribute to the sperm exclusion hypothesis, which is also referred to as the physiological “modified genitalia” tactic of mate choice. While vaginal length correlates with cetacean TL and not vaginal fold diversity (Orbach et al. 2017), intraspecific comparisons of vaginal fold diversity may provide some clues to the selective pressures that formed them (Orbach et al. 2021). Three species with complex vaginal morphology—long vaginal length and cumulative vaginal fold length—also have evidence of heavy investment in sperm competition by males. These are the pygmy and dwarf sperm whales (*Kogia breviceps* and *K. sima*, respectively) and harbor porpoise (*Phocoena phocoena*). The similarity in life history traits supporting relatively high reproductive output in these species (Read and Hohn 1995; Plön 2004) may provide future insights about the functionality of this morphology (Dines et al. 2014, 2015; Orbach et al. 2017, 2021). However, the role of female choice will likely remain unknown for most species.

6.4.2 Male Mating Strategies

Cetacean mating systems are predominantly classified as variations of multimale mammalian systems with male mating strategies inferred from traits shaped by sexual selection: behavior, phenotype, especially secondary sexual characteristics, SSD, and relative testes size. To sire as many offspring as possible, cetacean males are expected to compete with each other for access to mates directly using combat or display methods to exclude rivals or attract females (pre-copulatory behavior) or indirectly through sperm competition (post-copulatory behavior; Dines et al. 2015; Mesnick and Ralls 2018a; Orbach 2019). Aggressive intermale competition for mates is inferred from external scars on males of species with relatively small testes and marked secondary morphological characters (e.g., narwhal tusks and beaked whale teeth) (McCann 1974; Silverman and Dunbar 1980; MacLeod 1998; Dines et al. 2015; Loch et al. 2023, this book). Many morphological and physiological traits are likely the result of sexual selection producing variation ultimately associated with mating strategies as evolutionary pressures mold species to their environment. The resulting adaptations reflect access to resources: prey, predators, and mates influencing a species' distribution, range, group size, and social structure.

A minority (~30%) of toothed whales exhibit pre-copulatory mating behaviors with about half participating in aggressive combat and half displaying to attract mates, while the majority (~70%) exhibit post-copulatory traits associated with sperm competition (Dines et al. 2015). The tactics of sperm competition remain unknown, and the associated traits (e.g., penis length, penis shape, sperm quantity, and sperm morphology) are expected to vary among species as has been observed in other mammals (Gomendio and Roldan 1993b; Gomendio et al. 1998; Tourmente et al. 2011). Additional variability in mating strategies is also expected to be associated with mating behavior as has been observed in bottlenose dolphins (Connor et al. 2000b) and inferred for spinner dolphins (Perrin and Mesnick 2003). We will discuss these examples further below, because they suggest that mating tactics may contribute to operational variability in mating strategies within species.

The potential for sperm competition in some baleen whales is considered high because females have multiple mates per estrus (Brownell and Ralls 1986). However, longitudinal studies have revealed variability in male mating strategies for several species. For example, humpback whales exhibit intermale competition during the winter breeding season, which includes setting up three-dimensional leks in areas selected by females for calving and singing to attract mates (Clapham 2000; Connor et al. 2000a). Intermale competitions have also been observed in right whales with callosity-induced skin scarring resulting from aggressive encounters (Connor et al. 2000a; Kraus and Hatch 2001). Because establishing how intermale competitions control access to females has proven difficult, sperm competition is suggested as the primary mating strategy of right whales as it is for bowhead and gray whales. Little is known about blue (*Balaenoptera musculus*), Bryde's (*B. edeni*), fin (*B. physalus*), and minke (*B. acutorostrata*) whales' mating strategies, but songs recorded for these species may play a role in finding, attracting, or guarding potential mates (Brownell and Ralls 1986; Boness et al. 2002; Eichenberger et al. 2023, this book).

The mating strategies of toothed whales are somewhat better known than those of baleen whales largely due to the longitudinal studies of bottlenose dolphins, sperm whales, and killer whales. Male alliances have been observed in both the Shark Bay

(Australia) population of Indo-Pacific bottlenose dolphins (*T. aduncus*) and the Sarasota Bay (Florida, USA) population of common bottlenose dolphins. The alliances are temporary formations consisting of two or three males accompanying reproductively active females to control mating access to them, with intermale aggression also observed in the Shark Bay population. However, there is no evidence of male alliances being formed, or of any other types of male defense of females, to control reproductive access to females in two other common bottlenose populations: Moray Firth, Scotland, and Doubtful Sound, New Zealand (Connor et al. 2000b; Lusseau 2007). While male alliances are presumed to be a type of pre-copulatory behavior, paternity studies have revealed that alliance membership does not ensure mating or reproductive success (Duffield and Wells 1991; Wells et al. 1999; Krützen et al. 2004).

Studies of sperm whales have revealed that intermale aggression and sound occasionally play a pre-copulatory role but that males primarily rove among groups of females in search of mates (Whitehead and Weilgart 2000). Similarly, resident killer whales rove among pods brought together by summer prey aggregations to mate with receptive females not in their natal group. This behavior likely ensures outbreeding (Baird 2000). Long-finned pilot whales have a social structure similar to killer whales, and molecular genetics has confirmed that roving males ensure outbreeding by mating outside their natal groups (Amos et al. 1993).

SSD and relative testes size as proxies—Assembling comparative data sets to infer mating strategies from SSD and relative testes size is challenging because of differences in reported metrics among studies. For example, adult TL may be expressed as a mean, maximum, or an estimated asymptote, and characteristics of adults may differ depending on whether TL, appendage morphology, or reproductive organ data are used to identify them. Similarly, relative testes size may be calculated as the ratio of combined or singular testis weight with or without epididymis to body size: TL or weight. However, TL is used more frequently than body weight, because TL data are more readily available for most species, and correlates well with body weight (Brownell and Ralls 1986; Connor et al. 2000a). Consequently, the data compiled for mating strategy studies will differ, including which species were represented and which metrics were selected (Table 6.1). Even so, the overall conclusions of studies have been similar, because the focus has been on interspecific patterns, which are largely robust to the data metrics chosen.

Toothed whales adhere to Rensch's rule of allometry, which predicts that SSD scales with body size in mammalian lineages with male-biased SSD, with two notable exceptions (Casper and Begall 2022). The exceptions are the species that do not have male-biased SSD: the beaked whales (family Ziphiidae) and the Amazon river dolphin (*Inia geoffrensis*). The large size of beaked whales predicts that SSD will be male-biased, but instead the species have a predominantly female-biased SSD or are monomorphic. Male beaked whales also have relatively small testes and distinct dentition, which is a secondary morphological character, used in intermale combat and display behavior suggesting a significant investment in pre-copulatory mating behaviors in this family (Heyning 1984; Dines et al. 2015; Pitman 2018). On the other hand, a female-biased SSD is predicted for the Amazon river dolphin, but

Table 6.1 The number of baleen and toothed whale species included in studies using sexual size dimorphism (SSD) and testes size relative to male total body length as proxies to infer cetacean mating systems

	Adult total body length			Testes size			
Study	Baleen whale species	Toothed whale species	Metric	Baleen whale species	Toothed whale species	Metric	Analyses
Connor et al. (2000a)	4	25	Mean of sexually and physically mature and estimated asymptotic length	0	10	Maximum combined weight without epididymis	Allometry of SSD for cetaceans and relative testis size for toothed whales; one species per genus to mitigate phylogenetic bias
Plön and Bernard (2007)	3	15	Categorized as monomorphic, female-biased, or male-biased from literature	3	15	Combined testes weight as percent of total body weight	Proposed mating strategies using SSD, relative testes size, group size, and behavior
Dines et al. (2015)	11	47	Maximum	11	47	Maximum combined weight with and without epididymis	Multivariate approach to evaluating pre- and post-copulatory behavior
Casper and Begall (2022)	0	57	Mean; most extreme difference between sexes observed	0	0	None	Phylogenetic test of Rensch's rule for allometric scaling of SSD

their SSD is male-biased, and males have been observed with scars and injuries consistent with aggressive intermale competition for mates (Martin and Da Silva 2006). These examples demonstrate the unique evolutionary pressures molding cetacean species and the importance of considering the pre-copulatory role of mating behavior and secondary morphological characters in mating strategies.

The relative importance of pre- and post-copulatory behaviors in male cetacean mating strategies was furthered by Dines et al. (2015), who combined patterns in SSD and relative testes size with other traits likely molded by sexual selection, including secondary morphological characteristics and mating behaviors. Species with investment in pre-copulatory behaviors tend to have relatively small testes and distinct secondary sexual traits (e.g., dentition in most of the beaked whales and song in some baleen whales), which allow them to control access to females by engaging in combat or in ritualized displays to attract females. Examples of aggressive intermale combat include narwhals using their tusks in aggressive intermale interactions (Silverman and Dunbar 1980; Kelley et al. 2014b) and some beaked whales, especially *Mesoplodon* sp., using their teeth in combat (Pitman 2018). However, most (~70%) cetacean species (n = 58) in the Dines et al. (2015) study exhibited investment in predominantly post-copulatory traits. Among these species, most had limited male-biased SSD coupled with moderate to large relative testes size suggesting sexual selection favors sperm competition as the predominant post-copulatory investment. This negative correlation between SSD and relative testes size in toothed whales is consistent with that observed in all mammals and is one that correlates with mating systems (Kenagy and Trombulak 1986; Kelley et al. 2014a).

6.4.2.1 Intraspecific Comparisons

Relatively few studies have characterized the male mating strategies of subspecies, or populations, within cetacean species. However, geographic variation in the external morphology and molecular genetics has revealed evidence for long-term isolation of populations within species. The accumulation of differences in traits in isolated populations has been sufficient to support the recognition of discrete populations within species and interspecific and intraspecific taxonomic revisions (Perrin 2018). This geographic variation may be associated with variability in the mating tactics that have evolved within species.

Geographic variation in the external morphology of Eastern Tropical Pacific (ETP) spotted dolphins, spinner dolphins, and common dolphins resulted in the recognition of several populations and subspecies among them (Perrin et al. 1985; Dizon et al. 1994). Examining the mating strategy proxies for the ETP dolphin subspecies currently recognized to those published for small delphinids provides some context for assessing the variability in these proxies and identifying those that may have unique adaptations associated with their mating strategies (Fig. 6.5). For example, the study that compared male reproductive characteristics of the eastern spinner dolphin subspecies to those of the whitebelly (a hybrid of *S. l. orientalis* and *S. l. longirostris*) spinner dolphin revealed evidence to support the idea that different

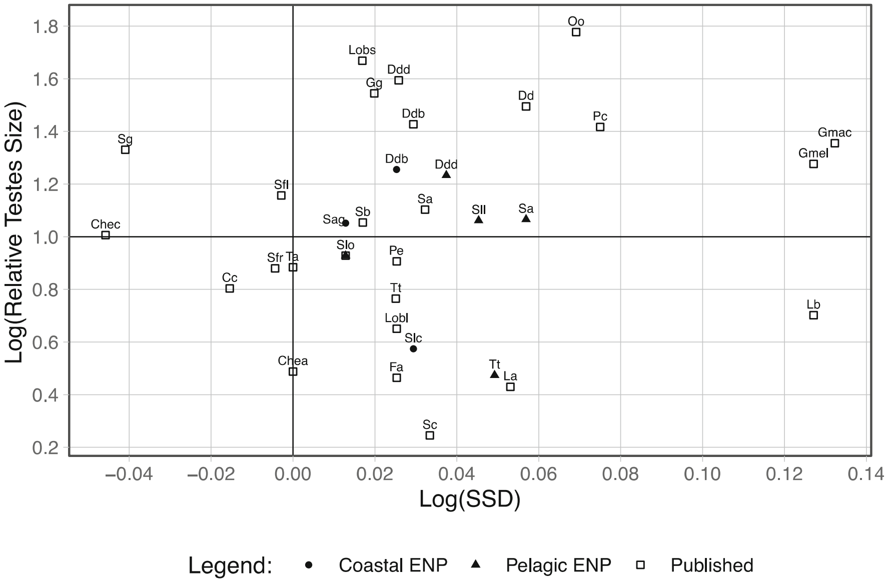

Fig. 6.5 Sexual size dimorphism (SSD) and relative testes size for subspecies of eastern North Pacific Ocean (ENP) spotted dolphins, spinner dolphins, and common dolphins using data collected from fisheries bycatch specimens are plotted together with published values for 35 delphinid species from Connor et al. (2000a) and Dines et al. (2015). The data point labels reflect the taxonomic name for each species and subspecies represented. For the ENP: pantropical spotted dolphin (Sa), coastal spotted dolphin (Sag), eastern spinner dolphin (Slo), whitebelly spinner dolphin (Sll), Central American spinner dolphin (Slc), short-beaked common dolphin (Ddd), long-beaked common dolphin (Ddb), and common bottlenose dolphin (Tt). For the published data, ordered by SSD: Hector’s dolphin (Chec), Guiana dolphin (Sg), Commerson’s dolphin (Cc), Atlantic spotted dolphin (Sfr), tucuxi (Sfl), Heaviside’s dolphin (Chea), Indo-Pacific bottlenose dolphin (Ta), eastern spinner dolphin (Slo), dusky dolphin (Lobs), rough-toothed dolphin (Sb), Risso’s dolphin (Gg), common bottlenose dolphin (Tt), melon-headed whale (Pe), Pacific white-sided dolphin (Lobl), pygmy killer whale (Fa), short-beaked common dolphin (Ddd), long-beaked common dolphin (Ddb), pantropical spotted dolphin (Sa), striped dolphin (Sc), Atlantic white-sided dolphin (La), common dolphin (Dd), killer whale (Oo), false killer whale (Pc), Northern right whale dolphin (Lb), long-finned pilot whale (Gmel), and short-finned pilot whale (Gmac)

polygamous mating systems were operating. Specifically, socially and sexually dominant male eastern spinner dolphins were identified as those with high sperm production, distinct secondary sexual characteristics (i.e., a post-anal hump, forward-canted dorsal fin), and a relative testes size about half that of whitebelly spinner dolphins. These observations are consistent with a more polygynous mating system in eastern spinner dolphins and a multi-male multi-female mating system in whitebelly spinner dolphins (Perrin and Mesnick 2003).

Selective pressures may be influencing the mating strategies of other toothed whale species that exhibit geographic variation in their external morphology (e.g., SSD and secondary sexual characters) and relative testes size. These species include the false killer whale, narwhal, beluga whale, common dolphin, and pantropical

Table 6.2 Sexual size dimorphism (SSD) calculated using the mean and maximum adult total body length (cm; TL) data for female and male common dolphins (*Delphinus delphis*) and pantropical spotted dolphins (*Stenella attenuata*) sampled from incidental bycatch and stranded specimens in the eastern North Pacific are presented along with relative testes size calculated from combined testes with epididymis weights (g) and maximum male adult TL. For the common dolphin, the subspecies and Eastern Tropical Pacific (ETP) populations recognized are presented: *D. d. bairdii* (eastern North Pacific long-beaked common dolphin, LBCO), *D. d. delphis* (short-beaked common dolphin, SBCO) from the northern (N), central (C), and southern (S) populations. For ETP pantropical spotted dolphins, the coastal subspecies (*S. a. graffmani*) and populations of *S. a. attenuata* (northeastern (NE), western (W) and southern (S)) are presented (Perrin et al. 1985). For reference, the data used in the analyses by Dines et al. (2015) are included

Common dolphin

Subsp./stock	N Female TL	N Male TL, Testes weight	SSD (TL mean)	SSD (TL max)	Relative testes size
LBCO	56	141, 6	1.040	1.057	12.22
SBCO—N	90	147, 6	1.041	1.097	8.82
SBCO—C	843	947, 613	1.020	1.113	10.89
SBCO—S	17	13, 11	0.989	1.106	18.53
LBCO—Dines				1.070	26.72
SBCO—Dines				1.140	31.26
Pantropical spotted dolphin					
Coastal	159	106, 48	1.028	1.025	11.26
NE	5754	4378, 1201	1.011	1.136	11.64
W	1777	1315 445	1.010	1.064	10.39
S	2092	1713, 504	1.016	1.059	10.27
Sa—Dines				1.070	11.27

spotted dolphin. As observed in the ETP spinner dolphins, the relative testes size of false killer whales off South Africa is about half that of those off Japan (7.7 versus 14.1), but unlike the ETP spinner dolphins, the SSDs of these populations are the same (Ferreira et al. 2014). These data suggest differences in their mating strategies may be revealed when more data are available. Similarly, comparisons of mating strategy proxies for Canadian Arctic populations of narwhal and beluga whales reveal interspecific and intraspecific differences. The larger relative testes size of beluga whales, which range from 2.01 to 3.63 among populations, suggests they are more polygynandrousthan narwhals, which have relative testes sizes ranging from 1.8 to 2.7. In contrast, the negative correlation of narwhal tusk length with testes size suggests tusks may play a role in display soliciting female choice and intermale aggression (Silverman and Dunbar 1980; Kelley et al. 2014b). In the ETP, populations of common dolphin (*Delphinus delphis*) and pantropical spotted dolphin exhibit relatively low SSDs (i.e., <15%) and relative testes size ranging from 8.8 to 12.2, which are characteristics consistent with sperm competition being the dominant mating strategy. However, the variability observed in these proxies among populations suggests other traits may have evolved to influence male mating success within this strategy (Table 6.2).

Additional studies quantifying sexual dimorphism in other biological and morphological characteristics contribute to inferring species' mating strategies when combined with SSD, relative testes size, and group size. For example, Plön et al. (2012) compared the sexual dimorphism in relative organ size for three small delphinid species off South Africa and found that the results were consistent with the overall differences in their body size, relative testes size, distribution and range, and group size and structure. In concert, the authors suggested the primary mating strategies differed with the Indo-Pacific humpback dolphin (*Sousa chinensis*) having a harem-like strategy, the Indo-Pacific bottlenose dolphin engaging in frequent copulations, and the long-beaked common dolphin sperm competition. Similarly, Yahn et al. (2022) characterized variability in the degree of dorsal fin sexual dimorphism in four species of toothed whales belonging to the subfamily Globicephalinae sampled off Hawaii: the false killer whale, short-finned pilot whale, melon-headed whale (*Peponocephala electra*), and pygmy killer whale (*Feresa attenuata*). Variability ranged from fairly extreme in short-finned pilot whales to more limited in false killer whales. The authors proposed that this evidence supported pre-copulatory mating behavior as likely in all of these species. This hypothesis differs from that of Dines et al. (2015), which listed pre-copulatory selection for short-finned pilot whales only. These examples illustrate some of the complexities associated with inferring mating strategies from proxies and the value of including multiple sexually dimorphic traits, especially those likely to be under sexual selection, along with group size and social behaviors to reveal how species likely implement their mating strategy.

6.5 Social Behavior

Mating is one aspect of cetacean life histories that contributes to group formation and the only one we will consider here. The size, dynamics, and behavior of individuals within groups reflect the spatiotemporal patchiness of resources in the environment and the benefit to individuals coming together to breed, forage, or avoid predators (Acevedo-Gutierrez 2018; Trillmich and Cantor 2018). Mating behaviors are a key component of mating strategies and remain poorly understood for most cetaceans. Our understanding of cetacean mating strategies is limited to the six species that have been the focus of longitudinal studies and includes the multi-decadal studies of sperm whales, killer whales, and bottlenose dolphins (McHugh 2019).

Baleen whales are largely solitary, and the aggregations that occur on summer feeding and winter breeding grounds are predominantly structured around the availability of resources: prey and mates. Similarly, aggregations of toothed whales are structured around the availability of these resources as well as the need to protect calves from predators during the extended lactation period of most species.

Successfully protecting calves contributes to an individual's lifetime reproductive fitness, which can be further enhanced by communal living and cooperating with kin (Rendell et al. 2019). Toothed whales are largely social with many of the smaller species living in groups characterized by fission-fusion dynamics with group size and membership frequently changing, while several of the larger species form matrilines (e.g., killer whales, pilot whales, and sperm whales) that are more stable (Christal et al. 1998; Ottensmeyer and Whitehead 2003; Gowans et al. 2008; Cantor et al. 2019; Gowans 2019). Long-term studies have contributed insights about the social behaviors associated with mating, including the formation of male alliances controlling access to reproductive females in bottlenose dolphins (Wells et al. 1999; Connor et al. 2000b), and how roving males find mates to ensure outbreeding in sperm whales (Whitehead and Weilgart 2000; Eguiguren et al. 2023, this book). Studies detailing social behaviors are essential to understanding mating strategies and tactics, and the data collected from longitudinal studies will aid in identifying the proxies most informative for inferring mating strategies of difficult-to-study species.

6.6 Conclusions and Future Directions

The apparent diversity among cetacean mating systems reflects the variability in their reproductive strategies, which differ markedly between baleen and toothed whales (Mesnick and Ralls 2018a). To date, cetacean mating systems are considered partially predictable from SSD and relative testes size as they are for other mammals (Kenagy and Trombulak 1986). These metrics, together with the role of secondary sexual characteristics and behavior, reveal the contribution of pre- and post-copulatory traits in mating strategies. Evidence of intermale competition through combat or display controlling access to females suggests that pre-copulatory traits play a significant role in mating in a minority of species (~30%). On the other hand, the investment in relatively large testes evident for the majority (~70%) of species suggests that post-copulatory traits, especially sperm competition, dominate cetacean mating strategies (Dines et al. 2015). One noteworthy exception among odontocetes is the franciscana (*Pontoporia blainvillei*). To date, the franciscana is the only cetacean to exhibit long-term patterns of social interaction consistent with a single male, or monogamous, mating system, which is rare among mammals (Connor et al. 2000a; Wells et al. 2013).

Mating systems for most cetaceans will likely continue to be predicted from proxies. The ability to identify additional proxies of traits molded by sexual selection will improve our understanding of mating strategies. Comparative interspecific and intraspecific studies using cross-sectional data combined with data obtained from techniques developed to study the reproductive biology of wild populations in situ will contribute to quantifying and evaluating potential proxies to infer mating strategies of the lesser-known species. The use of remote technologies such as application of existing molecular genetic techniques to reveal male reproductive success through paternity (e.g., Krützen et al. 2004) will play a greater role in these studies, particularly as the collection of biological samples for cross-sectional studies continues to decline. While the highly mobile, wide-ranging, largely pelagic nature of cetaceans will continue to limit our knowledge of most species, our understanding of the complexities of their reproductive and mating strategies will be expanded by on-going multi-decadal longitudinal studies.

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