Chapter 20
Reproductive Tactics in Baleen Whales

Franca Eichenberger, Ellen C. Garland, and Emma L. Carroll

Abstract While a variety of reproductive tactics are readily witnessed in odontocetes, such behaviors can be far more elusive in baleen whales and in some cases are yet to be observed. This leads researchers to study the reproductive behaviors in mysticetes using a variety of research methods which have improved greatly in recent years. Genetics and genomics tools can provide valuable information on maternity, paternity, age, diversity, and kinship, while acoustic tools can provide new insights into the function of sexual displays such as song. In this chapter, we explore what is known about reproductive strategies and tactics of baleen whales, with a particular focus on the comparatively well-studied right whales (*Eubalaena* spp.) and humpback whale (*Megaptera novaeangliae*). Finally, we showcase that by integrating multiple data types, we can explore the interactions between anatomy, physiology, reproductive success, age, population dynamics, and acoustic displays to better understand the mating systems of baleen whales.

Keywords Age · Baleen whale · Genomics · Molecular ecology · Reproductive strategy · Reproductive success · Sexual selection · Song · Tactics

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F. Eichenberger (✉) · E. C. Garland
Sea Mammal Research Unit, School of Biology, University of St. Andrews, St. Andrews, Fife, UK
e-mail: fe23@st-andrews.ac.uk; ecg5@st-andrews.ac.uk

E. L. Carroll
School of Biological Sciences, University of Auckland – Waipapa Taumata Rau, Auckland, New Zealand
e-mail: e.carroll@auckland.ac.nz

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20.1 Mating Systems and Reproductive Strategies of Baleen Whales

There are many gaps in our understanding of mating systems and strategies of marine mammals, in particular for many of the mysticete suborder (baleen whales). The species are often rare, endangered, or otherwise difficult to observe; few observations may have therefore been made of their mating behavior, especially at the temporal scale necessary to evaluate lifetime reproductive success. When mating behaviors are observed, understanding the full behavioral repertoire and its context is challenging due to the elusive nature of mammals that spend most of their time submerged.

Most baleen whales undertake seasonal migrations to feed, mate, and give birth. The distances of these migrations and the extent to which breeding and feeding areas are separated from each other vary greatly across species, sometimes even across populations (e.g., non-migratory Arabian sea humpback whales, *Megaptera novaeangliae*: Mikhalev 1997). While some of the largest lunge feeders (rorquals), blue and fin whales (*Balaenoptera musculus* and *B. physalus*), appear to breed dispersed across unobserved offshore areas (Simon et al. 2010; Sears et al. 2013), other baleen whales aggregate on distinct breeding grounds (e.g., humpback whale; gray whale, *Eschrichtius robustus*; southern right whales, *Eubalaena australis*). The reproductive behaviors of most baleen whales indicate a polygynous mating system (successful males mate with multiple females), yet variance in male reproductive success is relatively low in comparison to polygynous mammals on land (Cerchio et al. 2005; Frasier et al. 2007; Carroll et al. 2012). Parentage analyses have further revealed that females mate with different males across years (e.g., Clapham and Palsboll 1997; Frasier et al. 2007), thus hinting toward a polygynandrous mating system (both males and females mate with multiple partners). However, direct observations of females mating with multiple males within the breeding season have, so far, only been reported in bowhead whales (*Balaena mysticetus*, Tarpley et al. 2021), gray whales (Swartz 1986), and North Atlantic right whales (*Eubalaena glacialis*, Mate et al. 2005). Despite the similarities in reproductive strategies (i.e., polygynandry, polygyny) across species, the behaviors that individuals engage in within their species' mating system can vary considerably (Table 20.1).

Much of what we know about mysticete reproductive behavior comes from humpback, right, and gray whales. There are similarities in the reproductive behaviors between these species: males typically aggregate in groups of a few to a few dozen individuals, where they physically compete to be closest to a single female at the center of the group (Tyack and Whitehead 1982; Norris et al. 1983; Kraus and Hatch 2001; Parks et al. 2007). However, while male humpback whales produce one of the most complex acoustic and culturally transmitted displays in the animal kingdom (Payne and McVay 1971; Payne and Payne 1985; Noad et al. 2000; Garland et al. 2011), the acoustic displays of right and gray whales are much simpler (Crance et al. 2019; Matthews and Parks 2021; Parks 2022). Right whales have the largest testes to body mass ratio of any baleen whale, indicating the important role of

Table 20.1 Overview of the male reproductive tactics and the potential for female choice in baleen whales. “Distribution” refers to the distribution of individuals in space during the breeding season. “Pre-copulatory trait investment” was based on the presence of elaborate vocal displays (i.e., song) with higher investment for more complex songs (see Table 20.2). “Post-copulatory trait investment” was based on whether the phylogenetically controlled residuals of maximum testes mass regressed onto maximum body length were lower than expected (low), as expected (medium), or higher than expected (high), based on Dines et al. (2015). “Potential for female choice” indicates the hypothetical possibility for female choice to occur based on the species’ mating system and the observed or inferred male reproductive tactics, and whether female choice likely takes place before and/or after copulation

Family	Species	Distribution	Pre-copulatory trait investment	Post-copulatory trait investment	Male reproductive tactics	Potential for female choice	Source
Balaenopteridae	Bryde’s whale, *Balaenoptera edeni*	(dsp)	(Low)	Medium	(Sc, Sp)	u	1–3
	Omura’s whale, *B. omurai*	(dsp)	Low-medium	u	(Sc, S)	u	1–4
	Sei whale, *B. borealis*	(dsp)	(Low)	Medium	(Sc, Sp)	u	1–3
	Blue whale, *B. musculus*	disp	High	Medium	Sc, S	preC(+postC)	1–3, 5
	Fin whale, *B. physalus*	disp	High	Medium	Sc, S	preC(+postC)	1–3, 10
	Humpback whale, *Megaptera novaeangliae*	aggr	High	Low	C, S, Sc, E	preC	1–3, 6–11
	Antarctic minke whale, *B. bonaerensis*	(dsp)	(Low)	u	(Sc)	u	
	Common minke whale, *B. acutorostrata*	dsp	Medium	Medium	Sc, S	(preC+postC)	1–3
Eschrichtiidae	Gray whale, *E. robustus*	aggr	Low	High	Sp, Sc	postC	1–3, 12
Balaenidae	Pygmy right whale, *Caperea marginata*	(dsp)	(Low)	(Medium)	(Sc)	u	3
	NA right whale, *Eubalaena glacialis*	aggr	Low	(High)	Sp, Sc, E	postC	13–16
	NP right whale, *E. japonica*	(aggr)	Low-medium	High	Sp, Sc, S	postC(+preC)	1–3
	S right whale, *E. australis*	aggr	Low	(High)	Sp, Sc	postC	17–19

(continued)

Table 20.1 (continued)

Family	Species	Distribution	Pre-copulatory trait investment	Post-copulatory trait investment	Male reproductive tactics	Potential for female choice	Source
	Bowhead whale, *Balaena mysticetus*	aggr	High	High	Sp, S, Sc	preC+postC	1–3, 20, 21

Abbreviations: aggr, breeding aggregations; dsp, dispersed; C, contest competition; Sc, scramble competition; E, endurance competition; Sp, sperm competition; S, singing; preC, pre-copulatory; postC, post-copulatory; u, unknown or unclear; () for inferred or hypothesized

References: (1) Ralls and Mesnick (2019); (2) Dines et al. (2015); (3) Brownell and Ralls (1986); (4) Cerchio (2022); (5) Sears et al. (2013); (6) Tyack and Whitehead (1982); (7) Clapham and Palsboll (1997); (8) Cerchio et al. (2005); (9) Pack et al. (2012); (10) Simon et al. (2010); (11) Herman (2017); (12) Swartz (1986); (13) Kraus and Hatch (2001); (14) Mate (2005); (15, 16) Frasier et al. (2007, 2013); (17) Carroll et al. (2012); (18) Burnell (2001); (19) Rowntree et al. (2001); (20) Würsig and Clark (1993); (21) Tarpley et al. (2021)

Table 20.2 Overview of baleen whale song from species that have been suggested to sing. Seasonality refers to the act of singing within a given year. Estimates of song complexity levels (simple, low complexity, high complexity) are based on the general song structure and sound repertoire (as given in "Song description") and the temporal and spatial variation of song. Temporal and spatial variation refer to changes in song (e.g., structure, composition, frequency). Audio examples of each species are provided online (https://doi.org/10.1007/978-3-031-35651-3_20).

Family	Species	Song description	Seasonality	Frequency (Hz)	Song complexity	Temporal variation	Spatial variation	Sex of singer	Reproductive function	Source
Balaenopteridae (rorquals)	Omura's whale, *Balaenoptera omurai*	Amplitude-modulated vocalizations, rhythmically repeated	u	15–20	Simple but not much known	u	u	u	Suggested	1
	Blue whale, *B. musculus*	Low-frequency songs that consist of a series of phrases each comprised of 1–5 sounds units	(Year-round)	16–100	Relatively low	Worldwide decline in frequency	Geographically distinct	Male	Suggested, further hypothesized to indicate male body size	2–4
	Fin whale, *B. physalus*	Low-frequency pulses arranged into stereotypic sequences at regular intervals (i.e., inter-pulse intervals, IPIs)	20 Hz calls produced mainly during the breeding season	15–40	Relatively low	Increase in IPIs, decrease in peak frequency	Geographically distinct	Male	Suggested, further hypothesized to attract females to aggregations of prey	5–12
	Humpback whale, *Megaptera novaeangliae*	Highly stereotyped and hierarchically structured: a sequence of sounds ("units"), creates a "phrase," repeated phrases form a "theme," and several different themes in a particular order make a "song"	Mainly during breeding season, and migration, and to a lesser extent on feeding grounds	50–4000	High	Changes in song structure and complexity during cultural evolutions and revolutions	Geographically distinct, high population conformity	Male	Suggested, further hypothesized to serve as a multi-message display and to indicate male quality	13–21
	Common minke whale, *B. acutorostrata*	Low-frequency pulse trains with variable IPI structure and peak frequencies	Seasonal but unclear if due to changes in vocal behavior or	55–150	Relatively low	Limited variability between years	Geographical variability in pulse train duration	(Male)	Suggested	22–24

(continued)

Table 20.2 (continued)

Family	Species	Song description	Seasonality	Frequency (Hz)	Song complexity	Temporal variation	Spatial variation	Sex of singer	Reproductive function	Source
			absence of whales at recording sites							
Balaenidae	NP right whale, *Eubalaena japonica*	Stereotypic sequence of gunshot sounds	(Seasonal)	50–1500	Simple	u	Multiple song types within each region	Male	Suggested, further hypothesized to encode information on resource availability	25
	NA right whale, *E. glacialis*	Long patterned sequences of gunshots (unclear if song due to data deficiency)	(Seasonal)	50–1500	(Simple)	u	u	(Male)	Suggested to function as female advertisement or male–male agonistic signal	26–28
	Bowhead whale, *Balaena mysticetus*	High diversity of song types comprised of highly modulated sounds and biphonation	(Mainly during breeding season)	50–4000	High	Complete renewal of singing repertoire	Multiple song types within each region but shared among smaller clusters of animals	u	Suggested, further hypothesized to indicate male quality	29–32

Abbreviations: u, unknown or unclear; () for inferred or hypothesized

References: (1) Cerchio et al. (2017); (2) Cummings and Thompson (1971); (3, 4) McDonald et al. (2006, 2009); (5) Watkins et al. (1987); (6) Croll et al. (2002); (7) Delarue et al. (2009); (8) Simon et al. (2010); (9) Morano et al. (2012); (10) Oleson et al. (2014); (11) Širović et al. (2017); (12) Weirathmueller et al. (2017); (13) Payne and McVay (1971); (14) Winn and Winn (1978); (15) Payne and Guinee (1983); (16) Noad et al. (2000); (17, 18) Garland et al. (2011, 2013); (19) Herman (2017); (20) Allen et al. (2018); (21) Murray et al. (2018); (22, 23) Risch et al. (2013, 2014); (24) Risch (2022); (25) Crance et al. (2019); (26) Parks et al. (2005); (27) Matthews and Parks (2021); (28) Parks (2022); (29, 30) Tervo et al. (2011a, b); (31) Stafford et al. (2018); (32) Erbs et al. (2021)

sperm competition as their reproductive tactic (Brownell and Ralls 1986). Despite being in the same taxon and exposed to similar environmental pressures, baleen whales seem to have evolved different reproductive strategies and tactics. This raises the question of what behavioral strategies the lesser-studied baleen whales have evolved and what are the underlying ecological and social drivers that led to the variation in reproductive behaviors across baleen whales. The unique evolutionary history of the transition from land to sea, well-resolved phylogeny, and trait variation of cetaceans offer a great opportunity to test hypotheses on the evolution of mating systems and reproductive behaviors.

20.2 Ecological and Social Factors Shaping Reproductive Tactics in Baleen Whales

Baleen whales share many of the life history characteristics of their phylogenetic terrestrial relatives, yet their locomotion and sensory systems are strikingly different. Over more than 50 million years of evolution (Uhen 2010), the anatomy and physiology of marine mammals became specialized for the marine environment. It is reasonable to assume that the reproductive tactics of baleen whales too are adapted for a life in the ocean.

Baleen whales are highly mobile and undertake some of the longest migrations in any mammal. For example, Oceania (South Pacific) humpback whales travel more than 7000 km between their breeding grounds and Antarctic feeding grounds (Riekkola et al. 2019). While some species show clearly defined migration strategies and large-scale seasonal movements from their polar feeding grounds to clearly distinct breeding grounds closer to the equator (e.g., humpback, blue, and gray whales), others undertake shorter migrations, do not breed near the equator (e.g., fin and right whales), and/or remain at similar latitude year-round (e.g., Bryde's whale, *Balaenoptera edeni*; bowhead whale; pygmy right whale, *Caperea marginata*; Bannister 2018). These migration strategies may even vary across populations (e.g., Bering-Chukchi-Beaufort Sea bowhead whales: Insley et al. 2021). While seasonal migration to warmer waters with fewer predators could represent a female tactic to increase offspring survival (Whitehead and Moore 1982; Corkeron and Connor 1999), the exact reasons why baleen whales travel these sometimes vast distances remain unclear. Considering the diversity of migratory tactics across baleen whale species and populations, the driving forces underlying their movement patterns might vary similarly (Horton et al. 2022).

Many baleen whales are capital breeders; after migrating from productive feeding grounds, individuals at the breeding ground generally go through an elongated fasting period (Costa and Maresh 2018). Females provision themselves and their offspring by feeding on seasonally abundant food sources, often thousands of miles from where they give birth. The long migration and elongated fasting period further increase the costs of reproduction for female baleen whales as female body condition

Fig. 20.1 Southern right whale cow–calf pair, photo taken in the Auckland Islands Maungahuka in the Aotearoa New Zealand subantarctic by the University of Auckland Waipapa Taumata Rau southern right whale research team, under New Zealand Department of Conservation permit 84845-MAR

affects fetal and calf growth (Christiansen et al. 2014, 2018). The capital breeding strategy also means nursing a calf leads to rapid depletion of a female's fat stores and body condition; in southern right whales, females lose an estimated 25% of their body volume in their calves' first few months of life due to lactation (Christiansen et al. 2018; Fig. 20.1). At this stage of development, the calf grows up to 1 m/month, highlighting the effectiveness and cost of this provisioning (Best 1994; Christiansen et al. 2018). Females may build up energy reserves required for reproduction over multiple feeding seasons, resulting in the need for longer inter-birth intervals. This likely reflects a female reproductive tactic in which the female delays reproduction to build up sufficient energy storage that may ultimately increase the survival of herself and that of her future offspring. Flexibility in reproductive timing may provide females with a buffer for poor prey conditions in a single year (Christiansen et al. 2022b). It may be that many females can become pregnant annually but carry the fetus to term only if conditions allow. The early stages of pregnancy (first and second trimesters) only incur about 5% of the total energetic cost of gestation (Christiansen et al. 2022b). It could therefore be that females can (physiologically) "decide" if the amount of energy resources obtained during the summer feeding period is sufficient to continue with the pregnancy. There is evidence that calving rates of southern right whales relate directly to environmental conditions that impact prey availability at offshore feeding grounds (Leaper et al. 2006; Seyboth et al. 2016). Similarly, the annual pregnancy rates of humpback whales along the Western Antarctic Peninsula may represent a response to favorable ecological conditions at these feeding grounds (Pallin et al. 2018b).

Compared to females, male baleen whales carry little of the reproductive costs, and their mating and reproductive success are mainly limited by distribution of mating partners in space and time. Due to the lack of stable groups in mysticetes and the absence of prey resources at their calving grounds, individuals are typically widely distributed. To combat this, many baleen whale species aggregate on breeding grounds every year (Table 20.1), many show site fidelity to these locations (Baker et al. 2013; Carroll et al. 2013), and produce acoustic displays audible across vast distances to find mates (Sect. 20.2.2). The variable inter-birth intervals of females can produce a male-biased operational sex ratio (ratio of receptive adults at any time in a population) at these breeding grounds, and further increase male competition for breeding opportunities (Boness et al. 2002). The 3D underwater habitat and great dispersion of individuals across the breeding ground, or the absence of distinct breeding grounds in some species, make it challenging for males to monopolize and defend groups of females or territories against other male competitors. Considering that fasting at the breeding ground is typical of baleen whales, food sharing and resource defense are also unlikely tactics. By process of elimination, (1) direct male–male competition over mating access in the form of male contest, endurance, and/or scramble competition, (2) indirect competition by attempting to attract females via elaborate displays (e.g., song), or (3) sperm competition over successful female fertilization are all possible and non-mutually exclusive reproductive tactics. All of these reproductive tactics are inferred or have been observed in baleen whales, and below we discuss each of them.

20.2.1 Direct Male–Male Competition over Mating Access

In some species, direct male–male interactions are readily observed and allow insights into mating tactics. The temporary group formations of three or more adults in right, gray, and humpback whales often peak around the breeding season and offer opportunities for direct competition between males for female mating access despite a commonly scattered distribution and solitary behavior (Norris et al. 1977, 1983; Everitt and Krogman 1979; Tyack and Whitehead 1982; Clark 1983; Clapham et al. 1992; Würsig and Clark 1993; Kraus and Hatch 2001) (Figs. 20.2 and 20.3). The level of aggression and intensity of male–male interactions within such groups vary across species. In humpback whales, males often engage in agonistic fights to gain or maintain the privileged position closest to the female of the group (Tyack and Whitehead 1982; Clapham et al. 1992) and show high levels of surface activity and behavioral displays (e.g., charges and peduncle strikes) that indicate the aggressive nature and intensity of these interactions (Baker and Herman 1984; Fig. 20.3). Males also often escort a single female (with or without her newborn calf) to form a pair. It is unclear whether the male's defense and the escorting of the female result in copulation or reflect mate guarding following earlier copulation (Clapham 1996). In right, gray, and bowhead whales, male–male interactions within these temporary group formations appear to be much less aggressive than in humpback whales.

Fig. 20.2 A group of ten socializing southern right whales photographed by drone in the Auckland Islands Maungahuka in the Aotearoa New Zealand subantarctic by the University of Auckland Waipapa Taumata Rau southern right whale research team, under New Zealand Department of Conservation permit 84845-MAR

Although aggregations of several males within temporary group formations are most likely driven by intra-sexual selection among males, they may also offer females the possibility to assess multiple potential mates. In North Atlantic right whales and humpback whales, females may facilitate the formation or increase the size of male aggregations to incite competition among males by surface-active displays (Clapham 2000) or vocalizations (Kraus and Hatch 2001; Parks 2003; Parks and Tyack 2005; Parks et al. 2007). Females may thus use aggregations of competing males to secure the highest quality male by mating with (or being fertilized by, see Sect. 20.2.3) the winner of the competition or through active mate choice.

The traits that allow a male to outcompete rivals underwater are likely different from the traits determining the outcome of male–male competition on land. While large body size is often correlated with increased strength on land and a clear advantage in fighting, a large size might come at the cost of reduced maneuverability underwater (Le Boeuf 1991; Segre et al. 2022). Better agility due to small size may be more advantageous in male–male competition in baleen whales considering the 3D underwater habitat, in contrast to terrestrially mating mammals (Mesnick and Ralls 2018a). However, large body size could increase the duration a male remains on breeding grounds, which are devoid of food (Craig et al. 2003), therefore increasing mating opportunities. Apart from maneuverability, male endurance and stamina likely also play an important role in determining a successful competitor,

Fig. 20.3 Humpback whale competitive group on their breeding grounds off the coast of New Caledonia in the South Pacific. The photo was taken by Opération Cétacéas, under a permit issued by the Province Sud

considering the hours-long duration of competitive group formations. Interestingly, mature-sized females at times have a preference for large males (Pack et al. 2012), suggesting that sexual selection could still favor large body size in males through female mate choice. Large male body size may convey other advantages, such as large offspring size, which has been correlated with low mortality in the first year of life in southern right whales (Best and Rüther 1992). Considering the atypical mammalian sexual dimorphism in mysticetes, where females tend to be slightly larger than males, selective pressures for large body size in females resulting from their higher energetic demands for reproduction likely outweigh sexual selection pressures for large body size in males (Ralls 1976).

20.2.2 Indirect Competition to Attract Females via Male Song

Baleen whales have a high variety of sounds and acoustic displays ranging from the low-frequency sounds of fin and blue whales, some sounds of which are below human hearing, to the star-wars-like vocalization of dwarf minke whales (*Balaenoptera acutorostrata*), to the more complex and hierarchically structured songs of humpback whales (Clark and Garland 2022). While all baleen whales vocalize, some also produce male-only breeding vocalizations termed "songs"

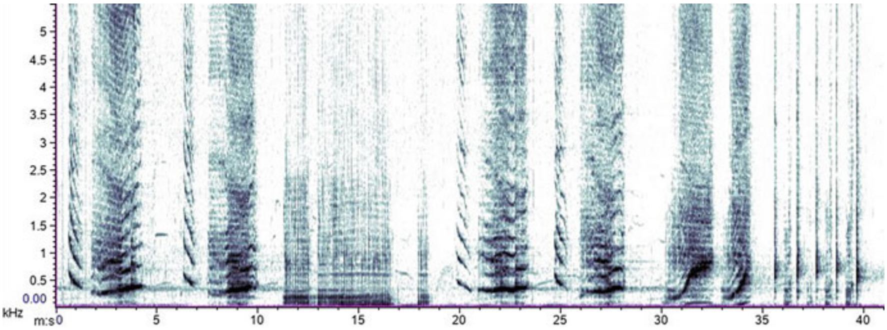

Fig. 20.4 Spectrogram of a small, continuous section of humpback whale song showing a variety of units recorded from a lone male on the breeding ground off the coast of New Caledonia in the South Pacific in 2018. Corresponding audio is provided online. The *x*-axis indicates time in seconds; the *y*-axis shows frequency in kHz. Spectrogram was generated in RavenPro 1.6 (Hann window, 75% overlap, 2048 point FFT, 16-bit)

(Table 20.2); these range in complexity from simple songs (comprised of a few sound types) of North Pacific right whales (*Eubalaena japonica*) to the highly complex songs of bowhead and humpback whales (Garland and McGregor 2020).

The highly stereotyped and hierarchically structured song of humpback whales is one of the most elaborate and complex vocal displays in the animal kingdom (Fig. 20.4). Songs typically last from 5 to 35 min; however, males may sing for many hours (Payne and McVay 1971; Winn and Winn 1978; Garland et al. 2013). Although songs change progressively each year through cultural evolution, all males within a population conform to the same song type at any given time (Winn and Winn 1978; Payne and Guinee 1983). In the South Pacific, a population's current song can be rapidly replaced by a novel song during so-called cultural revolutions (Noad et al. 2000; Garland et al. 2011). This indicates that despite the song's high complexity, males are able to learn entirely novel songs very quickly (i.e., within one season).

Humpback whale song has received considerable attention over the past 50 years, yet the underlying function(s) of song and its role within the mating system remain debated. There is clear evidence that singing is displayed solely by males which sing during the breeding season (including on migration and occasionally on the feeding grounds), and consequently singing is recognized as a male mating behavior (Glockner 1983; Baker and Herman 1984; Darling et al. 2006; Smith et al. 2008). Most studies have investigated the function of humpback whale song in the context of intra-sexual selection: (1) mediator of male–male interactions or male dominance relationships (Darling and Berube 2001; Cholewiak et al. 2018), (2) a spacing mechanism (Tyack 1981, 1983; Frankel et al. 1995), and (3) an index of association (Darling et al. 2006). Others suggest it is directed at females (inter-sexual selection): (4) female attraction to individual males (Winn and Winn 1978; Tyack 1981; Frankel et al. 1995) and (5) female attraction to an aggregation of communally singing males within the postulated lek mating system (Herman and Tavolga 1980;

Herman 2017). Although most studies on song function have focused on either intra-sexual or inter-sexual drivers, many conclude that both selective pressures are likely at play (Frankel et al. 1995; Clapham 2000; Darling and Berube 2001; Craig et al. 2002; Herman 2017; Cholewiak et al. 2018; Murray et al. 2018); song may thus serve more than a single function.

Humpback whale song contains both simple and complex phrase types, suggesting it might act as a multi-message display (Murray et al. 2018). Simple phrase types typically contain low-frequency sounds suitable for transmitting a signal across long distances and may thus facilitate a female's and/or male's ability to locate a singer over large distances (Bradbury and Vehrencamp 1998; Murray et al. 2018). The high-frequency sounds typical of complex phrase types convey information over a shorter range; thus, these shorter-range signals may be directed at females akin to how courtship usually occurs once potential mates are within close proximity (Bradbury and Vehrencamp 1998). Further, the high structural variability found in complex phrase variants appears ideal for conveying information on male quality, thus allowing the possibility of female mate choice to be the driver of song complexity (Hebets and Papaj 2005; Murray et al. 2018). However, female preference for any humpback whale song characteristic has yet to be investigated.

Compared to humpback whales, much less is known about the songs of other baleen whales, but several commonalities and differences across mysticete song are becoming apparent. The extraordinary diversity and variability of bowhead whale songs (Stafford et al. 2018; Erbs et al. 2021) suggest a complexity not dissimilar to the better-known humpback whale song. The songs of blue whales, fin whales, minke whales, North Pacific right whales, and Omura's whales are structurally simple, especially in the case of the latter two (Table 20.2). Although the songs of mysticetes show diverse levels of complexity and variability, they share several commonalities: (1) songs contain elements that aid long-distance communication across the ocean (e.g., contain low-frequency sounds and/or high redundancy; Payne and Webb 1971; Bradbury and Vehrencamp 1998; Clark and Ellison 2004; Risch 2022); (2) songs show some level of change across time (Noad et al. 2000; McDonald et al. 2009; Garland et al. 2011; Širović et al. 2017; Weirathmueller et al. 2017; Helble et al. 2020); (3) in at least rorquals, songs show some level of conformity within geographically distinct groups (Payne and Guinee 1983; McDonald et al. 2006; Garland et al. 2011, 2013; Darling et al. 2014; Risch et al. 2014; Širović et al. 2017; Weirathmueller et al. 2017); (4) song has been proposed to serve a reproductive function (Croll et al. 2002; Tervo et al. 2011b; Risch et al. 2013; Cerchio et al. 2017; Tyack 2022); and (5) for several species, song may convey individual-specific information and/or serve as a potential indicator of male quality (McDonald et al. 2006; Tervo et al. 2011b; Herman 2017; Clark et al. 2019; Crance et al. 2019; Erbs et al. 2021). For more detailed information by species, we direct readers to a recent review of baleen whale songs (see Clark and Garland 2022).

For species where the sex of the individual was determined, all singers were male (humpback whales: Payne and McVay 1971; fin whales: Croll et al. 2002; blue whales: McDonald et al. 2006; North Pacific right whales: Crance et al. 2019), and song mainly occurred during the breeding season (e.g., Smith et al. 2008), thus indicating that mysticete song likely serves a reproductive function and may therefore be under sexual selection. However, several species sing on the feeding grounds and during migratory stopovers (e.g., Owen et al. 2019). Singing outside the main breeding season might be driven by elevated testosterone levels during the spring or fall season while individuals are still on their high-latitude feeding grounds, as reproductive conditioning likely starts months before the peak breeding time (Vu et al. 2015). Such singing may represent a low-cost opportunistic advertisement by males to court females that failed to conceive, and/or possibly an intra-sexual display (Clark and Clapham 2004).

The 3D underwater habitat, the slightly larger body size of females relative to males (Ralls 1976), and the absence of organs to grab and force females into mating all promote female behavioral freedom and thus allow for a relatively strong influence of female mate choice compared to most other mammals. Male–male competition and female mate choice are possible and non-exclusive drivers for the function of whale song. More research is needed to better understand whether song signals the singer's quality and whether males and/or females adapt their reproductive choices or behaviors upon receiving that signal.

20.2.3 Sperm Competition for Successful Female Fertilization

Except for bowhead, right, and gray whales, few matings have been observed by humans, and it is not known whether females mate with multiple males. Relative testes size and penis length serve as a proxy for the role of sperm competition (Würsig et al. 2023, this book) and can shed light on the reproductive tactics of baleen whales. The relative testes size and penis length of right, bowhead, and gray whales are larger than those of all other baleen whales, and larger than expected based on their body mass, indicating the importance of sperm competition as their main reproductive tactic (Brownell and Ralls 1986; Dines et al. 2015). As mentioned in Sect. 20.2.1, interactions among males in these species are relatively unaggressive and females mate with multiple males during the breeding season (Swartz 1986), sometimes even simultaneously (Mate et al. 2005), suggesting that males are unlikely to monopolize access to females (Swartz et al. 2023, this book). Further, the higher-than-expected microsatellite heterozygosity in offspring of North Atlantic right whales indicates post-copulatory competition among males (Frasier et al. 2013). As relatedness of mating pairs was not lower than expected under random mating, this excess of heterozygous offspring does not appear to result from pre-copulatory mate choice for dissimilar mates (Frasier et al. 2013). Instead, the observed patterns indicate the presence of post-copulatory selection for dissimilar gametes. However, it remains unclear whether these patterns are due to biased fertilization (e.g., cryptic female choice for dissimilar sperm) or biased mortality of zygotes (Frasier et al. 2013).

In comparison, the relative testes size of male humpback whales is lower than expected based on their body mass (Dines et al. 2015). Male humpback whales appear to engage in direct contest competition (Sect. 20.2.1), which suggests that males attempt to monopolize and defend access to females, thus reducing opportunities for sperm competition (Lüpold et al. 2014). Together with their elaborate acoustic displays (Sect. 20.2.2), this indicates their investment in and reliance on pre-copulatory reproductive tactics. In most other rorquals (blue whale, fin whale, minke whale, Bryde's whale, and sei whale), relative testes size is within the range expected based on their body mass (Dines et al. 2015), and males are unlikely to be able to monopolize access to females due to their dispersed distribution (Table 20.1). Thus, sperm competition remains a possible male reproductive tactic in most rorquals.

20.3 Toolkit for Studying Reproductive Tactics

Considering the long lifespan of baleen whales, long-term data collection is crucial to cover a wide range of the species' life history and to make inferences on sexual maturity and how reproductive tactics may change with age, experience, and/or condition. Many long-term studies on baleen whales are focused on the assessment of the population, rather than focal follows of individual whales. However, the identification of individual whales enables researchers to follow them long-term to learn more about their life history patterns, and to ground truth and calibrate tools to study mating systems, reproductive tactics, and other factors such as population dynamics (e.g., epigenetic aging, photogrammetry).

An example of a study that has shed light on changes in reproductive patterns is the extensive long-term monitoring program on Oceania humpback whales that has allowed for reconstruction of recapture histories and modeling of reproductive parameters in females (Chero et al. 2020). The relatively high calving rates of females at their breeding ground in New Caledonia are consistent with high pregnancy rates inferred by blubber progesterone levels on their migratory corridors (Riekkola et al. 2018) and feeding grounds (Pallin et al. 2018b), and may partially be driven by an increased reproductive capacity of this population (Chero et al. 2020). Epigenetic aging of individuals at this breeding ground could reveal whether this increased reproductive capacity is related to the age structure of the population, and/or if the anthropogenic pressures caused by commercial whaling led to the modification of breeding parameters (i.e., age at maturity or birth interval) (Chero et al. 2020).

The combining of long-term behavioral observations with molecular data is also a powerful approach. For example, paternity analysis using a long-term dataset of photo-identification and molecular data of endangered North Atlantic right whales revealed low variation in male reproductive success (Frasier et al. 2007). Combining the paternity data with measures of neutral and functional genetic diversity further indicated the presence of post-copulatory selection for dissimilar gametes that may represent cryptic female choice (Frasier et al. 2013). This integration of genetic parentage and genetic diversity also unveiled a possible mechanism to mitigate the loss of genetic diversity after population exploitation (Frasier et al. 2013).

Research methods and technologies have greatly improved in recent decades, resulting in a variety of tools for data collection and analysis offering new and deeper insights into the life of mysticetes. The examples above integrated long-term observational datasets, genetics, and hormonal (physiology) datasets. Building on these multidisciplinary approaches will allow us to explore interactions among anatomy, physiology, reproductive success, age, and vocal displays, to better understand the reproductive tactics of baleen whales. In Table 20.3, we highlight tools that can increase our understanding of the reproductive strategies and tactics of baleen whales.

20.4 Conclusions and Future Directions

While the *Balaenidae* and *Eschrichtiidae* species appear to rely heavily on post-copulatory reproductive tactics by competing for successful fertilization rather than mating access, the morphology, behavior, and distribution of many species within the *Balaenopteridae* (rorquals) suggest their reliance on pre-copulatory tactics. The often aggressive interactions among males within competitive groups suggest that male humpback whales compete primarily via direct contest competition by attempting to prevent matings by other males. The more widely dispersed distribution and lack of breeding aggregations of blue and fin whales could indicate scramble competition, where males directly compete in their efforts and efficiency of searching for and locating receptive females as their reproductive tactic, and highlights the importance of acoustic cues to find mates. Based on the trade-off between pre- and post-copulatory trait investment, the lack of prominent pre-copulatory traits of many baleen whales (Dines et al. 2015), except for a few species with elaborate male songs (see Sect. 20.2.2), and the apparent lack of direct contest competition in most baleen whales (apart from humpback whales; Sect. 20.2.1) suggests that polygynandry (often mediated by sperm competition) may be more common within mysticetes than the lack of direct observational evidence to date suggests, outside of the *Balaenidae* and *Eschrichtiidae* families. Thus, irrespective of the reproductive tactics males employ, the elaborate acoustic displays and large testes size observed in several mysticete species suggest that female baleen whales may be able to exert a certain level of choice before and/or after copulation.

Much can be learned when taking a comparative perspective across marine mammals to understand reproductive tactics. While some species of pinnipeds and odontocetes show extreme levels of male-biased dimorphism in body size (e.g., elephant seals, *Mirounga* spp.; killer whales, *Orcinus orca*) and weaponry (e.g., walrus, *Odobenus rosmarus*; narwhals, *Monodon monoceros*) (Mesnick and Ralls 2018b), sexual size dimorphism in baleen whales is relatively moderate and female-biased, and further characterized by an absence of any dangerous male-specific weaponry. The temporal and spatial distribution and social structure of females

Table 20.3 Tools that can be used to delve deeper into the reproductive tactics of baleen whales

Tool	Description	Examples in baleen whales
Individual identification	Baleen whales can be individually identified by photo-identification of unique markings (e.g., ventral fluke patterns of humpback whales: Katona and Whitehead 1981; callosity patterns in right whales: Payne et al. 1983; Kraus et al. 1986; flank pigmentation patterns in blue whales: Sears et al. 1990) and/or genetic identification (e.g., microsatellite genotyping: Garrigue et al. 2004; Olavarría et al. 2007; Wade et al. 2011; Wiig et al. 2011; Baker et al. 2013; Carroll et al. 2013)	Reproductive histories of female humpback whales (Baker et al. 1987) Reproductive capacity of an endangered and recovering population of humpback whales (Chero et al. 2020)
Sex identification	Identifying the sex of individuals can be difficult in wild marine mammals; this can be done using behavioral observations and genetic markers	Identifying the sex of focal animals in southern right whale social groups (Best et al. 2003)
Genetic parentage analyses	Using Mendelian inheritance patterns of genetic markers to infer maternity and paternity patterns (see Chap. 4)	Patterns of maternity and paternity can provide information on the reproductive skew, and variation in reproductive success (Cerchio et al. 2005; Frasier et al. 2007), the strength of sexual selection, as well as reproductive interchange among populations (Garrigue et al. 2004; Carroll et al. 2012)
Genetic diversity	Genetic diversity not only offers valuable insights into the demography and gene flow across populations; it further can be used to identify genes under selection and to assess the role of female choice within a species' mating system (e.g., genetic compatibility: Mays and Hill 2004; Puurtinen et al. 2005). Untangling molecular patterns of non-random fertilization in the context of post-copulatory sexual selection can shed light on the role of female choice and the resulting impacts on population biology and evolutionary genetics (gamete compatibility: Springate and Frasier 2017)	Diversity and duplication of MHC genes in several mysticetes suggest that these genes are under positive selection (Baker et al. 2006; Moreno-Santillán et al. 2016) Linking parentage with genetic diversity revealed the post-copulatory reproductive strategy in North Atlantic right whales which might indicate cryptic female choice (Frasier et al. 2013)
Molecular age biomarker	Measurable changes in DNA or RNA abundance or sequence that change over the lifespan of an animal can be used to estimate age (Jarman et al. 2015) Epigenetic clocks make use of	Epigenetic age estimation has been applied to several baleen whale species (Polanowski et al. 2014; Goto et al. 2020; Tanabe et al. 2020; García-Vernet et al. 2021), and other cetaceans (Bors et al. 2021; Robeck

(continued)

Table 20.3 (continued)

Tool	Description	Examples in baleen whales
	age-related changes in DNA methylation levels to estimate the age of living whales using skin biopsy samples. Such epigenetic clocks need to be calibrated using individuals of known age, thus highlighting the crucial role of long-term data collection for the assessment and ground-truthing of such methods	et al. 2021). If related to other factors such as behavior, body size, hormone levels, and reproductive success, an individual's estimated chronological age can offer new insights into the reproductive strategies and life history parameters that, considering the lifespan of these animals, are out of reach of most datasets
Endocrinology	Estimating hormone levels in individuals can tell us more about their sexual maturity or reproductive state (see Hunt et al. 2017). Hormone concentrations can be measured using multiple matrices: blubber, respiratory vapor ("blow"), and fecal samples (Rolland et al. 2005; Hunt et al. 2013), and for the retrospective and longitudinal assessment of reproductive hormones: baleen plates (Hunt et al. 2014, 2016)	*Progesterone*: inference of pregnancy status and rates (e.g., Kellar et al. 2013; Hunt et al. 2016; Pallin et al. 2018a, b; Kershaw et al. 2021) *Testosterone*: can be used to infer reproductive maturity and status of individuals or seasonal changes in reproductive state (e.g., Kellar et al. 2009; Vu et al. 2015; Cates et al. 2019; Mingramm et al. 2020; Melica et al. 2021) *Estradiol*: can provide information on female reproductive maturity and receptivity (e.g., Mingramm et al. 2020; Lowe et al. 2022)
Bioacoustics	Baleen whale vocalizations can be recorded using handheld equipment taken at the individual whale through to passive acoustic monitoring using autonomously deployed recorders that are anchored to the seafloor. Sound units are typically quantified for multiple acoustic parameters to ensure consistent classification of sound types (Dunlop et al. 2007; Garland et al. 2017; see also Clark and Garland 2022)	A quantitative comparison of the similarity in arrangement, structure, and complexity in humpback whale song (Garland et al. 2012, 2013, 2017; Allen et al. 2018) can uncover song dynamics at large spatial scales such as the unidirectional cultural revolutions (discussed in Sect. 20.2; Garland et al. 2011), through to intricate intra- and inter-individual differences (Allen et al. 2018; Murray et al. 2018). By uncovering song differences, whether large-scale or extremely subtle, we may be able to tease apart aspects of the song that signal male quality and thus may serve in female mate choice
Animal-borne tags	There are a wide variety of tag types ranging from high-resolution behavior loggers to satellite tags that provide tracking data over large spatial and temporal scales (Goldbogen et al. 2013). Biologgers are tags equipped with additional sensors (e.g., accelerometer, hydrophones, video cameras,	Satellite tracking can tell us about the migratory routes and spatial usage of species and individuals and can reveal migratory and reproductive strategies (e.g., Garrigue et al. 2015; Derville et al. 2018; Mackay et al. 2020) Biologgers, regularly used to study the foraging ecology and diving

(continued)

Table 20.3 (continued)

Tool	Description	Examples in baleen whales
	magnetometers) making them a powerful tool to simultaneously track the behavior and environment of individuals (Watanabe and Goldbogen 2021). Such tools are extremely valuable for species that are more located offshore, deep diving, or live in environments that are otherwise hard to reach (e.g., ice shelf)	behavior of marine mammals, could reveal further insights into the cost of reproduction and vocal communication of marine mammals
Drone technology	Drones, or unoccupied aerial vehicles (UAVs), provide a cost-effective option for monitoring, photogrammetry, and behavioral observations of free-ranging marine species. Aerial photogrammetry can be used to estimate the body size and condition of individuals (e.g., Dawson et al. 2017; Burnett et al. 2019; Christiansen et al. 2019; Aoki et al. 2021). UAVs can be used to obtain acoustic measurements close to the whales (Lloyd et al. 2016; Frouin-Mouy et al. 2020) and respiratory blow samples for genetic, endocrine, and microbiological analyses (Atkinson et al. 2021)	As capital breeders, baleen whale body condition and reproductive costs likely play an important role in their reproductive strategies. UAV photogrammetry and long-term sighting histories can be used to establish growth patterns to estimate age based on body mass, explore the energetic costs of female reproduction (e.g., Christiansen et al. 2014, 2022a, b), or the relationship between migratory timing and body condition (Russell et al. 2022) Paring acoustic recordings and overhead visual observations could shed light on the behavioral context and function of acoustic displays (e.g., song)

increase the potential for single males to monopolize groups of females in land-breeding pinnipeds, and led to the evolution of male alliances and temporary courtships in several odontocetes (Mesnick and Ralls 2018b; Brightwell and Gibson 2023, this book; Chivers and Danil 2023, this book). Reproductive strategies and tactics across pinnipeds, odontocetes, and mysticetes are highly variable, yet the reproductive tactics within each suborder vary similarly. Understanding how the diversity of ecological and social factors across and within each suborder shape the reproductive behaviors of individuals will shed light on the evolution of reproductive strategies and tactics of baleen whales.

The emergence of new technologies has greatly enhanced the detail and scope of investigations that are now possible. Future directions include the employment of animal-borne tags and drone technology to study the behaviors of species and individuals that are difficult to observe or approach. The use of genomics, epigenomics, and endocrinology offers insights into the genetic quality, reproductive maturity and status, and physiological condition, providing a comprehensive picture at the level of the individual needed to untangle the multifaceted factors shaping their reproductive tactics and the role and mechanisms of female choice. Understanding the function(s) of baleen whale song is a largely unanswered question that is ripe for exploration through a multidisciplinary approach that offers insights into the proximate and ultimate causes of singing. This could then be expanded into a comparative perspective to investigate the evolution of song and complex communication in multiple taxa, both marine and terrestrial. By understanding reproductive tactics employed by large whales, we provide invaluable contributions to the wider understanding of mating behavior across taxa.

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