

# Chapter 16

## Sex in Killer Whales: Behavior, Exogamy, and the Evolution of Sexual Strategies in the Ocean's Apex Predator



Brianna M. Wright, Eva H. Stredulinsky, and John K. B. Ford

**Abstract** We present the current available knowledge about sexual behavior and mating systems in the killer whale, *Orcinus orca*, focusing primarily on the most well-studied ecotype, the Residents of the eastern North Pacific. Resident killer whales display lifetime natal philopatry of both sexes and thus form stable social groupings organized along maternal lines. Inbreeding is minimized via exogamous mating during multigroup aggregations that are diffusely seasonal. Male reproductive success in Residents is highly skewed, likely as a result of female mate choice or possibly intrasexual contest competition (or both), with only the largest and oldest males siring offspring. Female choice for males with large body and appendage sizes likely explains why killer whales as a species have evolved a high degree of sexual dimorphism. Scarring patterns and dorsal fin injuries indicate that breeding-aged males may occasionally engage in aggressive intrasexual competition to secure mates. Young male Residents appear to practice courtship behaviors by engaging in sociosexual play with other males. Coercive mating or mate-guarding in this species has not been observed and appears to be unlikely. Relative testes size, penis length, and penis tip morphology indicate that some sperm competition presumably exists in killer whales and likely co-evolved with female polyandry. Thus, both pre- and postcopulatory sexual selection may occur simultaneously in killer whales, and this species probably has a polygynandrous mating system in which both males and females can breed with multiple partners. Genetic pedigree studies of killer whale ecotypes besides Residents are needed to provide currently lacking but valuable information about mating patterns in other populations.

**Keywords** Exogamy · Female mate choice · Intrasexual aggression · Killer whale · Male-male sociosexual play · Matrilineal · Polygynandry · Sexual dimorphism · Sperm competition

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B. M. Wright (✉) · E. H. Stredulinsky · J. K. B. Ford  
Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC, Canada  
e-mail: [Brianna.Wright@dfo-mpo.gc.ca](mailto:Brianna.Wright@dfo-mpo.gc.ca)

## 16.1 Introduction

Killer whales (*Orcinus orca*) occur in all major oceans and are the most cosmopolitan of cetaceans (Forney and Wade 2007). Generally, killer whales are most abundant in higher latitudes, with a preference for productive colder waters (Morin et al. 2015). Although currently considered a single species, several distinct forms or “ecotypes” of killer whale have been described (Ford et al. 2000; Pitman and Ensor 2003; Foote et al. 2009; Pitman et al. 2010; Durban et al. 2016). These ecotypes are genetically isolated and are distinguished by differences in diet, habitat preferences, foraging strategies, social organization, vocalizations, and morphology/color patterns (Morin et al. 2010, 2015). Ecotypes are also socially isolated from one another, with no intermixing even when their geographic ranges overlap (Ford et al. 1998, 2000; Matkin et al. 2007; Zerbini et al. 2007; Filatova et al. 2019). As relatively few killer whale populations around the world are well known enough to allow for ecotypic classification (de Bruyn et al. 2013), our primary focus in this chapter is on the ecotypes and populations of the eastern North Pacific. The killer whales of this region have received the longest-running and most extensive research attention and thus provide the best available information relevant to sexual strategies and mating systems.

### 16.1.1 Population Structure, Genetic Diversity, and Gene Flow

The three sympatric killer whale ecotypes that occur in the eastern North Pacific are exceptional in their long-standing and steadfast ecological divergence and social segregation. Although killer whales as a species are generalist apex predators, with varying degrees of dietary diversity, flexibility, and niche partitioning among populations, eastern North Pacific ecotypes exhibit rigid and disparate dietary specializations. Bigg’s killer whales<sup>1</sup> are marine mammal eaters, while the Resident and Offshore ecotypes are both piscivorous, with Residents having a strong preference for salmon (*Oncorhynchus* spp.) and offshores appearing to specialize in shark predation (Ford et al. 1998, 2011a, 2014; Ford and Ellis 2006; Dahlheim et al. 2008). There is no evidence of social mixing or interbreeding among these ecotypes, despite their sympatric ranges (Hoelzel 1998; Barrett-Lennard 2000; Pilot et al. 2010). They diverged genetically from one another tens to hundreds of thousands of years ago (Morin et al. 2010) and are now reproductively isolated due to extreme social segregation and culturally inherited behavioral differences (e.g., dietary specialization and vocal dialects), which likely drive assortative mating (Barrett-Lennard

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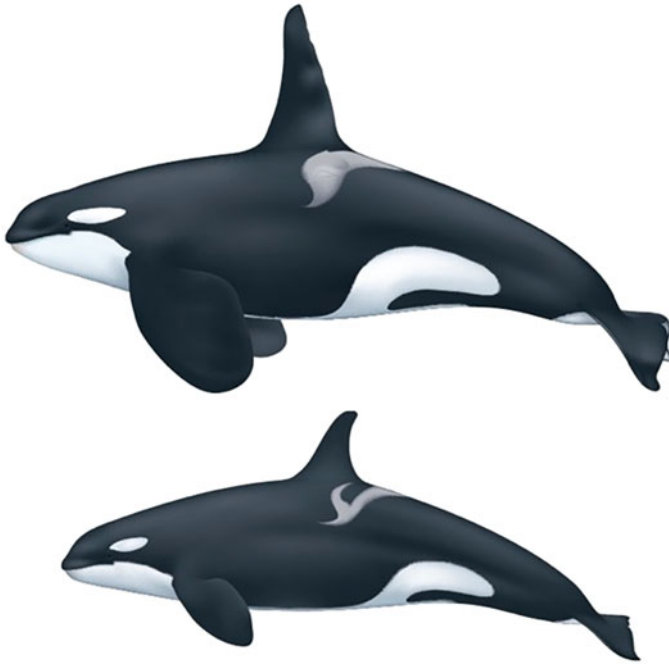
<sup>1</sup>Bigg’s killer whales were formerly known as Transient killer whales. Here we will use the term “Bigg’s” to refer to the ecotype as a whole but retain “Transient” when referring to specific populations within the Bigg’s ecotype, for instance, the AT1 Transients.

2000). This reproductive isolation has persisted for long enough that Bigg's killer whales are proposed to be a unique species (Morin et al. 2010).

Multiple populations can exist within an ecotype. For example, the Resident ecotype of the eastern North Pacific comprises three known populations: the southern, northern, and southern Alaska Residents. While these populations do not usually associate with one another, there is evidence of occasional interbreeding (Barrett-Lennard 2000; Ford et al. 2011b). For instance, microsatellite genotypes point to possible but rare instances of breeding between the northern Residents of British Columbia (BC) and the southern Alaska Residents (Barrett-Lennard 2000). However, these genetic patterns could also be due to historical associations and founding events, rather than being driven by contemporary mating patterns. Similarly, there is evidence of occasional gene flow in Bigg's killer whales between the inner West Coast Transient population (ranging coastally from southeastern Alaska to California) and the Gulf of Alaska Transient population (Barrett-Lennard 2000). Nevertheless, the vast majority of mating occurs within rather than between putative killer whale populations in the eastern North Pacific, and some of the smaller, more fragmentary populations are completely reproductively isolated (e.g., the endangered southern Residents and AT1 Transients) (Barrett-Lennard 2000; Pilot et al. 2010; Ford et al. 2011b; Parsons et al. 2013).

## 16.2 Life History Characteristics Relevant to Sexual Behavior in Killer Whales

Interpretation of the behavioral and social aspects of sexual interactions in killer whales requires an understanding of their physical characteristics, life history parameters, and reproductive physiology. Most detailed information on killer whale life history has been derived from long-term photo-identification studies of the two Resident populations in BC and Washington State (northern and southern Residents, respectively) (Olesiuk et al. 1990, 2005). The reliability and completeness of this information are due to the extremely stable matrilineal social structure of Residents, in which emigration from the natal group does not normally take place and individual mortalities can be documented with high confidence. Recent studies suggest that the life history parameters of these populations are also typical of at least one Resident population in Alaska (Matkin et al. 2014) and of sympatric Bigg's killer whales (Nielsen et al. 2021). Details of reproductive physiology in killer whales have mostly been obtained from studies on captive whales (Robeck et al. 1993; Duffield et al. 1995; Robeck et al. 2004; Katsumata et al. 2006; Robeck and Monfort 2006; Robeck et al. 2015; Katsumata et al. 2021) and may not always reflect patterns in wild populations.



**Fig. 16.1** Relative sizes of male (top) and female (bottom) Resident killer whales in coastal eastern North Pacific waters. Illustration courtesy of Uko Gorter

### ***16.2.1 Sexual Dimorphism***

Among the family Delphinidae, killer whales are noted for their body size and pronounced sexual dimorphism. They are the largest of the dolphins, with males attaining a maximum length of about 9.0 m and females 7.9 m, although average sizes are somewhat smaller in many populations (Pitman et al. 2007; Ford 2009; Groskreutz et al. 2019; Durban et al. 2021). Mature males are typically about 15% longer than females, but more significantly, males develop disproportionately larger appendages than females (Figs. 16.1 and 16.2). This includes the pectoral flippers, tail flukes, and dorsal fin, which may reach a height of 1.8 m in males, about twice that of females (Ford 2009). As discussed later, sexual dimorphism in killer whales is likely related to the mating system of these large dolphins.

### ***16.2.2 Female Life History Characteristics***

Like many cetaceans, female killer whales have a prolonged maturation period before becoming reproductive. They reach sexual maturity at about 10–11 y of

**Fig. 16.2** Breaching adult male southern Resident killer whale, showing the disproportionately large pectoral flipper characteristic of this sexually dimorphic species. Photograph by Brian Gisborne, taken under research permit issued by Fisheries and Oceans Canada



age, when they begin estrous cycles averaging 41 d in duration (Robeck et al. 2004). Ovulation in killer whales is spontaneous rather than induced (Katsumata et al. 2006). After conception and a gestation period of 17–18 months, they give birth to a single calf (Duffield et al. 1995; Robeck et al. 2015). Hence, a female's first calf is typically born when she is 12–14 years old (Olesiuk et al. 1990, 2005). In Resident killer whales, calving appears to be diffusely seasonal with a peak in late autumn or winter. Given the gestation period, this suggests a peak in conceptions in late spring through summer. Seasonal variation in estrous cycling activity supports this conclusion, as slight increases are observed between March and August (Robeck et al. 1993). Neonate mortality is high, with one-third or more of calves estimated to die within their first six months (Olesiuk et al. 1990). Calves are nursed for at least one year but may start taking solid food from their mother while still nursing. The typical age at weaning in wild killer whales is not known but is likely between one and two years. Juveniles continue to be provisioned by their mothers and other close kin for many years post-weaning and, in the case of male offspring, potentially for the rest of their lives (Wright et al. 2016).

Calving intervals can be as short as two years but more typically average about five years (Olesiuk et al. 2005, Matkin et al. 2014). Females continue to produce calves through their 20s, but by their late 30s to early 40s, they become reproductively senescent (Olesiuk et al. 2005). Because of high neonate mortality, females only have an average of about five surviving calves over their average 25-year reproductive life span (Olesiuk et al. 2005). Female longevity is about 50 years on average, but some may live to 70–80 years (Olesiuk et al. 2005). Thus, their post-reproductive period averages about 10 years but may extend to 30–40 years (Olesiuk et al. 2005). By the time a female becomes an elderly matriarch, she may have three or four generations of living descendants within her matriline.

### ***16.2.3 Male Life History Characteristics***

As with females, male killer whales spend a prolonged period as juveniles or subadults before becoming sexually mature. In the wild, males appear to reach sexual maturity on average at about 13 years, as indicated by a period of rapid growth of the dorsal fin (Olesiuk et al. 2005). Puberty, marked by an increase in serum testosterone, likely starts about two years before this accelerated fin growth (Robeck and Monfort 2006). Serum testosterone also fluctuates seasonally in both pubertal and sexually mature males, with the highest concentrations occurring during the spring and early summer (Robeck and Monfort 2006; Katsumata et al. 2021). This seasonal pattern, similar to that seen in female estrous cycles, probably corresponds to diffuse seasonality in mating opportunities. Sperm concentrations, however, appear to be relatively consistent regardless of season (Robeck and Monfort 2006). Body mass and dorsal fin size continue to increase in males until they reach physical maturity at about 19–20 years. Males may be sexually mature for many years before they become reproductively active and successfully mate when in their mid to late 20s. Average life expectancy for males is estimated to be about 30 years, with maximum longevity of about 50–60 years (Olesiuk et al. 2005).

## **16.3 Killer Whale Sociality**

Many stages of mammalian reproduction are influenced by social structure and dynamics, including mate selection, sexual behavior, mating success, and parental investment. Killer whales are gregarious mammals that exhibit matrilineal social organization, where core social units are composed of closely related females and their offspring. These maternal groups are considered the foundation of all described killer whale societies despite significant ecological differences among them, including fish-eating populations in the western North Pacific (Ivkovich et al. 2010), eastern North Pacific (Bigg et al. 1990; Matkin et al. 1999), and eastern North Atlantic (Bisther and Vongraven 1995; Esteban et al. 2016), mammal-eating populations in the eastern North Pacific (Baird and Whitehead 2000) and eastern North Atlantic (Beck et al. 2012), and generalist populations in subantarctic waters (Guinet 1991; Tosh et al. 2008; Tixier et al. 2021). This kin-based organization benefits an animal's inclusive fitness through cooperative behaviors promoting division of labor (e.g., shared rearing of offspring (Sear and Mace 2008; Konrad et al. 2019) and sharing of resources such as prey (Wright et al. 2016)). In Resident killer whales, females have been shown to markedly improve the survival of their offspring and grandoffspring (Foster et al. 2012a; Natrass et al. 2019), thus enhancing their inclusive fitness, particularly during their post-reproductive life span. Matrilineal social systems commonly arise when females mate with multiple males per estrous cycle; thus paternity is uncertain and consequently there is often little or no investment in offspring by fathers (Greene 1978). Males may increase inclusive

benefits by investing in the offspring of close matrilineal kin (i.e., a male investing in his sister's offspring instead of his own) (Wu et al. 2013). This bias in male investment may be particularly beneficial if resources are shared among the natal groups.

Generally, killer whales form fission-fusion societies, with temporally stable groups of maternally related individuals that may preferentially (i.e., nonrandomly) but temporarily associate with other groups. In fish-eating populations, these intergroup associations can result in multitiered social structures, where preferential but nonhierarchical, casual associations exist among groups (Tavares et al. 2017) or where preferential associations among groups are hierarchical, strong, long-lasting, and often predicted by maternal relatedness (Bigg et al. 1990; Matkin et al. 1999; Parsons et al. 2009; Ivkovich et al. 2010; Esteban et al. 2016). Conversely, more fluid social organization is also observed in some killer whale societies and is common in mammal-eating killer whales, where no definitive social structure beyond the core maternal unit exists and where social associations among groups are often weak and not necessarily predicted by kinship (Baird and Whitehead 2000; Beck et al. 2012; Reisinger et al. 2017; Denkinger et al. 2020). The social structure and dynamics of killer whale societies exhibit plasticity, often influenced by a population's ecology, as well as fluctuations in prey availability and demographics (Lusseau et al. 2004; Williams and Lusseau 2006; Parsons et al. 2009; Foster et al. 2012b; Esteban et al. 2016; Busson et al. 2019; Jordaan et al. 2021; Stredulinsky et al. 2021). For example, foraging strategies may dictate optimal group sizes, resulting in the core social units of mammal-eating populations being generally composed of fewer individuals than those of fish-eating populations (Baird and Dill 1996; Pitman and Ensor 2003; Zerbini et al. 2007; Beck et al. 2012; Higdon et al. 2012; Travers et al. 2018; Denkinger et al. 2020).

Killer whales exhibit natal philopatry, where individuals of both sexes remain with their natal group. The longevity of this group fidelity varies among killer whale populations and sexes. For example, in Bigg's populations, individuals of both sexes have been known to leave their natal groups at or near maturity (Baird and Dill 1996; Baird and Whitehead 2000). Dispersal in Bigg's killer whales appears to occur via female-biased budding events, with a decline in close social associations between daughters and their mothers as daughters age, beginning after a daughter has had at least one calf (Nielsen et al. 2023). Unlike females, male Bigg's killer whales tend to maintain strong social bonds with their mothers throughout life and are considered partially or fully philopatric (Nielsen et al. 2023). In contrast to Bigg's killer whales, Residents exhibit extreme bisexual social philopatry, where both sexes remain with their natal group throughout life and individual dispersal is exceedingly rare (Matkin et al. 1999; Ford et al. 2000; Parsons et al. 2009). Resident killer whales thus live in highly stable groups composed of a female, her offspring, and up to five generations of her descendants through maternal lines (Bigg et al. 1990). These maternal groups are the foundation of Resident killer whale society, which is hierarchically organized (Table 16.1). Since group size is not moderated by individual dispersal in Resident killer whales, matrilineal splitting provides the only mechanism by which new groups can form (Bigg et al. 1990; Stredulinsky et al. 2021).



**Table 16.1** Resident killer whale social organization

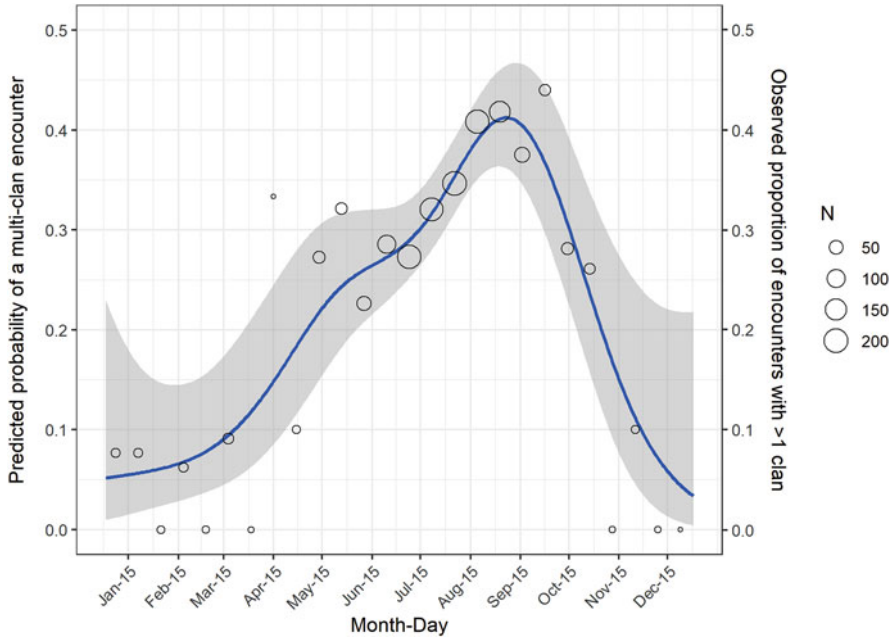
Term	Definition
Maternal group	Individuals descended from a common direct maternal ancestor (matriarch) that always travel together (Bigg et al. 1990). Maternal groups are named after the most recent matriarch of the group and are the core social unit of Resident killer whales.
Pod	An assemblage of maternal groups that, on average, spend more than 50% of their time together (Bigg et al. 1990). Pods are composed of one or more maternal groups. Maternal groups found in the same pod likely share a common maternal ancestor (i.e., belonging to the same matriline). New pods form when group splitting occurs. Pod membership is typically stable but not permanent (Parsons et al. 2009); this social grouping may only maintain cohesion for a decade or less, depending on group size, demographics, relatedness, and/or ecological factors (Stredulinsky et al. 2021).
Clan	Maternal groups with vocal dialects that include shared call types. Call repertoires of clans can persist for at least 60 years and likely longer. Different clans are acoustically distinct and may represent separate matriline (Ford 1991).
Population	A community of one or more clans that associate with one another. May be sympatric with but does not mix socially with other populations (Bigg et al. 1990).

A matriline denotes all individuals descended from a common maternal ancestor. Direct maternal ancestors refer to individuals from whom one descends in a direct line through mothers (i.e., mother, maternal grandmother, maternal grandmother's mother, etc.). Adapted from the "Social Groupings" section of Table 16.1 by Stredulinsky et al. (2021) – footnotes removed, used under CC BY

## 16.4 Exogamy and Inbreeding Avoidance in Eastern North Pacific Ecotypes

Little is known about mate choice and inbreeding in killer whales outside of the well-studied Resident ecotype of the eastern North Pacific, and so we focus on them here as a case study. We also briefly touch on possible mechanisms of inbreeding avoidance in the sympatric Bigg's killer whale. Despite neither sex dispersing from the natal group, Resident killer whales largely avoid inbreeding by mating with unrelated individuals during temporary multigroup associations (Barrett-Lennard 2000). These aggregations are sometimes termed "superpods" (Matkin et al. 1997) and are characterized by high levels of acoustic and social activity (Ford 1989) and reduced foraging rates (Hoelzel 1993). In northern Residents, the probability of encountering aggregations of whales from multiple acoustic clans increases during the summer and into the early autumn (Fig. 16.3). The majority of mating therefore likely occurs between June and October, a pattern that is also reflected in the seasonality of female estrous cycles, male serum testosterone levels, and calving. Copulation itself is rarely (if ever) observed in killer whales, likely because it happens underwater, can be hard to distinguish from other active social or play behaviors, and is thought to be very brief. Cetaceans have a fibroelastic (rather than vascular) penis, and thus it has been suggested that intromission is rapid and only lasts between 1 and 30 seconds; limited observations of mating behavior in wild





**Fig. 16.3** Predicted probability (blue line) of multi-clan northern Resident encounters as a function of day of the year, modeled using photo-identification data collected by the Fisheries and Oceans Canada between 1973 and 2021. Gray shading indicates 95% confidence intervals, and open circles indicate the proportion of observed encounters in each two-week bin that included whales from more than one clan (circle size indicates the total number of encounters per bin). Model uncertainty is greater in the winter months due to the paucity of winter encounter data; however, the available data indicate that multi-clan encounters are much less likely during this season

and captive delphinids appear to support this claim (Slijper 1966; Markowitz et al. 2023, this book).

Similar large, multi-pod, or multi-clan aggregations are also reported in southern Alaska (Olsen et al. 2020) and Russian Far East (Filatova et al. 2009) Resident killer whale populations. Social interactions are frequent and energetic during these aggregations, while time spent foraging and resting decreases (Filatova et al. 2009; Olsen et al. 2020). In southern Alaska Residents, observations of social interactions increase with the overall number of pods and number of rarely encountered pods present (Olsen et al. 2020), and in Russian Far East Residents, social activity increases with both number of pods and number of acoustic clans present. This suggests that large aggregations of other fish-eating killer whale populations provide outbreeding opportunities for unrelated individuals to mate with one another (Filatova et al. 2009; Olsen et al. 2020), just as they do in northern and southern Residents. Rarely encountered groups of southern Alaska Residents that travel long distances beyond their normal home ranges may do so for this purpose (for instance moving between southeastern Alaska and Prince William Sound, a distance of more than 800 km) (Matkin et al. 1997). During such aggregations, mature males often

temporarily abandon their natal groups to closely follow reproductive females from other groups (Matkin et al. 1997). As in the northern Resident multi-clan model (Fig. 16.3), southern Alaska Residents form multi-pod aggregations from May to October (Olsen et al. 2020) but most often in July and August (Matkin et al. 1997), and Far East Russian Residents aggregate in large groups from late June to early September (Filatova et al. 2009).

Bigg's killer whales also socialize more and forage less as group size increases, probably for the same reason as Residents. Large aggregations of multiple maternal groups likely provide increased mating opportunities and facilitate outbreeding (Baird and Dill 1995). Outbreeding in Bigg's killer whales is also promoted by (or potentially drives) this ecotype's greater fluidity in social group membership relative to Resident killer whales, and consequently, Bigg's killer whales have a higher level of genetic diversity (Barrett-Lennard 2000). Dispersing from the natal group either permanently or temporarily, which is observed in both sexes of Bigg's but is especially prevalent in females (Nielsen et al. 2023), may reduce intragroup sexual competition and increase the probability of finding unrelated mates (Baird and Dill 1996; Baird and Whitehead 2000; Towers et al. 2019). Dispersing male Bigg's that travel alone rather than integrating themselves into other social groups (also known as "roving" males; Baird 1994) may do so to increase their chances of encountering and mating with as many unrelated females as possible; however, only eight instances of this type of permanent dispersal have been documented so far for males with living mothers (Nielsen et al. 2023). Other Bigg's males may become solitary without dispersing, since some Bigg's social groupings consist of only a post-reproductive matriarch and her adult son, who travels alone after his mother's death (Towers et al. 2019). Bigg's killer whales do not have kin-specific dialects at the matriline or pod level (Deecke et al. 2005; Ford 2019); hence, they lack the potential benefit of an acoustic outbreeding mechanism as is believed to exist in Residents (Barrett-Lennard 2000).

Exogamous mating is assumed in many Resident killer whale populations based on increases in sociosexual behavior during multi-pod and multi-clan aggregations and has been proven to occur in northern Residents. Paternity analyses revealed that northern Resident calves are sired by males from maternal groups other than their own and are usually sired by males from different pods as well as different acoustic clans (Barrett-Lennard 2000). Females are likely to benefit by selecting the least related males as mates, as these pairings produce offspring with the lowest likelihood of deleterious mutations, which may reduce calf survival. Exogamous mating is evident in the negative inbreeding coefficients calculated at pod ( $-0.112$ ) and clan ( $-0.064$ ) levels, which indicate that individuals from the same northern Resident pod or clan are more heterozygous than expected if mating was random (Barrett-Lennard 2000). Conversely, mating in southern Residents appears to be random in terms of the maternal groups that breeding pairs belong to (Ford et al. 2018), which may be due in part to small population size (i.e., limited number of potential mates). In a recent genetic pedigree of southern Residents, intra-pod matings were relatively common, and of 81 offspring for which both parents had been identified, 4 were inbred (Ford et al. 2018). These individuals were the products of two parent/

offspring, one half-sibling and one uncle/half-niece mating. A weak relationship was detected between multi-locus heterozygosity and survival in southern Residents, suggesting that inbreeding depression could be impacting this population (Ford et al. 2018). The lack of discernible exogamy in southern Residents, as well as the occurrence of inbreeding and intra-pod mating, is probably due to this population having only a single acoustic clan and a relatively small number of reproductive individuals. Male reproductive success in northern and southern Residents is highly variable and positively related to body size (Fearnbach et al. 2011), with the oldest, physically mature males siring the vast majority of offspring (Barrett-Lennard 2000; Ford et al. 2011b; Ford et al. 2018). For instance, over half of sampled southern Residents born since 1990 were sired by one of only two males, and the median male age at successful reproduction was 31 years (range = 16–59 years) (Ford et al. 2018). Thus, the small number of physically mature males of prime breeding age may also play a role in the prevalence of inbreeding in the southern Residents.

Mating decisions in Resident killer whales are likely guided by various social cues that allow individuals to distinguish between kin and nonkin, thus facilitating outbreeding. These cues include visual recognition of close maternal kin through associative learning (i.e., familiarity), as well as acoustic recognition of individual (Nousek et al. 2006) and group-specific call repertoires (Ford 1989, 1991; Barrett-Lennard 2000). Because vocal dialects are learned within maternal groups, they do not provide a means of identifying paternal kin, as fathers belong to different groups than their offspring and therefore do not share acoustic repertoires. Despite this, father-daughter matings have never been detected in northern Residents (Barrett-Lennard 2000) and only one such mating has occurred in southern Residents (Ford et al. 2018), so heritable mechanisms of paternal kin recognition may also exist. Conversely, Resident killer whales may have no system of paternal kin recognition, and father-daughter matings are largely prevented because older males engage in the majority of breeding. It is probable that most fathers have died by the time their daughters become reproductively mature (Wright et al. 2016; Ford et al. 2018).

## 16.5 Sexual Strategies and Mating Systems in Killer Whales

The highly skewed reproductive success of male Resident killer whales suggests that some selective mechanism prevents all but a few males from siring offspring. Variable male reproductive success could be driven either by intrasexual selection (such as contest competition, mate-guarding, coercive mating, and sperm competition) or by intersexual selection in which females choose mates based on specific traits (i.e., signal discrimination). We discuss the current scientific evidence for these possible mating tactics as they relate to Residents and other killer whale populations.

### ***16.5.1 Female Mate Choice and the Evolution of Sexual Dimorphism and Modified Genitalia***

The sexual dimorphism in body length and mass in killer whales indicates that there is a selective advantage conferred on males that attain large body sizes. This advantage is likely the driving factor behind provisioning behavior by northern Resident matriarchs, who preferentially share fish with their adult sons, probably as a form of kin selection that enhances the body condition of sons and thus bolsters their likelihood of reproductive success (Wright et al. 2016). While large body size could benefit males during aggressive contest competition, as large males are expected to be more successful in physical confrontations, it is more likely that large males experience greater reproductive success due to female mate choice (Ford et al. 2011b; Caspar and Begali 2022). Female preference for large body and appendage size (i.e., signals of male quality) probably initiated runaway selection favoring males that exhibit these traits, which are energetically costly to maintain. Large appendages (flukes, pectoral flippers, and dorsal fins) may reduce male maneuverability (Fig. 16.2) during aggressive interactions and thus may have evolved as a result of display competition rather than contest competition. Female mate choice explains the large degree of skew in male Resident killer whale reproductive success (Barrett-Lennard 2000; Ford et al. 2011b), with females allowing only the oldest and largest males to sire their offspring. This skew would be further enhanced if females engage in mate choice copying (as suggested for another matrilineal species, the sperm whale (Orbach 2019)). It is not known whether mate choice copying exists in female killer whales, but paternity analysis for similar aged calves belonging to the same maternal groups could provide more evidence to prove or refute this hypothesis. In addition to visual signals of male quality, female mate choice in killer whales is also likely guided by signals that promote outbreeding, such as vocal dialects.

Female killer whales may also exert control over which males sire their offspring through the evolution of modified genitalia. Vaginal folds seem to allow female cetaceans to physically obstruct the depth of penile penetration and thus lower the likelihood of fertilization. Consequently, a female could cause an undesirable male's sperm to be deposited farther from the ovum into blind end vaginal recesses by changing her body orientation during copulation, in a type of cryptic mate choice (Orbach et al. 2017). This tactic may be less costly to females than direct resistance of mating attempts by lower-quality males (Orbach et al. 2017). Antagonistic coevolution of penis morphology in male cetaceans probably arose in response to the evolving complexity of the female genital tract (Orbach et al. 2017). In killer whales, the penis has a thin elongated tip, with a conspicuous curl or bend (Fig. 16.4) that likely assists males in overcoming the barriers to fertilization posed by vaginal folds. It is also possible that the exaggerated size of male pectoral flippers (Fig. 16.2) may assist males in holding onto females during copulation, thus countering evasive movements.



**Fig. 16.4** Male southern Resident killer whales engaging in sociosexual play behavior; the individual in the foreground is swimming on its side, with the pectoral fin and penis visible above the water's surface. The thin, elongated tip of the penis with its characteristic curl is also evident. A ten-year-old subadult male (J45) is visible swimming alongside. Photograph by Sara Tavares, taken under research permit issued by Fisheries and Oceans Canada

### ***16.5.2 Male Intrasexual Aggression***

While observations of aggressive interactions between male killer whales have not been reported, this may be partly due to the difficulty of detecting underwater behaviors. Such interactions may also escape notice if they are infrequent or of short duration, and because they are likely to occur during dynamic superpod encounters when large numbers of individuals are present, social groups are constantly mixing, and whales are engaging in other surface-active, percussive, or body contact behaviors. Aggression between males may fail to leave visible scars, for instance, if combatants strike one another with their flukes or use their rostrums as battering rams (Connor et al. 2000). However, tooth rake scars are reported in many odontocetes worldwide (McCann 1974; MacLeod 1998), including killer whales, and can be used to estimate the level of aggression between conspecifics (Scott et al. 2005; Robeck et al. 2019; Ham et al. 2021; Grimes et al. 2022). Tooth rake marks are common on the skin of both Resident and Bigg's killer whales of the eastern North Pacific and occur across all sex and age classes, indicating that at least mild aggressive behavior is a routine means of social communication (Robeck et al. 2019; Grimes et al. 2022). Since killer whales are apex predators, and since ecotypes actively avoid associating with one another (Bigg et al. 1990), tooth rakes are

assumed to arise from interactions between individuals belonging to the same population.

In northern Residents, rake mark frequency and density are significantly higher in adult males than in females or juveniles and also increase with male age (Robeck et al. 2019). This suggests that male northern Residents may engage in physical aggression as a means of competing for sexual partners or to establish dominance hierarchies related to reproduction. Aggressive interactions could function either to physically exclude other males from accessing females in estrus (i.e., contest competition) or could be ritualized displays meant to influence female mate choice (i.e., display competition). The latter is more likely, as previously discussed. Females might observe these interactions and allow the victor to mate or may select mates with more scarring as an indication of male quality (MacLeod 1998; Orbach 2019). Males may also use existing scars to evaluate the relative fighting ability or dominance rank of competitors and thus avoid costly aggressive interactions that they are unlikely to win (MacLeod 1998, Orbach 2019). The frequency of severe rake marks (covering >50% of the observable body area) was eight times greater in male northern Residents over 30 years of age than in males belonging to the next youngest age class (25–29 years) (Robeck et al. 2019). As the primary breeders, older males are the most likely to engage in aggressive contests with one another for access to females and thus would be expected to receive more rake marks than other demographic categories (Robeck et al. 2019). It is also possible that the higher incidence of rake marks and scarring evident on mature male northern Residents actually arises from adult females attempting to fend off unwanted mating attempts. Unless they are very deep, rake marks on killer whale skin heal over time and are generally thought to persist for <2 years (Bigg 1982; Robeck et al. 2019). Thus, the greater incidence of scarring on the oldest males reflects higher frequencies of recent aggressive interactions, rather than a lifetime accumulation of marks. Male-male aggressive interactions likely occur when multiple groups of Resident killer whales from different maternal groups aggregate temporarily for socializing and mating, given that males remain philopatric and mating is exogamous (Barrett-Lennard 2000).

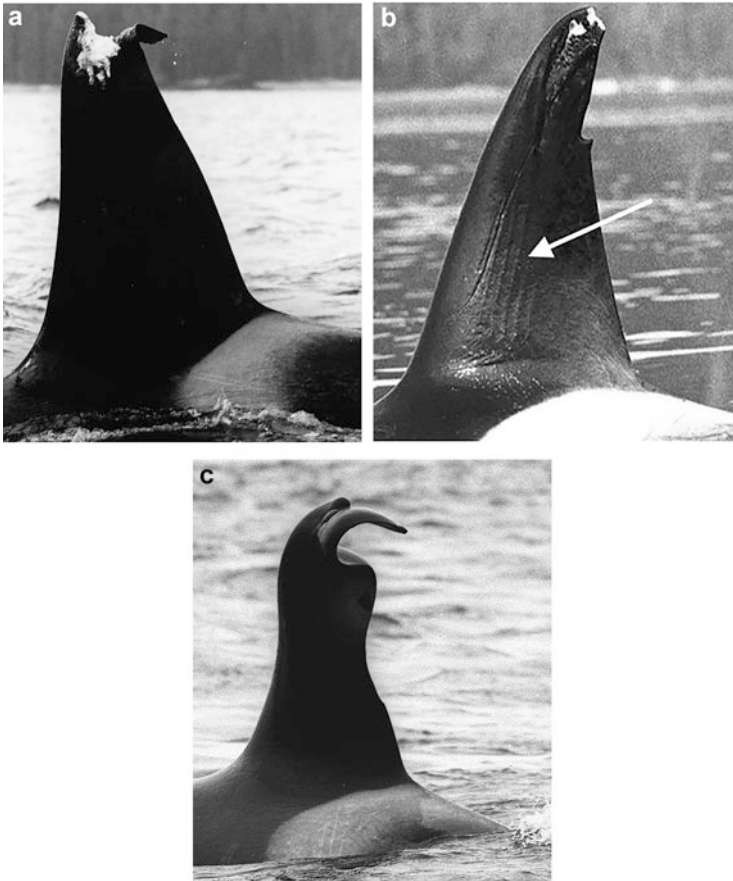
Male Bigg's killer whales show a similar increase in rake mark acquisition with age when compared to male northern Residents (Robeck et al. 2019). Male Bigg's could receive these rake marks during intrasexual competition as well, although under slightly different circumstances given the more fluid social structure of this ecotype. There is evidence that lone (or "roving") males occasionally disperse from their natal groups at sexual maturity (Baird and Dill 1996), a behavior that may be related to searching for mating opportunities. However, adult female Bigg's killer whales also show a similar degree of rake mark injuries to that of adult males. Tooth rake marks in this ecotype may therefore result from dominance interactions that occur whenever dispersing individuals attempt to integrate themselves into new groups, whether for breeding or other purposes (Robeck et al. 2019). As in northern Residents and Bigg's, rake marks are common in all demographic categories of the southern Resident population, and males exhibit higher densities and frequencies of scarring than females (Grimes et al. 2022). However, older adult male Southern

residents (>20 years) have fewer rake marks than younger individuals (Grimes et al. 2022), the opposite pattern to northern Residents, implying that little aggression occurs among males of breeding age in this population. This could be due to the smaller size of the southern Resident population, which currently (as of 2022) contains only nine males >20 years and of these only three are >30 years (Center for Whale Research 2019). Intrasexual competition between males may therefore be less prevalent in southern Residents if only the oldest and largest males are allowed to mate and there are very few animals in contention for these breeding opportunities. Young adult males that have yet to attain their full body size would be unlikely to initiate aggressive interactions with larger competitors if contests are expected to end in injury or defeat.

Observations of adolescent and adult male killer whales with moderate to severe dorsal fin injuries provide further evidence of potential male-male aggression in this species. These injuries often begin with bite or rake marks on the dorsal fin that are clearly made by the teeth of conspecifics (Fig. 16.5), producing fin disfigurements that can become progressively worse over a span of months or even years (Fig. 16.6). The dorsal fins of male killer whales are almost twice as tall as those of females (Ford 2014) and, as discussed previously, are a secondary sexual trait that likely evolved as a signal of male fitness valued by potential mates (i.e., intersexual selection via female mate choice; Alves et al. 2017). As such, they are undoubtedly physiologically costly to maintain and may be particularly vulnerable to buckling or collapse; even seemingly minor wounds can lead to fairly dramatic fin disfigurements, including significant tissue loss at the fin tip, buckling of the trailing edge (Fig. 16.5), and occasionally partial or complete dorsal fin collapse (Fig. 16.6).

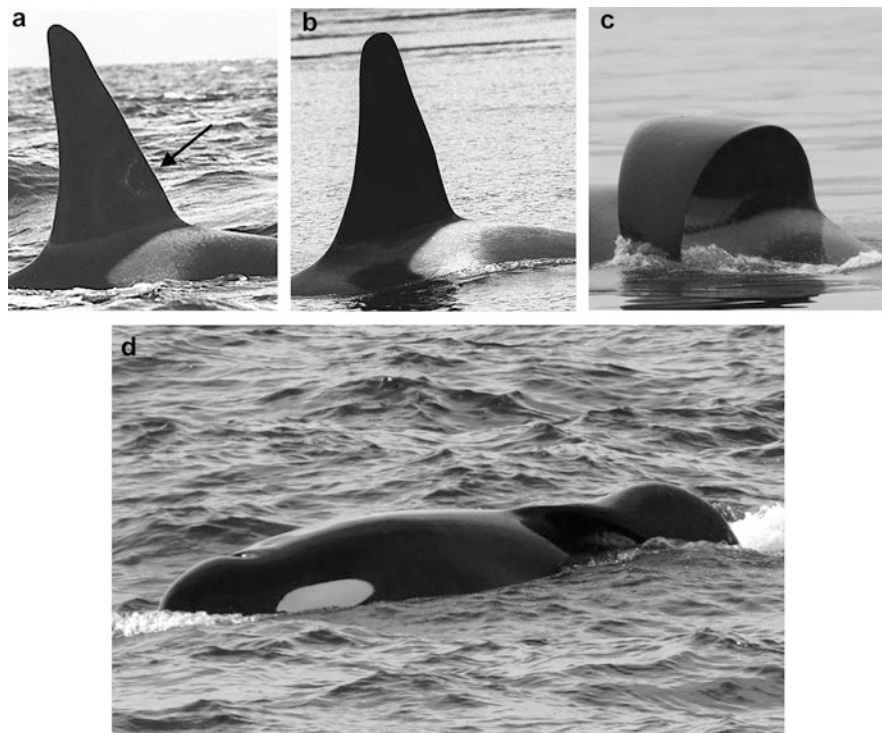
An analysis of photo-identification records from 2007 revealed that about 18% of northern Resident males and 4% of west coast Transient males (>12 years) display evidence of progressive dorsal fin injuries (Fisheries and Oceans Canada, unpublished report). On average, males are first injured at about 20 years of age (coinciding with the approximate onset of physical maturity, when they are more likely to compete with one another for breeding opportunities); however, these injuries do not appear to impact overall life span. Similar to northern Residents, 23% of adult males in a New Zealand fish-eating killer whale population showed evidence of abnormal, wavy, collapsing, or fully collapsed dorsal fins (Visser 1998). Two of the males with abnormal dorsal fins from New Zealand also had prolific tooth rake scars over large portions of their bodies. A more recent study of collapsed dorsal fins indicates that this type of abnormality is present in about 1–6% of photo-identified killer whales, depending on the region and population, and that the vast majority (>90%) of individuals with bent fins are males (Alves et al. 2017). The large size of male dorsal fins likely makes it an easy—and given its immobility, less dangerous—appendage for other whales to grasp with their teeth during aggressive interactions (see rake marks in Fig. 16.5, image *b*, and bite mark in Fig. 16.6, image *a*). For this reason, dorsal fins may be specifically targeted during such altercations if damaging another male's fin inflicts a future signaling (and therefore fitness) disadvantage. Once a male killer whale's dorsal fin has buckled or collapsed, photo-identification data suggest that it will not regain its previous shape. Because dorsal





**Fig. 16.5** Examples of dorsal fin wounds sustained by adult male northern Resident and Bigg's killer whales of the northeast Pacific, likely as a result of intrasexual aggression. Injuries include significant tissue loss (northern Resident killer whale H07 at 25 years old, photographed by Graeme Ellis, *a*), tooth rake marks (west coast Transient killer whale T74 at 24 years old, photographed by Dena Matkin, *b*), and buckling of the trailing edge (northern Resident H04 at 24 years old, photographed by John Ford, *c*). Photographs *a* and *c* were taken under research permit issued by Fisheries and Oceans Canada, and photograph *b* was taken under research permit issued to the North Gulf Oceanic Society by the National Oceanic and Atmospheric Administration (NOAA) and National Park Service (Glacier Bay National Park and Preserve)

fin injuries and associated cases of fin collapse are somewhat uncommon, we suspect that aggressive competition between males plays a minor role compared to female mate choice in killer whale mating systems. However, in populations where body scarring is more prevalent among mature males than other demographic classes (e.g., northern Residents) and where dorsal fin injuries appear to be inflicted by conspecifics, contest competition or ritualized displays of aggression may be occurring to some extent.



**Fig. 16.6** Progression of dorsal fin collapse in the adult male northern Resident B13, beginning with a bite mark visible along the trailing edge (indicated with arrow), probably sustained from male-male intrasexual aggression. The first wound appeared when this individual was 16 years old (*a*) and the fin tip displayed evidence of curling by the following year (*b*, both photographs by Graeme Ellis). The collapse of the dorsal fin progressed until it was folded over to the left side of the whale's body about three years after the original wound occurred (*c*, photograph by Jared Towers), and it had completely collapsed by the time the whale was 20 years old (*d*, photograph by Mark Malleeson); after which no further changes were observed. All photographs taken under research permit issued by Fisheries and Oceans Canada

### 16.5.3 Male-Male Sociosexual Play

In addition to potentially interacting aggressively, male northern Resident killer whales also frequently form male-only “play” groups in which males of all but the youngest age class (calves <3 years) engage in sociosexual behaviors (Rose 1992). These are temporary groupings, lasting from several minutes to hours. Groups typically consist of pairs, although groups of three or four killer whales occur in about a third of such events, and group membership is often fluid (Rose 1992). Adolescent males (12–25 years) participate more often than juveniles (<12 years) or adults (>25 years), and unrelated individuals are typically favored as partners over matrilineal kin (Rose 1992). Males in these groups exhibit active, at-surface behaviors including chasing, rubbing, head-butting, beak-to-urogenital slit body

orientations, percussive fluke slaps, aerial breaches, and penile displays (Fig. 16.4) (Jacobsen 1990; Rose 1992). On occasion, individuals attempt to insert their penises into the genital slits of other males in the group (Rose 1992). Physical contact is usually reciprocal rather than unilateral and declines in frequency with age (Jacobsen 1990; Rose 1992). Sociosexual play groups are an important component of male behavior in northern Residents, with individuals spending an average of >10% of their total activity budget in this manner (Rose 1992). As adolescents participate four times more often than adults, and because behaviors are typically reciprocal, it has been proposed that male-only social groupings in Resident killer whales represent affiliative play interactions, rather than functioning to establish or maintain dominance hierarchies (Rose 1992). These groupings likely allow young males that are sexually but not yet socially mature to practice their courtship skills and may provide an outlet for the libidos of adolescent males that are not yet old enough to successfully breed. While direct observations of mating behavior in killer whales are extremely rare (Barrett-Lennard 2000), adult male northern Residents have been observed interacting with females using stereotyped behaviors that mirror those performed in male-only play groups (e.g., reciprocal beak-genital body orientations) (Jacobsen 1990). This supports the hypothesis that play groups serve as practice opportunities for males to become proficient in courtship and mating behaviors (da Silva and Spinelli 2023, this book; Ham et al. 2023, this book). The purpose of reciprocal beak-genital body orientations in killer whale courtship behavior is currently unknown; however, similar contact behaviors have been observed in other delphinid species during sociosexual activity states (Bearzi and Politi 1999; Markowitz et al. 2023, this book). This behavior is unlikely to be related to olfactory or pheromone cues, as odontocetes lack the vomeronasal (Jacobson's) organ and associated receptor genes used by terrestrial mammals for detecting reproductive pheromones, and unlike mysticetes, anatomical and genetic evidence suggests that odontocetes have little to no sense of smell (Kishida et al. 2007; Berta et al. 2014; Suzuki et al. 2018).

#### ***16.5.4 Coercive Mating, Male Breeding Alliances, and Infanticide***

Coercive or forced mating by individual males seems unlikely in killer whales (or cetaceans in general), as herding or restraining females in an underwater, three-dimensional environment would prove difficult for a single male (Whitehead and Mann 2000). Adult female killer whales are also more maneuverable than mature males, given their smaller body and appendage sizes, and presumably this allows them to avoid unwanted mating attempts. In addition to greater maneuverability, females may also use physical aggression to defend themselves from unwanted copulations, possibly contributing to adult male body scarring (as described in previous section). Groups of males may employ social alliances to herd or gain reproductive access to females, a strategy that is rare in mammals but occurs in other

delphinids such as bottlenose dolphins (*Tursiops* sp.) (Wells et al. 1987; Connor et al. 2001; Möller et al. 2001; Parsons et al. 2003), Atlantic spotted dolphins (*Stenella frontalis*) (Elliser and Herzing 2014), and possibly Risso's dolphins (*Grampus griseus*) (Hartman et al. 2008). However, there is no evidence that this behavior occurs in killer whales. Alliance formation appears to be less prevalent in those bottlenose dolphin populations with more pronounced sexual size dimorphism (Connor et al. 2000), likely because selective pressure is acting on traits relevant to male contest competition, rather than on formation of male social bonds (Brightwell and Gibson 2023, this book). Consequently, male alliances are also unlikely to arise as a sexual strategy in killer whales, as they are the most sexually dimorphic of any dolphin species and display evidence of potential intrasexual aggression (tooth rake marks and dorsal fin injuries). Given the scarcity of observations of killer whale mating behavior in the wild, however, and the expected direct and inclusive fitness benefits (Krützen et al. 2003; Parsons et al. 2003) if brothers were to form mating coalitions within their maternal groups, it is still possible that male reproductive alliances could exist in this species. But it is much more probable that female killer whales have a large degree of control over which males they allow to mate, and their matrilineal social structure (resulting in strong bonds between female relatives) may also confer some protection if females band together to prevent forced copulations (Gowans et al. 2007).

Infanticide is a type of delayed sexual coercion in which adult males kill young that they are unlikely to have sired; this behavior may increase a male's reproductive success by causing postpartum females to return to estrus more quickly (Connor et al. 2000; Lukas and Huchard 2014). Although observed in other delphinid species (McEntee et al. 2023, this book), only one observation of infanticide has been reported in killer whales; a mature male Bigg's killer whale and his post-reproductive mother killed the neonate of a maternally unrelated female from the same population (Towers et al. 2018). With no other observations of infanticidal behavior, it is unclear whether infanticide is an aberrant behavior in killer whales or whether it serves an adaptive function by increasing a male killer whale's mating opportunities. Killer whales conform to some of the life history characteristics that promote the evolution of infanticide, namely, they are continuous breeders and relatively few males may monopolize the majority of reproduction (Lukas and Huchard 2014). However, it seems unlikely that infanticide constitutes a widespread sexual strategy if paternity is tenuous, because a male might kill his own offspring rather than a rival's. This is probably the case for many killer whale populations given their apparent lack of paternal kin recognition, the ephemeral nature of associations between mating pairs, and the likelihood that females mate with multiple males each estrous cycle. Mating with multiple males may constitute a sexual counterstrategy by which females confuse paternity to avoid infanticide (McEntee et al. 2023, this book), initiating an evolutionary arms race of male strategies related to sperm competition, such as increased relative testes size (Lukas and Huchard 2014), a trait which killer whales also exhibit. Species with large testes often experience secondary loss of infanticide (Lukas and Huchard 2014), so it is possible

that male killer whales engaged in infanticide more frequently in their evolutionary past but are currently transitioning away from this sexual strategy.

### ***16.5.5 Sperm Competition and Polygynandrous Mating***

The pronounced sexual dimorphism, signs of male-male aggression, and highly skewed male reproductive success evident in killer whales indicate a mating system in which males compete for access to estrus females (Connor et al. 2000). Competition to determine which males successfully sire offspring probably takes the form of displays that influence female mate choice, possibly in combination with occasional aggressive interactions between males. Selection for signals of male quality (e.g., body and appendage size) is therefore high. Additionally, female killer whales may mate with multiple males per estrous cycle, which is expected given their matrilineal social structure. It is likely that killer whales thus have a polygynandrous mating system in which individuals of both sexes mate with multiple partners, and therefore post-copulatory selection in the form of sperm competition may also occur. Sperm competition results when sperm from different males compete to fertilize the same ovum (Parker 1970; Smith 1984; Stockley and Purvis 1993). More sperm per ejaculate, greater ejaculate volume, and the ability to mate more frequently can all improve a male's likelihood of successfully siring offspring, and these traits are thus adaptive under sperm competition. Investment in testes mass as a percentage of body mass is used to infer the extent of sperm competition (and by association, the likelihood of females mating with multiple males) in mammals (Harcourt et al. 1981; Connor et al. 2000). Cetaceans tend to have slightly larger testes compared to similarly sized terrestrial mammals (Kenagy and Trombulak 1986; Aguilar and Monzon 1992), and most delphinids have larger testes than predicted by a regression of testes on body weights across all cetacean families (Aguilar and Monzon 1992). Killer whales are ranked intermediately (13th of 31 species analyzed) in this measurement (MacLeod 2010), suggesting that killer whale mating tactics involve some degree of sperm competition. Killer whales also have long penises relative to their body length (Carl 1946), a trait which occurs in cetacean species that engage in sperm competition, presumably because selection favors males that can deposit their sperm as close to the ovum as possible (Brownell and Ralls 1986; Dines et al. 2014). Furthermore, an elongated penis likely helps overcome the barriers presented by vaginal folds (Orbach et al. 2017) and may also have arisen as a counterstrategy for combating evasive movements by females during unwanted copulation attempts.

For continuous breeders like killer whales, larger males are predicted to achieve more favorable copulation timing, and smaller males should therefore invest more in sperm production to overcome this disadvantage (Stockley and Purvis 1993). Under this scenario, the correlation between testes and body size of individual males is predicted to weaken, which appears to hold true for killer whales (based on measurements from Norwegian and Antarctic populations) and further implies that sperm competition occurs to some extent (Stockley and Purvis 1993). In addition,

the transcription factor GATA4, which is involved in testes development (Kyrönlahti et al. 2011), shows a fixed difference in eastern North Pacific Residents compared to other killer whale ecotypes, a genetic change that could reflect increased sperm competition (Moura et al. 2014). Sperm competition may provide a selective advantage to male Residents, since mating occurs in large but temporary multigroup aggregations and it is presumably difficult for individual males to monopolize or guard access to receptive females. Unless females avoid mating with all but the highest-quality male they encounter, it is likely that they could mate with multiple males in quick succession during these superpod events.

### ***16.5.6 The Role of Acoustic Behavior in Killer Whale Reproduction***

Other than the role that acoustic dialects (Ford 1989, 1991) likely play in mate choice and inbreeding avoidance in Resident killer whales (Barrett-Lennard 2000), little is known about how vocalizations are used during courtship and mating in this species. Since killer whales are highly vocal and possess complex acoustic repertoires (Ford 1989, 1991), and given that acoustic signals travel much farther underwater than visual ones, vocal behavior is likely an important component of killer whale mating systems. Vocalizations by male animals can serve as displays of reproductive quality to attract nearby females (e.g., Eriksson and Wallin (1986)), stimulate female solicitation behaviors (e.g., McIntosh et al. (1978), Baker and Baker (1988)), influence female estrous cycles (McComb 1987), or advertise dominance to competing males (e.g., Krebs et al. (1978)). In cetaceans, male vocal behavior has been theoretically linked with mating strategies. Examples include mature male sperm whales using slow clicks (Weilgart and Whitehead 1988) and male Atlantic spotted dolphin alliances using synchronized vocalizations (Herzing 2015) to drive away potential competitors, male bottlenose dolphins using popping vocalizations as a threat signal to compel female consorts to remain close by (Smolker and Connor 1996), and male mysticetes using songs to either influence female mate choice or exclude competitors (Payne and McVay 1971; Glockner 1976; Croll et al. 2002; Schall et al. 2020; Kowarski et al. 2022). Vocalizations linked to reproduction could also be used by female killer whales—either to indicate to males that they are in estrus or conversely females might remain silent to avoid detection and mating attempts by undesirable males. Vocal behaviors are likely an incredibly important component of killer whale mating systems and one that remains to be explored fully.

## 16.6 Conclusions and Future Directions

This chapter summarizes the current available knowledge about sexual behavior and mating systems in the killer whale, largely based on data from the well-studied Resident ecotype of the eastern North Pacific. Killer whale mating patterns appear to be primarily driven by pre-copulatory intersexual selection, in which female preference for large body and appendage size in males has led to skewed male reproductive success and the evolution of extreme sexual dimorphism in this species. Displays of intrasexual aggression, as evidenced by tooth rake scars and dorsal fin injuries, may play a secondary role in determining which males successfully sire offspring. Females also appear to select mates based on maternal group membership, using acoustic and visual kin recognition to determine which males are least closely related to them, presumably as a means of inbreeding avoidance. Mating is thus more prevalent during the late spring through early fall, when large aggregations comprised of multiple maternal groups are more commonly observed. During adolescence, young male Resident killer whales practice courtship behaviors with other males in sociosexual play groups. Killer whales are probably polygynandrous (i.e., both sexes mate with multiple partners), and the coevolution of testes size, penis length, and penis morphology in males with genital tract complexity in females implies that post-copulatory sexual selection (i.e., sperm competition) may also occur in this species.

Additional genetic pedigree studies, particularly for ecotypes other than Residents, are needed to provide information about mating patterns for other populations of killer whales. Paternity analysis of similar-aged calves belonging to the same maternal groups could clarify whether female killer whales engage in mate choice copying, a behavior that could further skew male reproductive success. Focal-follows or other detailed behavioral studies of social interactions during multigroup aggregations (i.e., superpods), including the application of emerging data collection technologies such as unoccupied aerial vehicle (UAV, Ramos et al. 2023, this book) and underwater video footage, could provide the first descriptions of courtship and copulation behavior in wild killer whales. Acoustic recordings made in conjunction with these visual observation techniques would help clarify the role of vocal behaviors in killer whale mating systems. These approaches could also be used to confirm the existence of male intrasexual aggression and elucidate its potential role in breeding success.

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