Chapter 4
Sexual Strategies: Male and Female Mating Tactics

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Abstract Conflicting interests between the sexes to enhance their fitness potentials have resulted in several sexual strategies used by odontocetes under various social and ecological contexts. Mating tactics are diverse and non-mutually exclusive and can entail both precopulatory and postcopulatory mechanisms. Males typically rove between females, and their mating tactics include display, contest, endurance, scramble, and sperm competition. Female mating tactics to maintain mate choice and control paternity are less well documented but may include signal discrimination, mate choice copying, evasive behaviors, polyestry, multiple mating, and modified genitalia. Species-specific examples of mating tactics are reviewed, as are potential costs and benefits, to better understand the fitness trade-offs associated with odontocete sociosexual relationships.

Keywords Competition · Mate choice · Mating tactic · Odontocetes · Sexual selection

The mating behaviors of most species of cetaceans have not been described due to the logistical challenges of directly observing opportunistic copulation events in a clade that is submerged beneath the surface of the water most of the time (Schaeff 2007; Lanyon and Burgess 2014; Orbach et al. 2015a). Reproductive patterns are instead generally derived from studies of captive animals, anatomy, and endocrinology or inferred based on similarities to terrestrial models (Lanyon and Burgess 2014). The sociosexual behaviors of odontocetes frequently occur year-round and outside the breeding season. In addition to conception, the sociosexual behaviors of dolphins, toothed whales, and porpoises may facilitate social learning, play, and the establishment of social bonds and dominance relationships (Mann 2006). Accordingly, some caution has been warranted when considering anecdotal reports of copulations, and such reports may have hindered efforts to explore mating strategies

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of cetaceans. However, inferred mating tactics are continually being supported by new field evidence, and systematic studies of the mating behaviors of free-ranging cetaceans have been possible in some populations with conducive environments and overt behavioral traits. Through evaluation of the costs and benefits associated with varied mating tactics, it is possible to better understand fitness trade-offs and evolutionary constraints and thereby predict mating patterns.

A reproductive asymmetry exists between the sexes, likely related to anisogamy (females produce larger and more energetically costly gametes than males) and variation in parental investment (Bateman 1948; Trivers 1972). Females are generally limited in their reproductive success by the availability of resources for—and large temporal and energetic investments in—parental care and are consequently discriminatory of mate quality (Trivers 1972). Females distribute themselves relative to resources necessary for offspring survival, such as food and breeding site availability, while also balancing ecological factors with costs and benefits of group living, such as predation pressure and resource competition (Trivers 1972). Accordingly, the operational sex ratio (the male/female ratio among individuals searching for mates) is often male-biased in mammals, which leads to intrasexual variation in reproductive success among males and strong sexual selection (Daly and Wilson 1983). Males have the potential to increase their fitness by mating with multiple fertile females. Thus, males disperse themselves relative to the temporal and spatial distributions of receptive females and invest more in mating effort than parental effort (Emlen and Oring 1977), especially in internal fertilizing species where paternity is uncertain because of sperm competition. Paternal care of offspring has not been reported in any cetacean species (Connor et al. 2000a), although in some matriarchal societies where males do not disperse from their natal groups, males may help non-descendant young to survive (e.g., long-finned pilot whales, *Globicephala melas*, Augusto et al. 2017).

Across sexually reproducing animals, mating systems can be defined broadly as monogamous (one male and one female mate exclusively), polygynous (one male mates with multiple females), polyandrous (one female mates with multiple males), or polygynandrous (males and females mate with multiple partners; multi-mate or promiscuous). Cetaceans have a polygynous or polygynandrous mating system (Wells et al. 1999) with no confirmed example of obligate monogamy (Connor et al. 2000a). Odontocetes are polyestrous and give birth to one offspring per calving event (Chittleborough 1958). These factors, in addition to gregarious lifestyles and extensive behavioral plasticity, have resulted in a broad and diverse array of cetacean sexual strategies in both sexes. Male and female precopulatory and postcopulatory mating tactics (the behavioral, morphological, or physiological phenotype of a genetically based strategy) are reviewed for odontocetes to demonstrate mechanisms of paternity control in addition to potential costs and benefits experienced by both sexes.

4.1 Male Mating Tactics

In general, males compete for access to receptive females by defending territories of value to females (resource defense), following and defending females, or by roving (roaming between females) and mating briefly before departing to find more mates

(Clutton-Brock 1989). Territorial defense is not known to occur among cetaceans, likely because of the highly mobile nature of their prey in the marine environment (Connor et al. 2000a). Evidence is lacking of males defending mates from predators. In some populations of bottlenose dolphins (*Tursiops* sp.), males guard receptive females from mating with rival males (e.g., Connor et al. 1992, 1996). Male cetaceans most commonly rove for receptive females. Because females are highly mobile, a male's ability to prevent extra-pair copulations and assure paternity is limited (Boness et al. 2002). The benefits of roving and potentially mating with more females are predicted to exceed the costs of traveling and losing fertilizations to other males when the duration of estrus is longer than the time required to travel between females (Whitehead 1990). The duration of estrus is unknown for most wild odontocetes and only known for a few species in captivity (common bottlenose dolphins, *T. truncatus*, Robeck et al. 2005; Pacific white-sided dolphins, *Lagenorhynchus obliquidens*, Robeck et al. 2009; beluga whales, *Delphinapterus leucas*, Steinman et al. 2012; killer whales, *Orcinus orca*, Robeck et al. 1993). Other variables, such as the predicted number of females encountered by a roving male, may factor into the decision of when to leave a female (Magnusson and Kasuya 1997).

Whether defending resources, defending females, or roving between females, the male intrasexual behavioral-sperm competition spectrum can be broad. Several mating tactics have evolved across and within odontocete families that optimize reproductive success while decreasing associated costs. Connor et al. (2000a) assessed the relationship between testes size and sexual size dimorphism across the family Delphinidae to predict the intensity of fighting and/or sperm competition. For example, genera with high sexual size dimorphism but small testes-to-body mass ratios, such as pilot whales (*Globicephala* sp.), were predicted to fight to monopolize females more than compete by sperm competition and to be less promiscuous than species with large testes sizes (Connor et al. 2000a). However, mating tactics are not mutually exclusive and likely depend on environmental and social contexts. Five prominent male mating tactics and their associated costs and benefits discussed herein are display, contest, scramble, endurance, and sperm competition (Table 4.1).

Display Competition Males engage in courtship displays and compete for the attention of females using morphological or behavior signals that are assumed to reflect genetic quality, dominance, readiness to breed, or access to resources. Darwin's (1871) theory of sexual selection suggests that the presence of seemingly maladaptive male secondary sexual characters is a mechanism for epigamic selection (female mate choice) and differential male reproductive success. Sexually dimorphic morphological traits may not be used exclusively for displays and may also directly assist males to win battles by contest competition.

Sexual dimorphism of morphological characteristics is largely limited to variations in body shape and size, as toothed whales, dolphins, and porpoises have evolved fusiform bodies that increase laminar flow in the marine environment. Morphological variations that increase drag forces may significantly increase the energetic costs of swimming and reduce fitness. Social and ecological constraints may also affect the development of sexually dimorphic traits. For example, male

Table 4.1 General male mating tactics of odontocetes for intrasexual competition and potential fitness costs

Male mating tactic	Potential costs for males	Potential costs for females	Example	Species	References
Display competition	– Increased conspicuousness to predators – Time/energy not spent foraging or detecting predators	– Time/energy evaluating males – "Dishonest" signals – Lower offspring survival if inexperienced in evaluating males	Object carrying and posturing	Humpback dolphins (*Sousa sahulensis*)	Allen et al. (2017)
Contest competition	– High risk of injury – Increased conspicuousness to predators – Time/energy not spent foraging or detecting predators	– Not directly choosing mate – Risk of injury if male aggressive to female	Weaponry-"battle teeth"	Some beaked whale (family Ziphiidae)	McCann (1974), Heyning (1984), Pitman (2018)
Endurance competition	– Extensive temporal investment – Lost mating opportunities with other females – Reduced paternity in alliance	– Prevented from mating with preferred mate – Reduced socializing opportunity – Risk of injury risk if coerced	Mate guarding/consortships	Indo-Pacific bottlenose dolphins (*Tursiops aduncus*)	Connor et al. (1996)
Scramble competition	– Extensive energetic expenditure on challenging chases – Conditional on competitive sperm	– Time/energy actively evaluating male and avoiding rejected males	Maneuverability during mating chases	Dusky dolphins (*Lagenorhynchus obscurus*)	Markowitz et al. (2010), Orbach et al. (2014)
Sperm competition	– Tissue costly to maintain – Conditional on male copulation success	– Limited choice of copulation partners	Strong seasonal testes mass and cellular activity patterns	Short-beaked common dolphins (*Delphinus delphis*)	Murphy et al. (2005)

Table modified from Orbach (2016)

sperm whales (*Physeter macrocephalus*) are considerably larger and forage in more productive waters than females (Whitehead 2018). In contrast, dusky dolphins (*Lagenorhynchus obscurus*) are relatively sexually monomorphic, and as both sexes live and forage together (Würsig et al. 2007), they have likely evolved similar morphological adaptations that optimize foraging success in their shared habitat.

Display competitions often occur in odontocete species with strong sexual dimorphism and in which males have small relative testes sizes. Consistent with game theory predictions that males have fixed energy budgets to allocate toward traits that aid in reproduction (Parker et al. 2013), male cetaceans experience trade-offs between investments in precopulatory and postcopulatory traits (Dines et al. 2015). For example, Dall's porpoises (*Phocoenoides dalli*) have relatively small testes sizes, and compared to females, males have enlarged postanal humps, forward-canted dorsal fins, and deepened caudal peduncles, which could signal mate quality to females (Jefferson 1990). Other commonplace sexually dimorphic visual characteristics that may signal sexual maturity or quality to females include variations in the size or shape of fins, flukes, postanal humps, rostrums, and teeth, in addition to differences in thoracic girth, colorations, and ossification of the skull (Ralls and Mesnick 2018).

In many terrestrial animals, secondary sexual characteristics associated with male display competitions often increase and recede relative to the breeding period, suggesting that maintenance of morphological signals are metabolically expensive to males or increase predation risks and reduce survival probabilities (Daly and Wilson 1983). Similar trends are uncommon among odontocetes, suggesting that the displayed morphological traits are not costly for males to maintain, that the mechanisms to conditionally diminish secondary sexual characteristics have not evolved, or that it is more energetically expensive for males if the traits increase and recede seasonally than remain unchanged. Behavioral sociosexual displays, however, have been reported to peak and wane seasonally among odontocetes, potentially signifying associated costs for survival, such as predator detection. For example, some male Amazon River dolphins (*Inia geoffrensis*) carry sticks in their mouths, and the seasonal peaks in these apparent sociosexual displays to females may be correlated with increased conceptions (Martin et al. 2008). Adult male Australian humpback dolphins (*Sousa sahulensis*) display large marine sponges on their rostra/melons to adult females and pair these presentations with physical posturing (e.g., "banana pose"; Allen et al. 2017). Sexual displays enriched by object carrying are rare among nonhuman mammals, yet they may be more common than recognized among dolphins, as several species have complex cognitive abilities (Marino et al. 2007).

Sexual displays by sounds can also be an important mating tactic for cetaceans, as the marine environment provides an excellent medium for sound transmission. The click vocalizations of sperm whales (*P. macrocephalus*) may provide females with indicators of mate quality if whales have the capacity to measure each other's body lengths by the interpulse intervals of successive clicks (Norris and Harvey 1972; Growcott et al. 2011). Sperm whale "slow clicks" are typically produced only by large sexually mature males on breeding grounds and have been hypothesized to attract mates and establish dominance hierarchies among males (Weilgart and

Whitehead 1988; Whitehead 1993). If information about male quality is transmitted by acoustic communication, it can reduce female energy and time investments to travel to and assess roving males.

Display competition confers benefits to females at minimal costs if cues are "honest" and females are not coerced to mate with rejected males. When cues are not transmitted acoustically, some energetic and temporal costs of evaluating prospective mates may be incurred, in addition to decreased predator detection efforts. Females may discriminately select mates based on some social signal that reflects genetic quality, such as availability of resources, defense capabilities, or other indicators of survival potential. Elaborate male displays may increase conspicuousness to predators or require time and energy investments in signaling that could otherwise be directed toward foraging. The ability of males to survive despite their "handicap" may provide females with "honest" indicators of heritable genetic quality (Zahavi 1975). Selective forces often eliminate "dishonest" signals of quality. Thus, display competition is a relatively beneficial mating tactic for experienced females that can discriminate male quality from signals. Young female odontocetes, however, may make poor mate choice decisions based on inexperience assessing male displays. There is a general trend of low survival rates of firstborn offspring among mammals (Clutton-Brock 1984). This trend may reflect a young mother's inexperience in choosing "high quality" mates or at rearing offspring. Alternatively or concurrently, there may be physiological causes such as the inability of small primiparous female odontocetes to sufficiently meet the metabolic demands of lactation or the high transfer rates of lipophilic organochlorine to firstborn offspring (Cockcroft et al. 1989; Wells 2014).

Contest Competition Contest competitions involve one or more males limiting the access of other males to reproductive females through fights or aggressive behaviors. Females are considered high value resources that warrant "risky" behavior to establish dominance hierarchies and "win" access to mates. Males often develop armaments that aid in combat. High stakes intrasexual physical combats are common among male odontocetes, as evident through the evolution of "weaponry" in several species and scarring patterns in older males (MacLeod 1998). For example, male narwhals (*Monodon monoceros*) develop tusks (elongated upper left canines) used for jousting and intra- or intersexual displays. Fragments of tusks have been found embedded in conspecific males (Gerson and Hickie 1985). Beaked whales (family Ziphiidae) have cephalopod-rich diets and do not require teeth for feeding. Females are toothless, while males develop "battle teeth" (1–2 pairs of mandibular teeth) that they may use to attack other males and occasionally females (McCann 1974; Heyning 1984; Pitman 2018). Male northern bottlenose whales (*Hyperoodon ampullatus*) have large, squared, and flattened melons compared to females and headbutt each other with this enlarged surface area (Gowans and Rendell 1999). In several species of oceanic dolphins (family Delphinidae), males aggressively bite or injure each other, as evident from scarring patterns, rake marks, and opportunistic sightings of violent intrasexual interactions (e.g., Visser 1998; Parsons et al. 2003). The prevalence of physical combats may be underestimated among cetaceans, as

agonistic encounters involving strikes with flukes, peduncles, melons, or other body parts leave internal wounds not visible to observers. For example, Ross and Wilson (1996) reported that 36% of deceased harbor porpoises (*Phocoena phocoena*) with fractured bones or organ damage from antagonistic interactions with common bottlenose dolphins (*T. truncatus*) showed no external signs of skin damage.

Among cetacean species in which males evolved "weapons" or enhanced combat skills, the net payoff of increased reproductive success appears to exceed the costs of injury and potential mortality. Like most mammals, female cetaceans generally have longer lifespans than males (Ralls et al. 1980), and the costs of combats may contribute to reductions in male longevity. When the stakes are high, male cetaceans may discern and fight more aggressively for females in estrus (Tyack and Whitehead 1982). The number of violent intrasexual battles are predicted to be inversely related to the associated costs (Clutton-Brock et al. 1979), and males in species with "dangerous weapons" may signal their quality to each other rather than engage in physical combat. Body scars may also signal fighting abilities and serve as badges of status. Males may evaluate scars and determine their opponents' dominance ranks to avoid costly or lethal battles (MacLeod 1998). For example, the slow rate of scar tissue re-pigmentation in Risso's dolphins (*Grampus griseus*) has been hypothesized to accentuate scars for intrasexual competitor evaluation (MacLeod 1998). Females may also use scars to evaluate mate quality, as males with many scars tend to be older and have strong immune systems (MacLeod 1998).

Females gain more reproductive benefits than costs when males compete among each other to establish dominance relationships, as females may choose mates directly based on fighting abilities. Alternatively, if females choose mates indirectly by allowing males to establish social hierarchies and mate with the "winners" of contests (i.e., a lek, Emlen 1976), females potentially benefit through genetic transfer of "high quality" traits to their offspring. However, when contest competitions involve aggressive behaviors directed toward females, or when epigamic selection of a preferred mate is restricted, fitness costs can become substantial.

Endurance Competition In endurance competition, males attempt to outlast their rivals for the duration of a "war of attrition" despite accruing costs. For example, males may defend a female for at least the duration of her estrus and ovulation cycle (e.g., Indo-Pacific bottlenose dolphins, *T. aduncus*, Connor et al. 1996). Mate guarding occurs when males monopolize a female and competitively exclude rivals from mating with her and her from mating with a preferred male. In mate guarding contests, the female cannot be abandoned after copulation without risking the loss of a fertilization already won to another male. Thus, endurance competition costs females lost mating opportunities with preferred mates in addition to altered energy budgets, such as reduced group socializing opportunities. Endurance competition is the most temporally costly of the five reviewed male mating tactics. The time spent guarding one female to ensure paternity is time lost courting additional females or engaging in other activities such as foraging. For example, male Dall's porpoises (*P. dalli*) observed guarding females dove for shorter durations than non-mate guarding males, suggesting potentially reduced food intake (Willis and Dill 2007).

Although endurance competition is not known to occur among most species of odontocetes, it has been well-documented in one of the best studied populations of cetacean mating behavior. Male Indo-Pacific bottlenose dolphins (*T. aduncus*) off Shark Bay, Western Australia, engage in endurance competition paired with mate coercion, in which males chase a female, isolate her for periods that can span several months, and aggressively force her to copulate (Connor et al. 1992, 1996). Males form alliances of stable long-term associations that can last over seasons or years and coordinate activities to "herd" and sexually coerce reproductive females (Connor et al. 1992; Connor and Krützen 2015). Males can aggressively sequester and control females by charging, biting, or colliding into them (Connor et al. 1992) and use threatening "pop" vocalizations to constrain movement (Connor and Smolker 1996). As there is limited sexual size dimorphism in this population of dolphins, males in alliances benefit by their collective ability to overpower individual females, which is more challenging for a lone male (Connor et al. 2000b). However, paternity is skewed toward certain males within alliances, and fertilizations are not divisible (Krützen et al. 2004). Subordinate males appear to gain inclusive fitness benefits by kin selection, as genetic evidence indicates that many males in stable first order alliances are strongly related (Krützen et al. 2003).

Scramble Competition During scramble competition, males compete to quickly find and mate with as many fertile females as possible within typically brief time constraints. Males jostle for a proximate position near a sexually receptive female, followed by a series of actions directed toward her. Females subject to scramble competition are usually in estrus for short durations and are spatially aggregated. Often the most maneuverable or fastest male succeeds. Scramble competition is a prevalent mating tactic in odontocete species lacking strong sexual dimorphism, with the exceptions of enlarged caudal peduncles or pectoral fin sizes in males, which could be adaptive for increased agility. Females may benefit by overtly discriminating between different males. The mating chases are generally energetically expensive, although they are brief. However, scramble competition alone may not be an effective male mating tactic to secure paternity, as ejaculation does not guarantee siring offspring if other males have more competitive sperm. Similarly, a large sperm count does not ensure paternity if there are limited opportunities to copulate (Frasier et al. 2007).

Dusky dolphins (*L. obscurus*) engage in high speed and energetic mating chases, in which four sexually mature males typically chase one sexually mature female for around 10 min while some catch up and copulate with her (Orbach et al. 2015a). Both sexes incur substantial short-term energetic costs, as females lead males on challenging three-dimensional chases that include several leaps through the air, deep dives, and sudden changes in swimming speeds and directions (Orbach et al. 2014, 2015a). Males are not aggressive toward each other and appear to take turns mating with females but do not cooperate with each other (Orbach et al. 2015b). Dusky dolphins have a highly fission–fusion social structure (Würsig et al. 2007; Orbach et al. 2018), and new mating groups form throughout the day. The same female has been observed mating with different groups of males within and across days (pers. observ.).

Sperm Competition Sperm competition is a male postcopulatory tactic that occurs inside the female reproductive tract. Males with higher quality or quantities of sperm that can displace or dilute their rivals' sperm succeed in fertilizing the most ova and have the highest reproductive success (Parker 1970). Sperm competition is particularly prevalent among cetacean species in which females mate with multiple males, male intrasexual aggressive interactions are limited, and males have large testes-to-body mass ratios and corresponding high sperm counts (Brownell and Ralls 1986). Allometric relationships indicate that testes sizes vary greatly among mammals and that odontocetes generally have higher testes-to-body mass ratios than similarly sized terrestrial mammals (Kenagy and Trombulak 1986; Aguilar and Monzon 1992). However, there is a large range of relative testes sizes among odontocetes (Aguilar and Monzon 1992; Connor et al. 2000a; Dines et al. 2015), some of which invest >5% of their body weight into testes mass (e.g., dusky dolphins, *L. obscurus*, Van Waerebeek and Read 1994).

In cetacean species hypothesized to use sperm competition as a prominent mating tactic, such as short-beaked common dolphins (*Delphinus delphis*), testes mass and cellular activity regress considerably outside the seasonal reproductive period (Murphy et al. 2005). Sperm storage appears to be very metabolically costly to males, as large testes masses are not maintained year-round. Gonadal tissue maintenance and sperm development can account for 5–10% of basal metabolic rates (Kenagy and Trombulak 1986). The seasonal cycle of testicular growth and recession, combined with the males' substantial energetic investments in sperm volume, is indicative of a rut, which may be induced by females having brief estrus periods (Murphy et al. 2005). Females can benefit from sperm competition through increased genetic compatibility (Olsson and Madsen 2001) and increased fertilization success (Marconato and Shapiro 1996) or if good sperm competitors sire "higher quality" offspring or produce sons that are good at sperm competition.

4.2 Female Mating Tactics

Female mating strategies and tactics to control paternity remain unknown for most species of cetaceans (Connor et al. 2000a; Boness et al. 2002; Schaeff 2007; Mesnick and Ralls 2018). Females are often perceived to have passive roles in paternity control as sexual coercion and intrasexual male competition can mask female preferences (Clutton-Brock and McAuliffe 2009). Research on female reproduction in odontocetes has instead focused on the temporal and energetic investments used by mothers to raise reproductively viable offspring (Whitehead and Mann 2000). However, as the costs of mating with a "poor quality" mate are high (gestation and lactation can be lengthy in odontocetes), females likely demonstrate more mating tactics than recognized to confer advantages to their offspring. Females can respond to prospective mates by selectively copulating with preferred males, copulating with any male to reduce harassment, or using evasive tactics. Females may also engage in postcopulatory sperm selection or control the seasonality of conception and

Table 4.2 Hypothesized general female mating tactics of odontocetes for intersexual selection

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 (*Lagenorhynchus obscurus*)	Markowitz et al. (2010)
Mate choice copying	Suggested by patterns of paternal relatedness within matrilineal groups	Sperm whale (*Physeter macrocephalus*)	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 (*Lagenorhynchus obscurus*)	Orbach et al. (2015a)
Polyestry/multiple matings	Hypothesized mechanism to improve fertility, reduce sexual harassment costs, and obscure paternity	Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)	Connor et al. (1996)
Modified genitalia	Complex vaginal folds that occlude penetration of the penis	Harbor porpoise (*Phocoena phocoena*)	Orbach et al. (2017)

Table modified from Orbach (2016)

parturition to ensure that sufficient resources are available to support the physiological demands of reproduction (Whitehead and Mann 2000). Five female mating tactics that increase female control over paternity are reviewed for odontocetes—signal discrimination, mate choice copying, evasive behaviors, polyestry/multiple matings, and modified genitalia (Table 4.2).

Signal Discrimination Females evaluate prospective mates based on signaled cues that reflect heritable attributes including morphological characteristics, behavioral displays, competitive abilities, and access to resources. This form of epigamic selection is hypothesized to be the predominant female mating tactic across animals, a driving force behind the evolution of secondary sexual characteristics, and likely plays an important role in mate selection for odontocetes. Specialized adaptions to overcome challenges associated with living in marine environments may enable females to choose from among males and control paternity. For example, female dusky dolphins (*L. obscurus*) have the advantage of ventrum-down positioning during mating chases and ventrum-to-ventrum copulations (Markowitz et al. 2010), which allow them to breathe without major repositioning. Male dusky dolphins have the disadvantage of ventrum-up positioning and must curtail their chase because of the need to breathe. Accordingly, females may evaluate the vigor and agility of disadvantaged (ventrum-up) potential mates during extended chases. Although dusky dolphins engage in predominantly scramble and sperm competition (Markowitz et al. 2010), the mating chase also appears to function as a display competition subject to female mate choice. Despite the energetic investments associated with mating chases, the chase itself may benefit the female by providing her with "honest" indicators of potential mate fitness, as similar maneuverability attributes are necessary to capture

prey and evade predators (Markowitz et al. 2010). Among sexually monomorphic delphinid species, agility may be the preferred quality in a mate rather than large body size, unlike in many terrestrial breeding marine mammals (e.g., northern elephant seals, *Mirounga angustirostris*, Haley et al. 1994).

Mate Choice Copying Females may increase or decrease their likelihood of mating with a particular male based on observing the mating behaviors of other females. While mature female odontocetes may have experience selecting higher quality mates and discerning honest signals of their capabilities, young and inexperienced females risk making poorer mate selections that could result in nonviable or lower-quality offspring. Inexperienced females may develop the skills to select higher-quality mates through mate choice copying. Female sperm whales synchronize their estrus cycles within their social groups (Best and Butterworth 1980), and patterns of paternal relatedness occur (Richard et al. 1996), suggesting that multiple females within a group mate with a single male. While there is no direct evidence that older and more experienced females mate first followed by younger females, it is conceivably possible as cultural transmission has been well documented within matrilineal sperm whale clans (Rendell and Whitehead 2001), and communication codas within female groups increase in the presence of mature males on breeding grounds (Whitehead 1993).

Evasive Behaviors A female's ability to assess the quality of prospective mates increases her reproductive success if she can ensure that she copulates with her preferred suitor and evades copulations with rejected suitors. However, costs imposed by rejected males to resistant females can be substantial and include harassment, aggression, injury, and occasional infanticide (Watson 2005). Female cetaceans appear to actively avoid some attempted copulations through body positioning or use of their habitat. For example, during mating chases, female dusky dolphins (*L. obscurus*) evaded pursuant males with deep dives and inverted (ventrum-up) swims at the surface so that their genital opening was inaccessible (Orbach et al. 2015a; Fig. 4.1). Females also moved to shallow waters and raised their flukes in the air, as has been observed among female southern right whales (*Eubalaena australis*, Payne 1995). Females may cooperate to evade males. For example, the formation of dusky dolphin nursery groups (mothers with calves) is hypothesized to reduce male harassment (Weir et al. 2008). Female sperm whales (*P. macrocephalus*) adopt a group "marguerite" or "wagon wheel" formation to defend themselves and their young against heterospecific attacks (Whitehead and Weilgart 2000). Female sperm whales have the behavioral capacity to use this group formation to evade sexual advances from ardent males, although it has not been documented.

Polyestry and Multiple Matings When female odontocetes are coerced to mate with non-preferred males, they may have subtle mechanisms to control who sires their offspring, including polyestrous cycling and multiple matings. After being monopolized by an undesirable male, repeated estrus cycles with short durations of ovulation can facilitate mating and conceiving with a preferred mate. This hypothesis has been proposed as a mechanism for female Indo-Pacific bottlenose dolphins

Fig. 4.1 Female dusky dolphin, *Lagenorhynchus obscurus*, evades male by inverting her body at the surface so her genital opening is inaccessible to the male beneath her. (Photo by Dara Orbach)

(*T. aduncus*) trapped in aggressive consortships to control paternity (Connor et al. 1996). Repeated estrus cycles and mating with multiple males can induce sperm competition, prevent inbreeding, reduce the risk of mating exclusively with infertile mates, reduce sexual harassment, and confuse paternity (Furuichi et al. 2014). Non-parental infanticide (intentional killing of non-descendant young) has been reported in multiple species of dolphins (Towers et al. 2018) and can benefit males by prompting non-receptive females to resume estrus cycling sooner (Hrdy 1979). At minimum, female costs include non-recuperative time and energy invested in the killed offspring. Among some mammals with high infanticide rates, non-ovulating females have been observed actively soliciting copulations from multiple males (Hrdy 1977). Such proceptive behavior by females may obscure paternity and thereby deter infanticide (Connor et al. 1996; Wolff and Macdonald 2004).

Modified Genitalia Cryptic female choice is any behavioral, morphological, or physiological mechanism by which females bias paternity to favor particular mates after copulation (Eberhard 1996; Firman et al. 2017). It is a postcopulatory female

Fig. 4.2 Ventral view of dissected adult female harbor porpoise, *Phocoena phocoena*, highlighting the elaborate and extensive vaginal folds. (Photo by Dara Orbach)
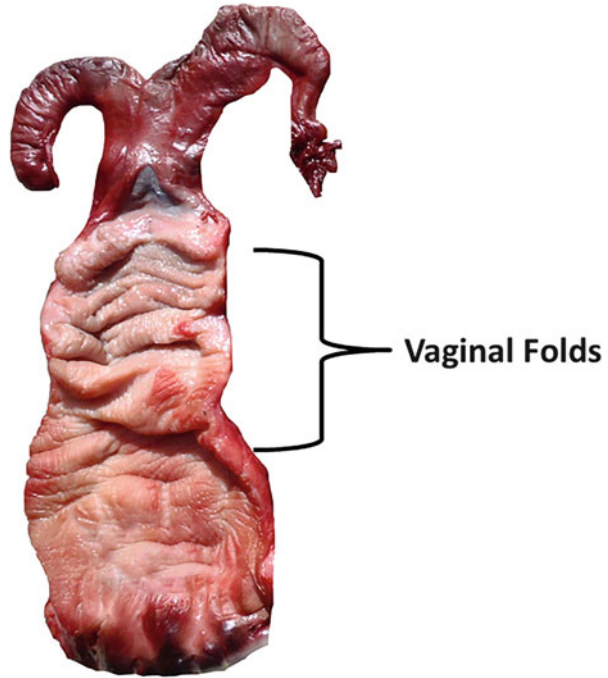
mating tactic that occurs inside the female reproductive tract and is a counter-adaptation to male sperm competition. Females may favor sperm with the best reproductive potential by having elongated and convoluted reproductive tracts. For example, a positive correlation was found between testes weight and oviduct length in 33 mammalian genera (Anderson et al. 2006), and studies of cetacean reproductive anatomy may yield similar patterns. Female cetaceans possess vaginal folds, which are muscular protrusions of the vaginal wall into the vaginal lumen that are unique to cetartiodactyls (Orbach et al. 2016; Fig. 4.2). It does not appear that common bottlenose dolphins (*T. truncatus*) can discriminately expel sperm from undesirable males by contracting reproductive tract muscles (Orbach et al. 2016), as has been demonstrated for some birds (Wagner et al. 2004) and moths (Curril and LaMunyon 2006). However, vaginal folds can occlude the penis and curtail the depth of penetration, thereby increasing the distance semen must travel to fertilize the ova (e.g., harbor porpoise, *P. phocoena*, Orbach et al. 2017).

4.3 Summary

Cetaceans have multi-mate mating systems, in which the sexes behave differently to optimize their respective reproductive success. Sexual selection and conflict entail males employing varied strategies to fertilize females, while females use counter-

strategies to maintain mate choice. Male odontocetes display diverse mating tactics that are not mutually exclusive, may vary among populations and species, and may be conditional rather than fixed. The "decision rules" of when to use a certain tactic likely depend on environmental conditions (e.g., season), social conditions (e.g., the tactics used by rival competitors or the number of reproductive females nearby), and the competitor's capacity to succeed at a given tactic, which may vary with age, experience, size, physiological condition, and dominance rank. In certain circumstances, males may make the "best of a bad job" and change tactics as new opportunities become available.

Most male odontocetes rove between receptive females and use display, contest, endurance, scramble, or sperm competition. Predictions of male mating tactics have been made based on characteristics such as mating systems, sexual dimorphism, evidence of aggressive interactions, behavioral observations, and testes-to-body mass ratios. Several intrasexual male mating tactics that commonly occur among terrestrial species have not been reported for odontocetes. For example, male odontocetes have not been observed provisioning prospective mates with direct benefits such as food, territory defense, or parental care and have not been observed exhibiting alternative reproductive tactics such as female mimicry or sneaky copulations. However, further field observations may provide evidence otherwise. As unmanned aerial vehicles become more popular to study cetacean behavioral patterns (Fiori et al. 2017), opportunities to gain new insights into mating behaviors are concurrently increasing without influencing the behaviors of the target marine mammals.

Female mating strategies are not typically as overt as male strategies and have generally been overlooked in cetacean research. Instead, counter-adaptations to male tactics are occasionally described, including evaluating cues that signify heritable fitness benefits, actively avoiding rejected males through behavior and body positioning, inducing pre- or postcopulatory male–male competition, and repeated estrus cycling. Known female mating tactics likely underrepresent the repertoire of mechanisms odontocetes use to control paternity. As our understanding of the diversity and complexity of cetacean mating strategies continues to expand in exciting novel directions, it is critical to consider how the behaviors of one sex alter the other, as male and female strategies can be strongly interdependent (Bro-Jørgensen 2011), and offer a window to explore underlying processes of evolution (Orbach 2016).

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