

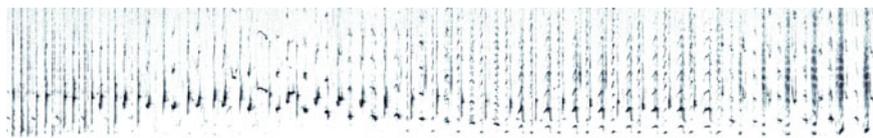
Chapter 11

Humpback Whales: Exploring Global Diversity and Behavioral Plasticity in an Undersea Virtuoso



Danielle Cholewiak and Salvatore Cerchio

... it does give one pause to realize that the ocean has been resounding with whale song for millions of years, and that the ocean's inhabitants have long been swimming in the midst of the echoing choruses. It is not altogether surprising to find that humans nearly extinguished the whole source and only in the last few years have we begun to hear the music. (Payne and Payne 1985)



Abstract It has been fifty years since Payne and McVay's seminal publication on the strange and beautiful sounds of the humpback whale (*Megaptera novaeangliae*), the study which inspired decades of research into their complex, underwater acoustic world. In the subsequent five decades, there probably have been more research projects and publications on humpback whale song than on the vocal behavior of any other baleen whale. What makes humpback song so unique? What have we learned? What questions remain? With this chapter, we explore these questions with an eye toward the overarching theme of studies that address proximate mechanisms (*the "how do humpback whales do this?" questions*) versus those that inquire about ultimate causes (*the "why do humpback whales do this?" questions*). We draw a distinction between studies that focus on singing behavior, versus those that use song as a proxy to investigate other biological processes. We take the reader through a

D. Cholewiak (✉)

Northeast Fisheries Science Center, NOAA Fisheries, Woods Hole, MA 02543, USA
e-mail: danielle.cholewiak@noaa.gov

S. Cerchio

African Aquatic Conservation Fund, Chilmark, MA 02535, USA
e-mail: scerchio@africanaquaticconservation.org

© Springer Nature Switzerland AG 2022

C.W. Clark and E. C. Garland (eds.), *Ethology and Behavioral Ecology of Mysticetes*,
Ethology and Behavioral Ecology of Marine Mammals,
https://doi.org/10.1007/978-3-030-98449-6_11

247

historical review of the literature, ending with a series of observations about the unanswered questions intended to provoke new ideas and new lines of inquiry. Through this exploration, we hope to synthesize a global body of research to identify common themes and probe the lingering gaps in our understandings of humpback whale song.

Keywords Humpback whale · Acoustics · Song · Sexual selection · Cultural transmission · Cultural evolution · Breeding behavior

11.1 Early Song Studies: Laying the Foundations from 1960s Through 1980s

Humpback whales (*Megaptera novaeangliae*) are almost cosmopolitan, occurring in all major ocean basins. Individuals in all but one or two populations are known or believed to undertake long-range seasonal migrations between high-latitude feeding and low-latitude breeding areas. By the mid-twentieth century, humpback whales had been hunted nearly to extinction throughout most of their range (reviewed in Baker et al. 1993). In 1955, commercial whaling for humpbacks was banned in the North Atlantic, followed by the Southern Hemisphere in 1963–64, and the North Pacific in 1966. How many animals were taken, and what the pre-whaling population sizes were, is not entirely clear. However, the populations that remained were a fraction of their original sizes, and in some cases occupied perhaps only a fraction of their original ranges (e.g., Reeves et al. 2001). The impacts of this population decimation on humpback whale movements, interchange, and communication structures are unknown. When the earliest acoustic recordings were made of humpback whales in the 1950s, US naval researchers and scientists were just beginning to learn about whale acoustic behavior by listening in on remnant populations left after post-industrial whaling. We are still unraveling the implications of impacts from the whaling era and considering how our interpretations of acoustic communication are affected by the study of populations that are recovering and expanding back into old and possibly new habitats. As we explore the processes that govern humpback whale singing behavior, it is important to keep in mind that our understanding of humpback communication dynamics may be influenced by these population-level changes.

By 1964, it was known that humpback whales make sounds during the breeding season, and also that these sounds were different than those heard on feeding grounds. As Schevill (1964) eloquently wrote, “The sonorous moans and screams associated with the migrations of *Megaptera* past Bermuda and Hawai’i may be an audible manifestation of more fundamental urges, for in New England waters and at other seasons we do not hear anything nearly so spectacular from this species.” It would be a few more years before the breeding sounds of humpbacks would be recognized as “song”, and by the time Roger Payne and Scott McVay published their seminal paper (Payne and McVay 1971), multiple researchers were already recording and exploring this newly documented acoustic phenomenon.

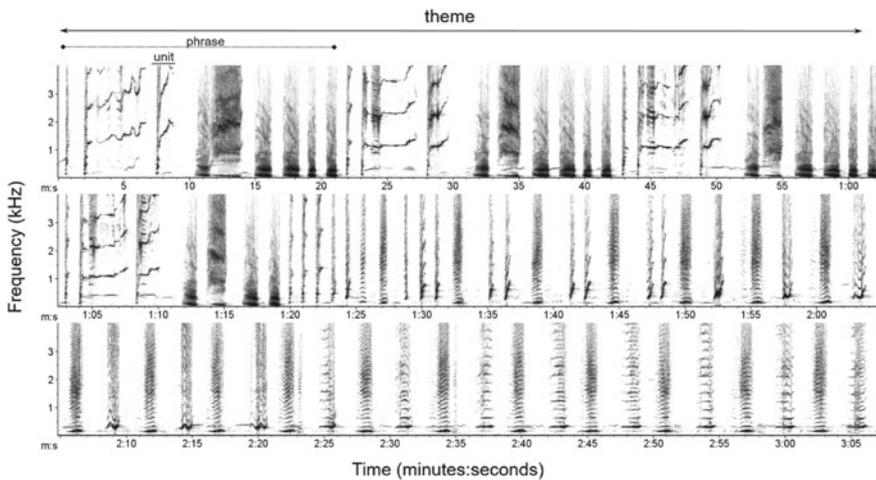


Fig. 11.1 Spectrogram showing a partial song sequence from one humpback whale, recorded off Hawai'i in 1990 (1024 pt FFT, Hann window, 80% overlap). This image reveals a diversity of song units as well as the hierarchically patterned structure of humpback song

The pioneering work in the 1970s developed a framework by which to analyze and understand humpback song structure. Payne and McVay (1971) described the well-structured hierarchy of song sequences, composed of individual units, organized into repeated patterns (“phrases”), repeated a variable number of times (“themes”) before a singer switches to a new set of phrases and themes (Fig. 11.1). This type of singing had already been defined in the avian song literature as “eventual variety” (Kroodsmas 1977; Fig. 11.2), which was also later applied to humpback whales (Cholewiak et al. 2013). Payne and McVay laid the groundwork for describing the hierarchical structure of humpback song, and explored variability in the singing behavior of individual singers, documenting, for example, that singers vary the number of times they repeat a phrase within a theme, resulting in themes and song sequences of varying lengths. These observations of plasticity in song production underlie an important behavioral mechanism that we continue to explore. Payne and McVay also speculated on the possible role of song in mate attraction or group cohesion and speculated that singing may be common in baleen whales. While their insights were seminal for humpback whale research, they also had clear influence on baleen whale song research worldwide.

The mid-1970s through the 1980s saw an explosion of research on humpback whales. By 1979, preliminary descriptions of acoustic signals had been produced for many baleen whale species (Thompson et al. 1979), but work on humpback whales was more advanced than on other species. Perhaps largely due to their accessibility in warm water coastal habitats and their charismatic vocal displays, humpback whales attracted dedicated and consistent study. Our understanding of humpback whale song and singing behavior during this era was shaped almost entirely by studies conducted in the Northern Hemisphere; most research was being conducted off Bermuda, around

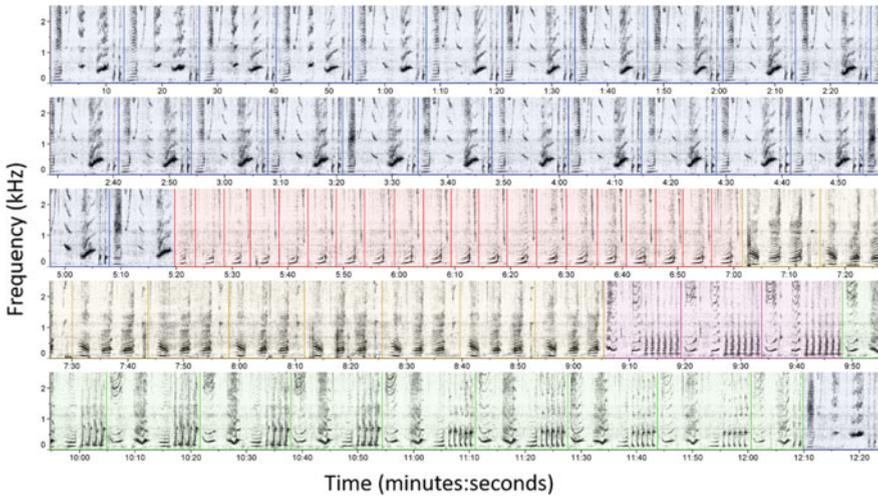


Fig. 11.2 Spectrogram showing partial song sequence from one humpback whale recorded off the Sultanate of Oman in 2012 (4096 pt FFT, Hann window, 50% overlap), with phrases delineated and colored by theme, showing how humpback singing behavior fits into the framework of “eventual variety” singing. Recording courtesy of the Environment Society of Oman

the Caribbean, and around the Hawaiian Islands. Scientists were exploring concepts related to individual identification based on song characteristics (Hafner et al. 1979), diel periodicity in song production (Thompson et al. 1979), and the use of song to assess population distribution and size (Winn et al. 1975; Levenson and Leapley 1978), recognizing that it was possible to monitor portions of a population in breeding areas using passive acoustics as a scientifically robust methodology. Work was also underway to assess geographic variation in song. In the first published comparison of song structure between populations, Winn et al. (1981) found strong similarities among songs in widely separated wintering grounds, recognizing that within the North Atlantic, songs recorded in the West Indies and Cape Verdes shared the same themes, as did songs recorded between Hawai'i and México in the North Pacific. In contrast, between ocean basins, North Atlantic songs shared no themes with those from the North Pacific, and both were different from one sample obtained from Tonga in the South Pacific.

In 1983, the book “Communication and behavior of whales” (Payne 1983) was published, which contained an important compilation of detailed studies on humpback whale song and singing behavior. These laid out the basic concepts that are still considered foundational to our understanding of humpback whale singing, that: singers are males (Glockner 1983); all individuals within a local breeding aggregation (e.g., the Hawaiian Islands) share the same phrases at any given time (Payne et al. 1983); there exists distinct individual variation such that some singers diverge from the typical ordering of themes and may be considered “aberrant” (Frumhoff 1983); songs change progressively over time (Payne et al. 1983); songs of individual singers

change through time in the same ways that songs from their regional “population” of singers change through time (Guinee et al. 1983); and singers in a completely different breeding aggregation located across an ocean basin, e.g., in México, sing songs composed from some of the same phrases and change those phrases in a similar manner across seasons as the singers in the Hawaiian Islands (Payne and Guinee 1983). An important concept running through many of these studies was that humpback whales change their song in different ways over time, but the subtleties, dynamics, and scales of such changes were just beginning to be appreciated.

Two fundamental papers on song structure and changes in song were published by Katharine Payne and her colleagues (Payne et al. 1983; Payne and Payne 1985). These papers, built on multiyear studies of humpback song in two different ocean basins, provided profound insights that shaped the research community’s understanding of humpback singing behavior. At their core, these studies examined the patterns and dimensions of variability of temporal change at the organizational level of song structure. Payne et al. (1983) observed that most of the structural changes in song do not occur between seasons, but rather during the breeding season, dismissing an early notion of “forgetfulness” as the root cause of song change. They observed that singers change their song structure at different rates over time, that “chaotic” themes could become organized, and that song structure goes through periods of instability and stability. Entire themes die out and new ones appear, and the birth of new themes most often occurred through a process by which stable themes become variable and later begin to differentiate. Payne and her colleagues described the humpback song system as “at once highly organized and also labile”. Payne’s observations and insights were influenced by contemporary research on oscine songbirds, in particular, the work in Peter Marler’s lab at Rockefeller University, with which the Paynes were associated. This was an era of intensive study on song learning in avian species, utilizing captive-bird laboratory experiments and field manipulations to develop a better understanding of the innate and environmental influences on acoustic repertoire development (e.g., Marler and Peters 1981; Marler 1984, 1990).

The Paynes’ observations were remarkable, as at the time the idea of song learning in baleen whales had not yet been considered. Importantly, Payne et al. (1983) recognized that progressive changes in humpback song, which imply that whales continuously learn song changes from conspecifics, represent a process of *cultural transmission* and *cultural evolution*. Cultural transmission and song evolution had already been well-documented in a number of oscine avian species (i.e., “songbirds”) by the 1970s (e.g., Lemon 1975; Jenkins 1978; Slater and Ince 1979), and researchers were developing frameworks to describe the process conceptually and quantitatively (Mundinger 1980; Cavelli-Sforza and Feldman 1981). Cultural evolution of a vocal behavior is the process by which a song tradition is changed over time, and changes are transmitted between individuals. This is the consequence of an individual having the capability to learn, coupled with the transmission of acoustic elements between individuals. These changes in a song pattern, sometimes referred to as “cultural mutations” (Jenkins 1978; Mundinger 1980), are believed to result from an “error” in copying, improvisation, innovation, or some combination of each of these. In most songbirds, changes accumulate slowly across generations, such as the

typical “vertical” transmission described in New Zealand’s South Island saddlebacks (*Philesturnus carunculatus*; Jenkins 1978) and indigo buntings (*Passerina cyanea*; Payne et al. 1981). However, in exceptional cases, “horizontal” transmission between individuals within the same generation, coupled with continual copying of individual innovations within singing seasons and throughout an individual’s lifetime, results in what has been termed “rapid cultural evolution”, as displayed by humpback whales (Chap. 8). The remarkable phenomenon of population continuity for a form of song undergoing rapid cultural evolution, in which emergent changes are adopted among individuals within a population to maintain the same song patterns, is not unique to humpback whales. Several avian species also exhibit similar phenomena in their acoustic breeding displays, such as the village indigobird (*Vidua chalybeata*, Payne 1979), and the yellow-rumped cacique (*Cacicus cela*, Trainer 1989).

There are likely multiple mechanisms by which such changes can be maintained by individual humpback whales in breeding areas thousands of kilometers apart. At least three mechanisms were proposed for the exchange of song material between individuals from different breeding populations: Singers from different breeding areas may overlap on the feeding grounds; they may interact and hear one another during migration; and/or they may move between breeding areas within a season or inter-annually (Payne and Guinee 1983). However, song similarity within an ocean basin is more complicated than originally believed (explored in more detail in Sect. 11.2).

Payne and Payne (1985) described humpback whale song structure patterns from 19 years off Bermuda, defining the concept of “transitional phrases”, as well as three types of themes: “static”, “shifting”, and “unpatterned” (Fig. 11.3). These categories are still used today in characterizing variation in humpback song. However, in many more recent papers, these distinctions are often not observed or described,

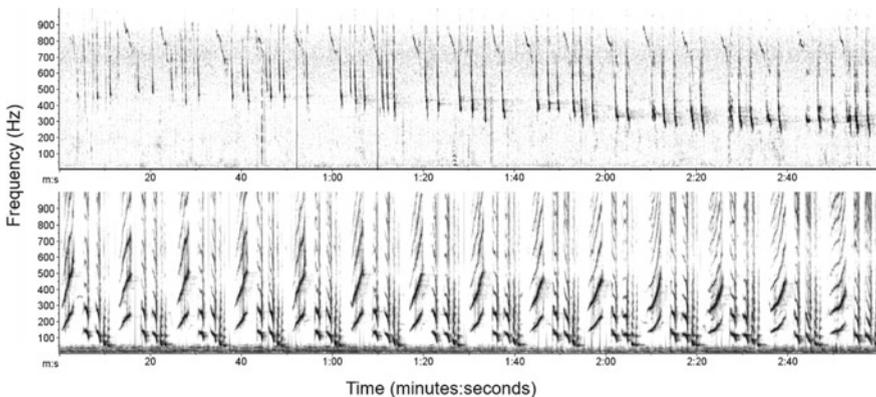


Fig. 11.3 Two excerpts from humpback song showing a shifting theme (top) and static theme (bottom). In the top panel, note both the progressively decreasing frequency and the increasing temporal spacing of the song units with each phrase repetition. In contrast, in the bottom panel, the spectral-temporal features of the song units are consistent among phrases. Recording sites: top panel: Madagascar, 2018; bottom panel: México, 2006

leaving us to wonder if some of the variation in song is either not accounted for or is misinterpreted. For example, without recognizing that transitional phrases are composed of components of different phrases from consecutive themes, and that in shifting themes the phrase structure changes progressively from the first to last repetition of the phrase, there exists the potential to “over-categorize” or split themes, leading to potentially erroneous interpretations.

The long time series of the samples used by the Paynes allowed them to recognize commonalities in humpback songs across years. Some of these commonalities have to do with the finer details in song units—such as the inclusion of both “simple” and “complex” sounds (defined as ranging from tonal to noisy bursts), and other types of contrasting sounds, such as those that are frequency-modulated and relatively constant in frequency, very long and very short in duration, and abrupt and gradual in onset. In examining the processes of theme evolution, the Paynes found that themes had dissimilar rates of extinction; while about half the themes were present in more than one year in their study, some were present for 7 or 8 years. Between adjacent years, the ratio of new to previous material varied; theme content in some adjacent years was very similar, while songs in other adjacent years had few themes in common. In fact, every 5–6 years, a period of stability seemed to be reached in which songs remained very similar between years. The Paynes also observed variation among themes and years in the “rhythm” of the song, the song tempo; a feature that students of humpback whale song studies recognize, but is difficult to capture in words. Finally, the Paynes recognized that despite inter- and intra-individual variation, overall, all songs from one breeding season are more similar to other songs from that same season than to songs from other seasons. Many of these insights were possible due to the expansive sample analyzed by the Paynes, and their insights have had lasting impacts on our understanding of the strengths and limitations of using song analyses to evaluate population structure.

In his book “Sociobiology”, E.O. Wilson (1975) stated “the most elaborate single display known in any animal species may be the song of the humpback whale *Megaptera novaeangliae*.” Among the balaenopterid whales, this observation holds true. None of the other rorquals produces a song that comes close to rivaling the complexity of humpback whale song. It has become clear that most (if not all) mysticete species sing; therefore, song can be considered an ancestral synapomorphic trait for this branch of cetacean evolution. When considering the acoustic frequency range and variety of unit types, and the complexity of song structure, humpback whale song is the most highly derived among the balaenopterid clade. What are the evolutionary drivers for this elaboration and complexity?

Early studies of humpback breeding behavior considered the question of evolutionary drivers. The existence of a trait that is highly derived and elaborate within a comparative phylogenetic framework is a typical indication of sexually selected exaggeration. In recognizing that the choruses of singers that they observed on the breeding grounds could function as a local “communal” display, Herman and Tavolga (1980) made the first connection between the humpback mating system and the lek mating systems described in terrestrial taxa (Emlen and Oring 1977). In lek mating systems, males aggregate and display to attract females, and females visit display

arenas for the purposes of evaluating males and choosing a mate based on their displays. Leks evolve in situations where males cannot directly control females or access to resources, where female movements to an area are predictable, and where females are relatively asynchronous in their periods of sexual receptivity, thereby skewing the operational sex ratio toward males. Many of these features are good descriptors of the typical humpback whale breeding system. Females arrive on the breeding grounds over a protracted period of several months (Dawbin 1966), and have an average two-year reproductive cycle (Mackintosh 1972), thus strongly skewing the operational sex ratio among sexually active adults toward males. Furthermore, during the breeding season, individuals are primarily or exclusively fasting (Chittleborough 1965); therefore, selective pressures with respect to defending food resources are unlikely to play a role in breeding behavior. Tyack (1981) put sexual selection at the forefront when considering the evolution of humpback singing behavior, noting that female choice may have been a driving force for song complexity (Chap. 7). Payne et al. (1983) took this concept one step further, drawing the analogy to the process by which female choice in some songbird species has led to the evolution of complexity in the form of large vocal repertoires.

Perhaps the most important insights to come out of this early period of work have to do with not only characterization of the intricate nature of humpback song structure and patterns of song sharing and rapid cultural evolution, but the exploration of hypotheses related to the underlying evolutionary drivers of song complexity. Therein lies the distinction between asking questions about the proximate processes that explain how an observed pattern develops, versus asking questions about the ultimate reasons for why these processes evolved. The foundational work of this early period of research, with its descriptions of song structure and the dynamics of humpback whale singing behavior, falls primarily into the proximate category. Based on these explorations, these authors cited above began to speculate on the ultimate questions of why humpback whales have evolved such a complex and dynamic singing behavior, which set the stage for further considerations of the selective forces and evolutionary drivers of the complexity in humpback singing behavior.

11.2 The Next Generation: Further Description of Patterns During the 1990s–2010s

The first phase of research on humpback whale song and singing behavior was conducted primarily by just a few research groups. Starting in the 1990s, humpback whale research in the ensuing three decades has focused on a broad range of topics by an ever-expanding number of researchers. Much of this more “modern” work has focused on exploring proximate mechanisms of how song patterns change and are transmitted between populations. Often song similarity has been used as a proxy metric to describe potential interactions among populations, supplementing early knowledge derived from whaling data and photo-ID mark recapture studies.

While earlier work concentrated on the Northern Hemisphere, Cato (1991), Dawbin and Eyre (1991), and Mednis (1991) confirmed that Southern Hemisphere humpback whales exhibit similar song structure and variable rates of song change to those of the Northern Hemisphere, undergoing periods of stability and of substantial change. Initial studies indicated that songs from east and west Australia showed little similarity, indicating that the geographic barrier of Australia may be more important than overall distances apart, as shown by the greater distances between breeding assemblages within the South Pacific with similar songs.

Passive acoustic studies have shown that patterns of physical movement (i.e., interchange) of individuals within and between populations can be more complex than previously thought. Within the North Pacific Ocean, initial studies showed that songs recorded from the breeding assemblages in Hawai'i and México shared all phrase types (Winn et al. 1981; Payne and Guinee 1983). Further ocean-basin-scale studies in the North Pacific revealed fluctuations in similarity among songs recorded from different breeding areas, sometimes resulting in the occurrence of temporary, regional differences in the number of shared versus "private" themes (Helweg 1990; Cerchio et al. 2001; Darling et al. 2014, 2019a). For example, Darling et al. (2019a) found that some themes were present across the entire North Pacific from the Philippines to México during a 3-year study, but others were only present in certain regions (e.g., "private themes"), and ocean-basin-scale similarity in song content varied across years. The variation in rates of song change and development of temporary, regional differences in song composition likely reflect variable levels of interchange and mixing of singers from different breeding areas over time. Within an ocean basin, therefore, humpback population structure could be described as a "metapopulation" (Levins 1969; Hanski and Gilpin 1991), within which there exists a complex pattern of site fidelity and overlap of individuals between feeding and breeding areas that varies across years. Similarly detailed song studies have not been conducted between the main breeding areas of the North Atlantic West Indies and Cape Verde Islands, though comparable fluctuations in similarity of song content between breeding regions may be present.

North Pacific and North Atlantic populations are separated by a continental land mass, with no movement of individuals between oceans. But the Southern Hemisphere is more open, with the high-latitude (>60° S) circumpolar "Southern Ocean" connecting separate ocean basins, and large expanses of lower latitudes dotted by islands. This allows for enhanced opportunities for whales mixing both between ocean basins across seasons, and within ocean basins during a season. The first example of consequent song sharing came from Noad et al. (2000), where humpback whales migrating along the east coast of Australia (western South Pacific Ocean), adopted the songs of animals from the west coast of Australia (southeast Indian Ocean) across two singing seasons. The process by which higher level song features (i.e., themes) are transferred between populations or aggregations is termed "*cultural diffusion*" (Mundinger 1980; Whiten et al. 2016). Mundinger (1980) applied this term to describe the process by which novel behaviors are introduced to one population by immigrants from a different population, as a cultural analog to gene flow between different populations. In the case of the Australian humpback whale populations,

immigrant individuals from the Indian Ocean (the origin population) introduced their song (the novel behavior) into the South Pacific population, which then adopted it. This is distinct from rapid cultural evolution that occurs incrementally and progressively as individuals from *within* a population gradually modify their existing song as they copy innovations made by one other. Noad et al. (2000) coined the term “cultural revolution” (perhaps due to the appeal of rhyming with cultural evolution, rather than drawing a parallel with other biological phenomena) for the transmission of song traditions between different populations. We maintain the original term “cultural diffusion” in this chapter.

During cultural diffusion from western to eastern Australia, there was complete replacement of all phrase types previously sung by the eastern Australian South Pacific population. There are also examples of cultural diffusion of partial songs, with only some novel phrase types being introduced and adopted, as described above in the North Pacific (e.g., Darling et al. 2019a). The phenomenon of cultural diffusion and complete replacement of songs has also been occasionally observed in other species, such as between social groups with distinct dialects in village indigobirds (Payne 1985). As in humpback whales, village indigobirds otherwise exhibit progressive rapid cultural evolution of songs during the singing season via individuals making innovations within songs that are copied and transmitted within their social group. However, Payne (1985) documented at least one case in which males from a neighboring social group permanently emigrated and introduced their origin social group’s song dialect into their new social group, whose previous dialect entirely disappeared.

Since 2000, the cultural diffusion of changes in song content between humpback breeding populations in the western and central South Pacific has been demonstrated repeatedly through a number of studies (e.g., Eriksen et al. 2005; Garland et al. 2011, 2015; Owen et al. 2019; Chap. 8). Other studies have shown limited song sharing across the Indian Ocean (Murray et al. 2012), and variable rates of song sharing across years between the southeast Atlantic and southwest Indian Oceans (Rekdahl et al. 2018). Song comparisons between breeding regions in the western and eastern South Atlantic (Darling and Sousa-Lima 2005) have shown that there is some song sharing between populations on opposite sides of the Atlantic Ocean, similar to patterns in the Northern Hemisphere (e.g., Darling et al. 2019a). Taken together, these studies reveal complex patterns of interchange between individuals both within and between breeding populations and subpopulations. These studies extend our early understanding of population movements derived from the whaling period (e.g., Dawbin 1966) as well as what has been shown through satellite telemetry and photo-ID studies (e.g., Calambokidis et al. 2001; Hauser et al. 2010; Garrigue et al. 2011, 2015).

While it is not clear which mechanisms for song transmission (as first proposed by Payne and Guinee 1983) are at work, it is likely that multiple mechanisms exist. Numerous studies have documented the occurrence of singing activity on feeding grounds in Northern Hemisphere and Southern Hemisphere (e.g., Gabriele and Frankel 2002; Clark and Clapham 2004; Vu et al. 2012; Stimpert et al. 2012; Garland et al. 2013; Van Opzeeland et al. 2013; Magnúsdóttir et al. 2014; Kowarski et al. 2018). Several studies have also documented singing in the open ocean, away

from breeding aggregations, presumably from migrating animals (Norris et al. 1999; Clark and Gagnon 2002; Darling et al. 2019b), as well as potential mixing between populations during migration (Owen et al. 2019). Finally, interannual movements of individuals between breeding areas have also been documented by individual recapture studies in both hemispheres (Dawbin 1966; Darling and Jurasz 1983; Darling and Cerchio 1993; Pomilla and Rosenbaum 2005; Stevick et al. 2016). All of these are likely mechanisms by which song sharing and cultural diffusion of song elements occur within and between populations. Levels of interchange between individuals appear to vary over time; thus, relatively short-term studies of only one or a few years cannot capture the full picture. Long-term, broad-scale studies (e.g., Garland et al. 2011) are needed to appropriately interpret what the patterns in song structure reveal about population interactions.

The 1990–2010 period also showed that changes in singing behavior can be used as an indicator of behavioral disturbance from human activities. Whereas numerous studies have assessed the impact of acoustic disturbance on movement patterns of individuals or distribution of populations (e.g., Frankel and Clark 2000, 2002; Dunlop et al. 2018), comparatively few have addressed behavioral impacts on singing activity or an acoustic response in the form of alteration of a vocalization. Humpbacks respond acoustically to a wide variety of anthropogenic sounds, such as vessel noise (Norris 1995; Sousa-Lima and Clark 2008; Tsujii et al. 2018), naval sonar (Fristrup et al. 2003; Risch et al. 2012), and seismic surveys (Cerchio et al. 2014), by altering song structure or decreasing singing activity. Subsequent studies modeling the potential communication space for humpbacks engaged in vocal interactions (both song and non-song) have demonstrated how noise from human activities can reduce the area over which individuals can communicate with one another (Cholewiak et al. 2018a; Dunlop 2019), a disturbing consequence of the expansion of human use of the oceans. Collectively, these studies have important implications, particularly considering cases when intense noise is generated in breeding habitat during the peak of reproductive activities; for example, seismic surveys occurring in tropical African waters during the austral winter. Since singing is a breeding display, disturbance in breeding habitats has the potential to impact the reproductive success of males and the ability of females to make important mate choice decisions.

11.3 The Next Phase of Research: Progress Toward Ultimate Questions

Many studies since the 1990s have documented cultural transmission of songs between humpback whale populations. Song is used in these cases as an indicator variable to study individual movements and population dynamics, rather than for the study of singing behavior itself. These studies reveal some of the proximate mechanisms of song transmission, but rarely address ultimate reasons for the evolution of song complexity, or the evolution of a system that favors a changing song

along with the rapid assimilation of changes in song units and patterns by individual males within a population. Compared to the numerous studies examining patterns of geographic variation in song, relatively few have been conducted in the past five decades that explore ultimate evolutionary hypotheses.

Why did the complexity that we observe in humpback whale song and singing behavior evolve in the first place? Evolutionary theory can give us some clues. While natural selection shapes signals that are important for survival, sexual selection shapes signals that are important within the context of reproduction. In some species, females show preferences for song characteristics even though these do not seem related to direct benefits to a female. The preference for traits that indicate indirect benefit is traditionally thought to arise through one of three types of selection: (1) traits that indicate “good genes”, which might result in higher offspring survivorship (Hamilton and Zuk 1982), (2) traits for which males incur a cost, thereby indicating male viability (the “handicap principle”, Zahavi 1975), or (3) indirect selection for an arbitrary trait that has no particular benefit other than increasing reproductive success for males who possess the trait (Fisher 1930, 1958). The latter involves the linkage between the male trait and female preference for the trait and is often referred to as “self-reinforcing” selection (Andersson 1994); this may lead to the evolution of highly exaggerated traits, such as the extravagant plumage of male peacocks (e.g., *Pavo cristatus*) or birds-of-paradise (family *Paradisaeidae*, e.g., *Parotia lawesii*), or the elaborate vocal performance of the common nightingale (*Luscinia megarhynchos*).

To address the adaptive function of rapid cultural evolution of songs in passerine birds, Trainer (1989) contrasted the reproductive behaviors of caciques and village indigobirds (species that are flexible learners with songs that are culturally transmitted horizontally and undergo rapid evolution), with the reproductive behaviors of chaffinches (*Fringilla coelebs*) and indigo buntings (*Passerina cyanea*) (species with stable songs that are transmitted vertically and change slowly across generations). Caciques and village indigobirds are polygynous, males are not territorial and frequently engage in competitive contact, males disperse widely, and songs can be learned as adults. In contrast, chaffinches and indigo buntings tend to be monogamous, males are territorial and engage in less social contact, males usually return to the same territory throughout their lifetimes, and learning ability is restricted to a period in early life. Trainer (1989), therefore, suggested that rapid cultural evolution of bird song occurs in species with a high degree of male-male competition. Payne (1985) suggested that the male village indigobirds with the most matings were those that sometimes initiated changes in song composition and were imitated most by other males. Trainer (1989) did not directly observe this in caciques, but proposed a process based on the preferential adoption of songs of successful males by less successful males, in which dominant males innovate on an existing song model to produce a song distinguishable from other males. This song variant from a high-ranking male acts as a strong stimulus to either threaten males or attract females. Other males try to imitate this song to confer its selective advantage upon themselves. Once all males share the song, it is no longer effective, and the dominant male makes a new improvisation. Therefore, there is continual incentive to improvise, and the repeating cycle

results in non-random, directional change in the details of the song composition. In humpback whales, this specific mechanism of copying dominant males cannot be the primary driving force behind song evolution; thousands of males spread across an ocean basin sing similar songs, and it is unlikely that a male's reproductive success in one breeding aggregation is affected by males in another breeding aggregation. However, humpback whales exhibit similar processes to some passerine songbirds in the rapid cultural evolution in song characteristics, suggesting that there may be similarities in the general underlying selective pressures.

In a comparative phylogenetic context and relative to other balaenopterids, the song system of the humpback whale clearly fits into the category of exaggerated traits, shaped by strong sexual selection. Singing is one of a suite of alternative mating tactics employed by males on the breeding grounds (Clapham 1996; Cerchio 2003; Cerchio et al. 2005). One of the main hypotheses is that female choice is the selective force driving both rapid cultural evolution and the complexity observed in humpback song (Tyack 1981; Payne et al. 1983; Clapham 1996; Cerchio et al. 2001; Cholewiak et al. 2018b); however, few studies have yet to document the role of intersexual selection. Medrano et al. (1994) documented two cases of females joining male singers, and Darling and Bérubé (2001) documented one case of a male–female pair in which the male was singing, and several instances of males singing in the presence of a female with calf. Smith et al. (2008) found that singers off eastern Australia were more likely to join mother–calf pairs than other types of groups and sang longer in the presence of a mother–calf pair than other group types. Anecdotal evidence from Kaua'i suggests that mothers accompanied by singers altered their respiratory behavior in response to the singers' presence by surfacing with the male (whose surfacings were timed to occur during a specific theme in the song), thus suggesting the female was listening to the singer and synchronizing her behavior with him (Cerchio 2003). Successful males participate in a variety of breeding tactics, and singing to mothers with calves may be one of them (Cerchio 2003; Cerchio et al. 2005). Molecular determination of paternity of calves off Socorro, México, matched the paternity of a female's second calf in consecutive years to a male observed escorting her in the previous year (Cerchio 2003). Estimated rates of post-partum estrus range from 3 to 20% of females giving birth in consecutive years (Clapham and Mayo 1987; Glockner-Ferrari and Ferrari 1990; Cerchio 2003) to 40%, based on whaling data (Chittleborough 1965); therefore, courtship of a mother with calf may be an important male breeding tactic.

These studies provide a glimpse of insight into potential intersexual selection. Studying the behavior and interactions of non-parous females with males on the breeding grounds could be quite revealing, but is unfortunately very challenging. Females are often the center of attention in competitive groups, which can involve many males vying for the position closest to her (Tyack and Whitehead 1982; Clapham et al. 1992), precluding the opportunity to study their behavior in the absence of interference by males. When unaccompanied, single individuals can be difficult to visually locate and track, as they can be relatively cryptic compared to other types of groups (singers being a notable exception). Therefore, although lone

females may well be within acoustic detection range and listening to (or even interacting acoustically with) male singers, their behavior is difficult to document. These challenges have thus far limited our ability to study potential female choice relative to singing males.

Studying singer behavior to examine the potential role of intrasexual selection has been a more fruitful line of inquiry. From the intrasexual perspective, using song to mediate interactions may allow males to assess potential rivals and avoid physical conflict. In taxa from ungulates to birds, escalation or de-escalation of agonistic interactions can be based on an individual's motivation and perception of one's own quality or competitive ability compared to that of a rival. Several studies have examined the spatial and acoustic responses of singers to interactions with other males. Frankel et al. (1995) found that singers generally maintained greater separation distances between one another than non-singing individuals in a breeding area off Hawai'i, leading to the idea that males may use song to maintain spacing between other singers (also observed in minke whales, Gedamke 2004). Darling et al. (2006) found that 89% of singers in their study sang until they were "joined" by non-singing males (143/161 observed interactions), often leading to brief interactions (<10 min) that typically appeared to be non-agonistic. This is consistent with other observations of lone males interacting with singers, who then often ceased to sing (Smith et al. 2008). Darling et al. (2012), using an experimental playback design, also found that a singing male approached a playback of song that was similar to his own song 7 out of 9 times (78%), and stopped singing in 8 out of 9 trials (89%). In considering these types of interactions, Darling et al. (2006) hypothesized that males may assess one another using details of song content as an index of association, and that this information may allow individuals to determine whether to interact antagonistically or otherwise with another singer. Only one study has examined the response of singers to one another by evaluating not only their spatial movements and singing persistence, but also by examining whether males are responding acoustically—specifically, changing the details of their song structure in response to other singers (Cholewiak et al. 2018b). If male singers are using song interactively to mediate interactions with one another, then it should be possible to measure the responses of one individual singer relative to the actions of another singer. With song, this could take the form of acoustically "pointing" at specific receivers, via timing or pattern changes (Todt and Naguib 2000). Cholewiak et al. (2018b) found that 11 out of 12 singers modified their song presentation in the presence of a singing rival, changing the rate at which they switched between phrase types, and the overall "evenness" of their song presentation. A similar result was found via a controlled playback study, in which singing males were presented simplified versions of their own songs (Cholewiak 2008). Similarly to previous studies, Cholewiak et al. (2018b) also found that some singers (5 of 12) approached other singers. Rapid approaches were associated with one or both males ceasing to sing (in 3 out of 3 cases), suggesting that the combination of singing while approaching could be a form of threat. This hypothesis suggests that males are interrupting the display of their rivals as a form of competition, as is commonplace on bird leks (Wiley 1991; Höglund and Alatalo 1995).

If humpback whale males are using their singing behavior and song characteristics to mediate potential competitive interactions, then there should be strong selection for song characteristics that allow males to assess one another, and these characteristics should be both costly and an honest reflection of male quality (i.e., difficult to cheat). Costs may be incurred either through production (e.g., energetic costs) or through enforcement of honesty by conspecifics (Bradbury and Vehrencamp 1998). Song elements or behavior that are difficult to produce, or those that indicate body size might be useful for male–male assessment. For example, differences in the spectral or amplitude characteristics of song units (Frankel 1994), or speed of swimming while singing as observed in fin whales (*Balaenoptera physalus*; Clark et al. 2019), could be features that convey male quality. The quality of a male’s song itself may also reflect experience and age of the singer, if some features of signal production or adherence to the “optimal” pattern require a skill level only acquired through repetitive practice and experience. Additionally, graded song characters (such as switching rates) that allow males to predict the likelihood of escalating aggression are also important in some species (e.g., Searcy et al. 2000).

It is likely that humpback whale song may have evolved in response to both inter- and intrasexual selective pressures (Herman 2017; Cholewiak et al. 2018b). In many avian species, song has been shown to serve both functions within the breeding system, where males may use different song types or change presentation style depending on the primary audience (e.g., Kroodsma et al. 1989; Searcy and Yasukawa 1990). Furthermore, both males and females may eavesdrop on acoustic interactions, which may also play a strong role in sexual selection (Naguib et al. 1999; Mennill et al. 2002). Individuals can gain information about another individual’s quality or motivation through eavesdropping and use this information to make subsequent decisions (Bartsch et al. 2014). Females may use the same types of song traits to assess male quality. The combination of stereotypy and complexity in humpback song may indicate that it is a multimessage display (Murray et al. 2018), and both males and females may be listening in on male–male interactions (Cholewiak 2008; Dunlop and Noad 2016; Cholewiak et al. 2018b).

A potential approach to exploring selective forces that have shaped humpback whale singing behavior is to use comparative studies from non-interacting populations and different periods of time (e.g., different decades), to distinguish between aspects of the singing behavior and song that are heritable versus entirely learned (Chap. 2). Several researchers have suggested that some aspects of singing behavior may follow innate templates, as opposed to those features of songs (e.g., the patterns themselves) that appear to be learned and transmitted between individuals and thus subject to the processes of cultural evolution. The continuity of humpback whale song structure and singing behavior on a global scale was first recognized by Payne and Guinee (1983). Populations in all ocean basins follow the same hierarchical song structure, change their songs progressively through time, and have similar levels of complexity, so Payne and Payne (1985) argued that there are innate constraints guiding the form of song. This is not entirely surprising, as all species of whales have their own recognizable species-specific song structure that is clearly a heritable trait.

Humpbacks are set apart from at least the other balaenopterids by the predisposition for flexible learning, apparent innovation, and aptitude for copying conspecifics; these traits are also clearly heritable, found in all populations currently studied, and apparently unique within the Balaenopteridae clade (Chap. 12). Therefore, it is clear that some evolutionary force has selected for the process of dynamic temporal change in humpback song. Another level of questioning is to ask whether these same evolutionary forces may have selected for specific ways in which singers change their songs over time, and thus constraining the observed variation in song patterns. Cerchio et al. (2001), during a study of geographic variation between Hawai'i and México, observed that some quantitative variables of unit and phrase structure changed in parallel in the two distant breeding areas over a single singing season. Since it was concluded that singers in these distant breeding areas could not interact during the study time period, the authors suggested that this may be evidence for an innate template that could govern some aspects of how singers change song over time, in the same manner as innate processes determine song structure. It was argued that progressive change therefore could be explained as a combination of cultural transmission overlaid on a set of innate rules for change. The prediction of such a system would be recurring patterns of how songs are changed over time, when comparing songs from distant populations or different periods of time (e.g., different decades). Other more recent studies have examined song samples from such non-interacting populations and similarly suggested "constraints" on what song elements are copied (Mercado III et al. 2003) and persistent recurring patterns of both phrase structure and how songs are changed over time (Green et al. 2011). Together, these studies expand upon the concept of genetic predispositions for song structure and flexible learning that were first proposed in the early studies (Payne and Guinee 1983; Payne and Payne 1985) and extend it to propose innate components to how these patterns change over time. Studies exploring a heritable component to song structure and temporal change have been relatively few in comparison to studies of cultural transmission and the resultant patterns of geographic variation. If in fact there are constraints on song variation and behavior, and definable patterns of temporal change, the description of these patterns could inform what has been selected during the evolution of the behavior, and in turn reveal those aspects of song that are important to reproductive success and inclusive fitness, driving the development of the observed complex system.

11.4 Where Do We Go Now? Open Questions for Future Work

In the fifty years since humpback whale song was first described, there have been well over 100 papers published in the scientific literature describing the content and patterns of song across space and time, the occurrence of singing activity, the behavior of singers, as well as speculations about the form and function of song within the

humpback breeding system. The beauty and complexity of humpback whale song have captivated many hearts and minds.

Yet, despite decades of research, fundamental questions remain. What are the evolutionary drivers that have resulted not only in a highly exaggerated acoustic display, but also the predisposition for life-long learning and incorporation of new features into an individual's song? Which features of humpback song and singing behavior are culturally transmitted, and which are genetically constrained? How do individual whales develop and change their own songs, and what are the social factors and thresholds for hearing new material that prompts an individual male to adopt new song patterns into his own song (e.g., Beecher 2017)?

For the most part, these questions have not been addressed because it is extremely difficult to study sexual selection. To do so would require documenting mate choice by females, quantifying the reproductive success of individual males, and identifying specific quantifiable male traits that contribute to reproductive success. Unlike songbirds, where individuals can be raised in captivity and the influences on a male's song development (and his subsequent reproductive success) can be tested in a controlled environment, no such research opportunity exists with free-ranging, long-lived large whales (or other large mammals, for that matter). Mating has been nearly impossible to observe in humpback whales, and there have been few molecular genetic studies of paternity and/or male reproductive success. Only three such studies have been published (Clapham and Palsboll 1997; Nielsen et al. 2001; Cerchio et al. 2005). The insights from these studies have revealed only mild skew in male reproductive success beyond what would be expected from a random mating model (with many males siring single calves and few males siring multiple calves), and indicate that successful males use a variety of mating tactics, singing being among them (Cerchio 2003; Cerchio et al. 2005). Studies of male reproductive success are particularly challenging in species with large populations that cover broad ranges, where the chances of sampling successful males are low.

There are multiple avenues for further study that have not been fully explored and could reveal new insights into both the proximate mechanisms and ultimate drivers of humpback whale singing behavior. From a comparative perspective, only one other species of cetacean has evolved a similarly complex song—the bowhead whale (*Balaena mysticetus*; Chap. 12). Bowhead whales are part of the family Balaenidae, which represents a separate evolutionary lineage within mysticetes, having diverged from the lineage that gave rise to the balaenopterids over 30 million years ago (Marx and Fordyce 2015). Within the four species of extant balaenids, it was previously thought that right whales (*Eubalaena glacialis*, *E. japonica*, *E. australis*) did not exhibit male acoustic reproductive displays, although recent studies have revealed that right whales do produce patterned sequences of gunshot sounds that have been characterized as song (Crance et al. 2019). Bowhead whales, on the other hand, are well known for their varied song repertoire, with extreme diversity in song types reported in some populations (Stafford et al. 2018; Chap. 12). Male bowhead song is generally comprised of one to three themes, but many different song types have been recorded within and between breeding seasons, suggesting potentially strong selective pressure for novelty (Stafford et al. 2018). In addition, bowheads incorporate

biphonation into some of their song units (Tervo et al. 2011), essentially singing with two voices. Given the phylogeny of mysticete whales, the occurrence of an exaggerated, complex acoustic display in both bowhead and humpback whales likely represents convergent evolution rather than shared ancestry. Of further consideration, the breeding systems of these two species are quite different; the bowhead whale mating system likely relies on sperm competition, given their larger-than-predicted testes size (Brownell and Ralls 1986) and observed mating behavior (Everitt and Krogman 1979), whereas humpback whales are believed to have a form of a polygynous mating system with alternative male mating tactics (Clapham 1996; Cerchio 2003). Further exploration of bowhead behavior and song within a comparative framework may reveal commonalities between the species, indicating similarities in sexual selection.

Within studies of humpback song and humpback singing behavior, several topics remain understudied. One of these is the ontogeny of song, both developmental, as a juvenile male matures into adulthood, and seasonal, i.e., with the increase and decrease in song production at the beginning/end of the breeding season. Studying the developmental ontogeny of song within individual males would require directed effort to record vocal production by juvenile males at various stages during their growth and maturation, an undertaking which has not been attempted, to our knowledge. Studies of calves with their mothers on the breeding grounds have revealed the production of non-song sounds by calves (Zoidis et al. 2008; Saloma 2018), but documentation of song production and song structure of sexually immature males is lacking. Such studies would reveal insights into how individual males develop and learn their songs. Areas where juvenile humpbacks occur during winter months, such as the mid-Atlantic coast of the US eastern seaboard (Swingle et al. 1993), could provide study areas where such targeted research could take place.

Recent work describing the seasonal ontogeny of song structure on feeding grounds in the western North Atlantic (Kowarski et al. 2019; Kowarski 2020) has revealed patterns in the onset and cessation of song production prior to and post breeding season. In the autumn, there appeared to be a gradual onset of singing behavior, with the production of song fragments prior to full song sequences. Song fragments were composed of individual phrases or subphrases, repeated a variable number of times, and were detected for several weeks prior to the detection of full song sequences. In contrast, during spring months, presumably when males would have been returning from the breeding grounds, the cessation of singing behavior was abrupt, with fewer instances of song fragments being detected. The authors discuss these patterns within the context of singing and hormonal development in oscine birds, suggesting that the production of song fragments is similar to the production of “subsong” (or perhaps more accurately, “plastic song”) in songbirds (Kowarski et al. 2019). More detailed analysis of complete songs throughout the autumn on the feeding ground, into the winter on Caribbean breeding grounds, indicated a steady increase in repetition number of phrases and consistency in order of themes, suggesting an analogous progression from “plastic song” to “crystallized song” (Kowarski 2020). While these studies were not able to discern the seasonal ontogeny of song development for individual males, they provide information on population-level patterns. Interestingly, the most common forms of song fragments

detected by Kowarski et al. (2019) were comprised of single or multiple song themes, with singular phrases or subphrases rarely detected.

Another line of inquiry that has not been well explored is that of the commonalities in the compositional organization and spectral content of humpback song found in songs worldwide. The Paynes first noted that all songs include “a remarkable range of contrasting frequencies, dynamics, and rhythms” (Payne and Payne 1985). Beyond simply the inclusion of contrasting frequencies and rhythms, our own observations are that completely unrelated songs (i.e., songs from different ocean basins and different years) may share similar compositional characteristics when examined from a broad view; for example, the production of themes with relatively higher frequency units (e.g., 300–500 Hz) followed by themes with consistently lower frequency units (e.g., <200 Hz), as though the themes are somewhat “ordered” by spectral content. These organizational features can be seen in example spectrograms of songs recorded from two different ocean basins (North Pacific vs. Indian Ocean) across a nearly 40-year time period (1990 vs. 2019) (Fig. 11.4). A similar pattern in overall spectral composition has been observed in other ocean basins, such as in the songs recorded in the North Atlantic (pers. obs.) as well as in the South Pacific (Mercado III and Perazio 2021) in different time periods. While the finer details of the spectral features and song composition are clearly different between these regions and periods, there appear to be similarities in the broad pattern that is greater than the individual components. These attributes describe what could be considered an emergent property of humpback whale song, which is often (though not always) observed. This observation may be one of the indications distinguishing what may be innate structural rules governing humpback song organization, versus the details of song composition that may be culturally transmitted (Cerchio et al. 2001).

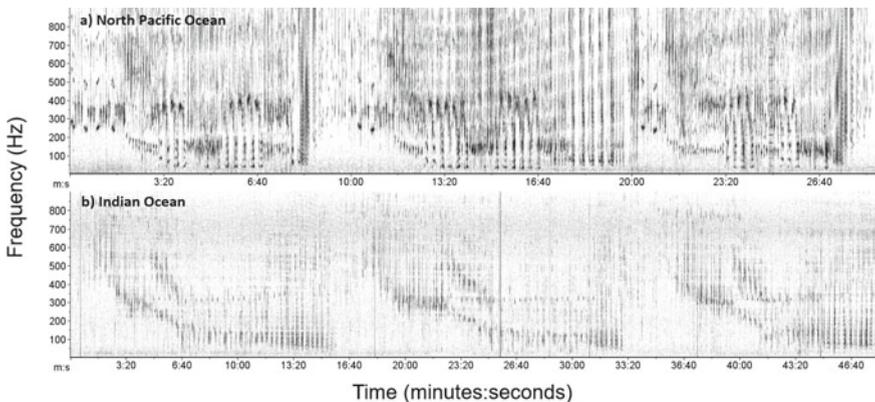


Fig. 11.4 Spectrograms showing examples of humpback song from two different ocean basins (**a** North Pacific Ocean, **b** Indian Ocean), and two different years (1990, 2019, respectively). Note the general similarity in the spectral-temporal organization of frequency content in both examples, demonstrating what appears to be a periodically recurring phenomenon in thematic organization in humpback song structure

The cultural diffusion and song convergence episodes documented in the South Pacific (e.g., Noad et al. 2000; Garland et al. 2011) provide another opportunity to study song learning, cultural transmission, and patterns of change. As individual males in one breeding aggregation appear to have learned and sung the songs from males in a different breeding aggregation, how is the new material incorporated into an individual's own song, and consequently the song of the population as a whole? One study has provided a glimpse into these mysteries, examining the song sequences of four males during periods of cultural diffusion (Garland et al. 2017). In each example, males incorporated complete phrases from new themes into their existing song pattern, and in some cases sang transition phrases that incorporated material from both the old and new themes. This suggests that the salient component for males incorporating new material into their song may be song phrases, rather than individual units. The observations of song hybridization and song convergence raise a new set of questions related to the cultural evolution of song patterns. After a song convergence episode between two breeding aggregations that had previously sung different songs (i.e., different sets of themes), there appears to be a period of isolation of the two aggregations during which song divergence occurs once again (Darling et al. 2019a). While some studies have examined measures of song "complexity" within a population before and after such convergence episodes (Allen et al. 2018), no studies have yet examined the differential patterns of song change between breeding aggregations after such convergence. Since cultural diffusion and song convergence are reported to occur repeatedly over decadal scales in both the Southern Hemisphere and Northern Hemisphere (Darling et al. 2019a; Garland and McGregor 2020), it is apparent that when males in one breeding aggregation are isolated from males in a different aggregation, some song changes must occur in different directions between the two separate aggregations. Therefore, studies on the temporal progression of song changes after convergence could provide valuable insights into cultural evolution, allowing one to potentially tease apart changes that are purely the result of cultural transmission of individual innovations (which one would predict to be divergent between aggregations), from those types of changes that may occur according to an innate heritable template, that would appear as similar parallel trends in the two diverging populations (Cerchio et al. 2001; Green et al. 2011).

As humpback whale populations increase after their decimation during the industrial whaling era, there may be increased opportunities for mixing of individuals from different breeding aggregations during migration or on the feeding grounds. Climate change and the resulting effects on the distribution and abundance of prey will continue to impact the movements and potential interchange between individuals from what had been different breeding aggregations on the foraging grounds. Observed variations in primary productivity have been correlated with fluctuations in humpback singing activity (Ryan et al. 2019), and the seasonal distributions of multiple species of large whales have already shifted in recent years in some regions (e.g., Davis et al. 2020). In addition, some breeding areas near to but north of the equator are utilized by individuals from both the Northern and Southern Hemisphere populations, in opposing breeding seasons. In the Cape Verde Islands and western African coast in the North Atlantic, and along the coast of Costa Rica in

the North Pacific, both Northern and Southern Hemisphere populations have been documented at different times of year (Acevedo and Smultea 1995; Rasmussen et al. 2007; Hazevoet et al. 2011; Van Waerebeek et al. 2013). While simultaneous utilization of those breeding areas by individuals from opposite hemispheres has not been documented, overlap of breeding males at the extreme temporal limits of their respective breeding seasons could be a possibility. Each of these factors (population recovery, shifts in distribution and potential overlap in breeding habitats) could facilitate increased cultural transmission of song features between males from different breeding aggregations. What is the threshold of exposure before an individual singer decides to incorporate a new song type into his own, and how does that relate to what is happening at the level of the breeding aggregation? Some breeding aggregations have appeared more “acoustically dynamic” than others (e.g., Darling et al. 2019a), and in the South Pacific, cultural transmission of new song types appears to spread from larger to smaller breeding groups (Garland et al. 2011, 2015). However, in some cases new song types were detected but failed to be adopted by the breeding aggregation as a whole (Garland et al. 2011). We are reminded that the changing dynamics of populations that are growing in a post-whaling era provide opportunities, but also complications, to our understanding of the factors driving the observed patterns in humpback song structure.

Finally, we reflect on a unique population of humpback whales that inhabits the Arabian Sea. Unlike all other humpback populations, the animals in the Arabian Sea comprise an extremely small population of year-round residents. They follow a Northern Hemisphere breeding cycle (Mikhalev 1997), but have no physical access to high-latitude feeding areas: Biannual periods of monsoon-driven productivity allow them to remain in the Arabian Sea and feed throughout the year (Minton et al. 2011). Therefore, they do not undertake the latitudinal migrations typical of other populations. This population was subjected to intensive illegal Soviet whaling in the 1960s that reduced a population that was thought to be already small in size, on the order of hundreds of animals (Mikhalev 1997); current estimates suggest the remaining population could be less than 100 animals (Minton et al. 2011) and has significantly lower genetic diversity than Southern Hemisphere populations (Pomilla et al. 2014). What can studies of an isolated, non-migratory population of humpback whales tell us about the mechanisms and underlying drivers for song complexity and change? Passive acoustic monitoring over a two-year period off the Arabian Sea coast of Oman indicated that singing activity followed the same boreal seasonal pattern typical of other Northern Hemisphere populations (Cerchio et al. 2016), despite the lack of latitudinal migration and the population having been derived from a Southern Hemisphere population approximately 70,000 years ago (Pomilla et al. 2014). Initial analyses of acoustic data from the region found that while patterns in song and phrase structure at any given time fit within the range of variation seen in other populations globally, temporally the population exhibited an unusually low rate of song change over a 3-year period, possibly representing a form of temporal “stasis” (Cerchio et al. 2018). The authors speculate that one potential explanation could be that the small population size has resulted in a low level of innovation in song patterns. Furthermore, during the study period, songs from the southwest

Indian Ocean humpback population were recorded on several days during the Boreal summer (Austral winter) off the coast of Oman, indicating a low level of occurrence of animals from the Southern Hemisphere population. However, the Arabian Sea animals did not incorporate or adopt any elements from the southwest Indian Ocean song into their own song, similar to the observation by Garland et al. (2011) in French Polynesia (where new songs were recorded but failed to be adopted by the breeding aggregation as a whole). Cerchio et al. (2018) propose three hypotheses for their observation: that no Arabian Sea animals were in the area during the time that the Southern Hemisphere animals appeared, that the number of the Southern Hemisphere singers was too few to result in cultural diffusion (i.e., for the local males to adopt the new elements into their song), or that the Arabian Sea population was either not receptive or possibly has partially lost the trait for adoption of novel material. The combined observation of comparatively slow change of songs over three years and the lack of cultural diffusion despite the presence of the immigrants' songs suggest that there may be some unique selective drivers for this population's singing behavior.

11.5 Afterword

Looking back on the past half century of research, it is clear that we have uncovered fascinating mysteries about the captivating songs of humpbacks whales. The growing availability of acoustic recording and analytical technologies in the past few decades has facilitated our ability to listen in on the ocean in many remote parts of the world, revealing new and interesting insights into the acoustic behavior of not only humpback whales, but many marine species. However, as our ability to remotely collect passive acoustic data has increased, there seems to have been a corresponding decrease in field efforts dedicated to the focal study of individual animal behavior; a line of inquiry that is essential if we are to further unravel some of the lingering questions that we have described in this chapter. Without continued study of humpback breeding behavior, and in particular the behavior of singers and how individual males change their songs over time, our understanding of the processes and forces that drive the beautiful complexity in humpback song will always be constrained. It is only through combining our collective efforts and observations, and retaining a deep connection to the animals that we study, that we can reflect on the most interesting and in-depth questions that inspire us, and pay homage to the wonders of the natural world.

Acknowledgements We acknowledge and appreciate over half a century of work by dozens of researchers around the globe that have contributed to the body of knowledge that has allowed us to explore the intricacies of humpback whale song in so many different ways. In particular, we thank Dr. Christopher Clark for many years of support, thought-provoking discussions, and insightful reflections that have profoundly influenced our thought processes and understanding of not just humpback whale song, but baleen whale acoustic ecology as a whole. Finally, we dedicate this

chapter to Katharine Payne, for inspiring generations of curious minds, including our own, to listen a little more closely to the world around us.

References

- Acevedo A, Smultea M (1995) First records of humpback whales including calves at Golfo Dulce and Isla del Coco, Costa Rica, suggesting geographical overlap of northern and southern hemisphere populations. *Mar Mamm Sci* 11:554–560
- Allen JA, Garland EC, Dunlop RA, Noad MJ (2018) Cultural revolutions reduce complexity in the songs of humpback whales. *Proc R Soc B Publ* 285(1891). <https://doi.org/10.1098/rspb.2018.2088>
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ
- Baker CS, Perry A, Bannister JL, Weinrich MT, Abernethy RB, Calambokidis J, Lien J, Lambertsen RH, Urban Ramirez J, Vasquez O, Clapham PJ, Alling A, O'Brien SJ, Palumbi SR (1993) Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proc Natl Acad Sci* 90:8239–8243
- Bartsch C, Wenchel R, Kaiser A, Kipper S (2014) Singing onstage: female and male common nightingales eavesdrop on song type matching. *Behav Ecol Sociobiol* 68(7):1163–1171
- Beecher M (2017) Birdsong learning as a social process. *Anim Behav* 124:233–246
- Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer Associates Inc.
- Brownell RL, Ralls K (1986) Potential for sperm competition in baleen whales. *Rep Int Whaling Comm* 8:97–112
- Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Jorge UR, Jacobsen JK, Ziegeler OV, Balcomb KC, Gabriele CM (2001) Movements and population structure of humpback whales in the North Pacific. *Mar Mamm Sci* 17:769–794
- Cato DH (1991) Songs of humpback whales: the Australian perspective. *Mem Queensland Museum* 30:277–290
- Cavalli-Sforza LL, Feldman M (1981) Cultural transmission and evolution: a quantitative approach. Princeton University Press, Princeton, NJ
- Cerchio S (2003) Paternity, polygyny and alternative mating tactics in humpback whales (*Megaptera novaeangliae*)
- Cerchio S, Jacobsen JK, Norris TF (2001) Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Anim Behav* 62(2):313–329
- Cerchio S, Jacobsen JK, Cholewiak DM, Falcone EA, Merriwether DA (2005) Paternity in humpback whales, *Megaptera novaeangliae*: assessing polygyny and skew in male reproductive success. *Anim Behav* 70(2):267–277. <https://doi.org/10.1016/j.anbehav.2004.10.028>
- Cerchio S, Strindberg S, Collins T, Bennett C, Rosenbaum H (2014) Seismic surveys negatively affect humpback whale singing activity off northern Angola. *PLoS ONE* 9(3):e86464–e86464. <https://doi.org/10.1371/journal.pone.0086464>
- Cerchio S, Willson A, Muirhead C, Minton G, Collins T, Baldwin R, Sarrouf Willson M, Al Harthi S (2016) Preliminary report on long-term detection of Arabian Sea humpback whale vocalizations off Oman
- Cerchio S, Willson A, Muirhead C, Al Harthi S, Baldwin R, Bonato M, Collins T, Di Clemente J, Dulau V, Estrade V, Latha G (2018) Geographic variation in song indicates both isolation of Arabian Sea humpback whales and presence of Southern Hemisphere whales off Oman
- Chittleborough RG (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Mar Freshw Res* 16(1):33–128. <https://doi.org/10.1071/MF9650033>
- Cholewiak D (2008) Evaluating the role of song in the humpback whale (*Megaptera novaeangliae*) breeding system with respect to intra-sexual interactions

- Cholewiak DM, Sousa-Lima RS, Cerchio S (2013) Humpback whale song hierarchical structure: historical context and discussion of current classification issues. *Mar Mamm Sci* 29(3):E312–E332. <https://doi.org/10.1111/mms.12005>
- Cholewiak D, Clark CW, Ponirakis D, Frankel A, Hatch LT, Risch D, Stanistreet JE, Thompson M, Vu E, Van Parijs SM (2018a) Communicating amidst the noise: modeling the aggregate influence of ambient and vessel noise on baleen whale communication space in a national marine sanctuary. *Endang Species Res* 36:59–75
- Cholewiak DM, Cerchio S, Jacobsen JK, Urban RJ, Clark CW (2018b) Songbird dynamics under the sea: acoustic interactions between humpback whales suggest song mediates male interactions. *R Soc Open Sci* 5(2):171298. <https://doi.org/10.1098/rsos.171298>
- Clapham PJ (1996) The social and reproductive biology of humpback whales: an ecological perspective. *Mamm Rev* 26(1):27–49
- Clapham PJ, Mayo CA (1987) The attainment of sexual maturity in two female humpback whales. *Mar Mamm Sci* 3(3):279–283
- Clapham P, Palsboll PJ (1997) Molecular analysis of paternity shows promiscuous mating in female humpback whales (*Megaptera novaeangliae*, Borowski). *Proc R Soc Lond B* 264(264):95–98
- Clapham P, Palsboll PJ, Matilla D, Vasquez O (1992) Composition and dynamics of humpback whale competitive groups in the West Indies. *Behaviour* 122(3–4):182–194
- Clark CW, Clapham PJ (2004) Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. *Proc R Soc Lond B* 271(1543):1051–1057. <https://doi.org/10.1098/rspb.2004.2699>
- Clark CW, Gagnon C (2002) Insights from IUSS detections, locations and tracking from 1992 to 1996. *J Underw Acoust (USN)* 52:609–640
- Clark CW, Gagnon GJ, Frankel AS (2019) Fin whale singing decreases with increased swimming speed. *R Soc Open Sci* 6(6):180525. <https://doi.org/10.1098/rsos.180525>
- Crance JL, Berchok CL, Wright DL, Brewer AM, Woodrich DF (2019) Song production by the North Pacific right whale, *Eubalaena japonica*. *J Acoust Soc Am* 145(6):3467–3479. <https://doi.org/10.1121/1.5111338>
- Darling JD, Bérubé M (2001) Interactions of singing humpback whales with other males. *Mar Mamm Sci* 17(3):570–584
- Darling JD, Cerchio S (1993) Movement of a humpback whale (*Megaptera novaeangliae*) between Japan and Hawaii. *Mar Mamm Sci* 9(1):84–88
- Darling JD, Jurasz C (1983) Migratory destinations of North Pacific humpback whales. In: Payne R (ed) *Communication and behavior of whales*. Westview Press, pp 359–368
- Darling JD, Sousa-Lima RS (2005) Songs indicate interaction between humpback whale (*Megaptera novaeangliae*) populations in the western and eastern South Atlantic Ocean. *Mar Mamm Sci* 21(3):557–566
- Darling JD, Jones ME, Nicklin CP (2006) Humpback whale songs: do they organize males during the breeding season? *Behaviour* 143:1051–1101
- Darling JD, Jones ME, Nicklin CP (2012) Humpback whale (*Megaptera novaeangliae*) singers in Hawaii are attracted to playback of similar song. *J Acoust Soc Am* 132:2955–2958
- Darling JD, Acebes JMV, Yamaguchi M (2014) Similarity yet a range of differences between humpback whale songs recorded in the Philippines, Japan and Hawaii in 2006. *Aquat Biol* 21(2):93–107
- Darling JD, Acebes JMV, Frey O, Jorge Urban R, Yamaguchi M (2019a) Convergence and divergence of songs suggests ongoing, but annually variable, mixing of humpback whale populations throughout the North Pacific. *Sci Rep* 9(1):7002. <https://doi.org/10.1038/s41598-019-42233-7>
- Darling JD, Goodwin B, Goodoni MK, Taufmann AJ, Taylor MG (2019b) Humpback whale calls detected in tropical ocean basin between known Mexico and Hawaii breeding assemblies. *J Acoust Soc Am* 145(6):EL534–EL550
- Davis GE, Baumgartner MF, Corkeron PJ, Bell J, Berchok C, Bonnell JM, Bort Thornton J, Brault S, Buchanan GA, Cholewiak DM, Clark CW, Delarue J, Hatch LT, Klinck H, Kraus SD, Martin B, Mellinger DK, Moors-Murphy H, Niekirk S, Nowacek DP, Parks SE, Parry D, Pegg N, Read

- AJ, Rice AN, Risch D, Scott A, Soldevilla MS, Stafford KM, Stanistreet JE, Summers E, Todd S, Van Parijs SM (2020) Exploring movement patterns and changing distributions of baleen whales in the western North Atlantic using a decade of passive acoustic data. *Glob Change Biol* 26:29. <https://doi.org/10.1111/gcb.15191>
- Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In: Norris KS (ed) *Whales, dolphins, and porpoises*. University of California Press, pp 147–170
- Dawbin WH, Eyre EJ (1991) Humpback whale songs along the coast of Western Australia and some comparison with east coast songs. *Mem Queensland Museum* 30:249–254
- Dunlop RA (2019) The effects of vessel noise on the communication network of humpback whales. *R Soc Open Sci* 6(11):190967. <https://doi.org/10.1098/rsos.190967>
- Dunlop RA, Noad MJ (2016) The “risky” business of singing: tactical use of song during joining by male humpback whales. *Behav Ecol Sociobiol* 70(12):2149–2160
- Dunlop RA, Noad MJ, McCauley RD, Kniest E, Slade R, Paton D, Cato DH (2018) A behavioural dose-response model for migrating humpback whales and seismic air gun noise. *Mar Pollut Bull* 133:506–516. <https://doi.org/10.1016/j.marpolbul.2018.06.009>
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197(4300):215–223
- Eriksen N, Miller LA, Tougaard J, Helweg DA (2005) Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. *Behaviour* 142:305–328
- Everitt RD, Krogman BD (1979) Sexual behavior of bowhead whales observed off the north coast of Alaska. *Arctic* 32(3):277–280
- Fisher RA (1930) *The genetical theory of natural selection*, 1st edn. Clarendon Press, Oxford
- Fisher RA (1958) *The genetical theory of natural selection*, 2nd edn. Dover, New York
- Frankel A (1994) Acoustic and visual tracking reveals distribution, song variability and social roles of humpback whales in Hawaiian waters. University of Hawaii
- Frankel AS, Clark CW (2000) Behavioral responses of humpback whales (*Megaptera novaeangliae*) to full-scale ATOC signals. *J Acoust Soc Am* 108(4):1930–1937
- Frankel AS, Clark CW (2002) ATOC and other factors affecting the distribution and abundance of humpback whales, *Megaptera novaeangliae*, off the north shore of Kauai. *Mar Mamm Sci* 18(3):644–662
- Frankel AS, Clark CW, Herman L, Gabriele CM (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawai‘i, determined using acoustic and visual techniques. *Can J Zool* 73:1134–1146
- Fristrup KM, Hatch LT, Clark CW (2003) Variation in humpback whale (*Megaptera novaeangliae*) song length in relation to low-frequency sound broadcasts. *J Acoust Soc Am* 113(6):3411–3424. <https://doi.org/10.1121/1.1573637>
- Frumhoff P (1983) Aberrant songs of humpback whales (*Megaptera novaeangliae*): clues to the structure of humpback songs. In: *Communication and behavior of whales*, pp 81–127
- Gabriele C, Frankel A (2002) The occurrence and significance of humpback whale songs in glacier bay, southeastern Alaska. In: *Arctic research of the United States*, pp 42–47
- Garland EC, McGregor PK (2020) Cultural transmission, evolution, and revolution in vocal displays: insights from bird and whale song. *Front Psychol* 11:2387. <https://doi.org/10.3389/fpsyg.2020.544929>
- Garland EC, Goldizen AW, Rekdahl ML, Constantine R, Garrigue C, Hauser ND, Poole MM, Robbins J, Noad MJ (2011) Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. *Curr Biol* 21(8):687–691. <https://doi.org/10.1016/j.cub.2011.03.019>
- Garland EC, Gedamke J, Rekdahl M, Noad MJ, Garrigue C, Gales N (2013) Humpback whale song on the southern ocean feeding grounds: implications for cultural transmission. *PLoS ONE* 8(11):e79422
- Garland EC, Goldizen AW, Lilley MS, Rekdahl M, Garrigue C, Constantine R, Hauser ND, Poole MM, Robbins J, Noad MJ (2015) Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. *Conserv Biol* 29(4):1198–1207

- Garland EC, Rendell L, Lamoni L, Poole MM, Noad MJ (2017) Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales. *PNAS* 114(30)
- Garrigue C, Constantine R, Poole M, Hauser N, Clapham P, Donoghue M, Russell K, Paton D, Mattila DK, Robbins J, Baker CS (2011) Movement of individual humpback whales between wintering grounds of Oceania (South Pacific), 1999 to 2004. *J Cetac Res Manage Spec Issue* 3:275–291
- Garrigue C, Clapham PJ, Geyer Y, Kennedy AS, Zerbini AN (2015) Satellite tracking reveals novel migratory patterns and the importance of seamounts for endangered South Pacific humpback whales. *R Soc Open Sci* 2
- Gedamke J (2004) Minke whale song, spacing, and acoustic communication on the Great Barrier Reef, Australia. Ph.D., University of California, Santa Cruz
- Glockner DA (1983) Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. In: Payne R (ed) *Communication and behavior of whales*, vol 76. Westview Press, Boulder, CO, pp 447–464
- Glockner-Ferrari DA, Ferrari M (1990) Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975–1988: the life history, reproductive rates and behavior of known individuals identified through surface and underwater photography. *Rep Int Whaling Comm (spec Issue)* 12:161–169
- Green SR, Mercado E, Pack AA, Herman LM (2011) Recurring patterns in the songs of humpback whales (*Megaptera novaeangliae*). *Behav Proc* 86(2):284–294. <https://doi.org/10.1016/j.beproc.2010.12.014>
- Guinee LN, Chu K, Dorsey EM (1983) Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). In: Payne R (ed). Westview Press, Boulder, CO, pp 59–80
- Hafner GW, Hamilton CL, Steiner WW, Thompson TJ, Winn HE (1979) Signature information in the song of the humpback whale. *J Acoust Soc Am* 66(1):1–1. <https://doi.org/10.1121/1.383072>
- Hamilton WD, Zuk M (1982) Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387
- Hanski I, Gilpin M (1991) Metapopulation dynamics: brief history and conceptual domain. *Biol J Lin Soc* 42:3–16
- Hauser N, Zerbini A, Geyer Y, Heide-Jorgensen MP, Clapham P (2010) Movements of satellite-monitored humpback whales, *Megaptera novaeangliae*, from the Cook Islands. *Mar Mamm Sci* 26(3):679–685
- Hazevoet CJ, Gravanita B, Suárez PL, Wenzel FW (2011) Seasonality of humpback whale *Megaptera novaeangliae* (Borowski, 1781) records in Cape Verde seas: evidence for the occurrence of stocks from both hemispheres? *Zool Caboverdiana* 2(1):25–29
- Helweg DA (1990) Comparison of songs of humpback whales (*Megaptera novaeangliae*) recorded in Japan, Hawaii and Mexico during in the winter of 1989. *Sci Rep Cetac Res* 1:1–20
- Herman LM (2017) The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. *Biol Rev* 92(3):1795–1818
- Herman LM, Tavolga W (1980) The communication systems of cetaceans. In: Herman LM (ed). Wiley Interscience, New York, pp 149–209
- Höglund J, Alatalo RV (1995) *Leks*. Princeton University Press, Princeton
- Jenkins PF (1978) Cultural transmission of song patterns and dialect development in a free-living bird population. *Anim Behav* 26:50–78
- Kowarski K (2020) Humpback whale singing behavior in the western North Atlantic: from methods for analysing passive acoustic monitoring data to understanding humpback whale song ontogeny. Dalhousie University, Halifax, Nova Scotia
- Kowarski K, Evers C, Moors-Murphy H, Martin B, Denes SL (2018) Singing through winter nights: seasonal and diel occurrence of humpback whale (*Megaptera novaeangliae*) calls in and around the Gully MPA, offshore eastern Canada. *Mar Mamm Sci* 34(1):169–189. <https://doi.org/10.1111/mms.12447>

- Kowarski K, Moors-Murphy H, Maxner E, Cerchio S (2019) Western North Atlantic humpback whale fall and spring acoustic repertoire: insight into onset and cessation of singing behavior. *J Acoust Soc Am* 145(4):2305. <https://doi.org/10.1121/1.5095404>
- Kroodtsma DE (1977) Correlates of song organization among North American wrens. *Am Nat* 111(981):995–1008. <https://doi.org/10.1086/283228>
- Kroodtsma DE, Bereson RC, Byers BE, Minear E (1989) Use of song types by the chestnut-sided warbler: evidence for both intra- and inter-sexual functions. *Can J Zool* 67:447–456
- Lemon RE (1975) How birds develop song dialects. *The Condor* 77(4):385–406
- Levenson C, Leapley WT (1978) Distribution of humpback whales (*Megaptera novaeangliae*) in the Caribbean determined by a rapid acoustic method. *J Fish Res Board Can* 35(8):1150–1152
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15(3):237–240
- Mackintosh NA (1972) Biology of the populations of large whales. *Sci Prog* 60(240):449–464
- Magnúsdóttir EE, Rasmussen MH, Lammers MO, Svavarsson J (2014) Humpback whale songs during winter in subarctic waters. *Polar Biol* 37(3):427–433. <https://doi.org/10.1007/s00300-014-1448-3>
- Marler P (1984) Song learning: innate species differences in the learning process. In: Marler P, Terrace HS (eds) *The biology of learning*. Springer, pp 289–309
- Marler P (1990) Song learning: the interface between behaviour and neuroethology. *Philos Trans R Soc Lond B Biol Sci* 329(1253):109–114
- Marler P, Peters S (1981) Sparrows learn adult song and more from memory. *Science* 213(4509):780–782
- Marx FG, Fordyce RE (2015) Baleen boom and bust: a synthesis of mysticete phylogeny, diversity and disparity. *R Soc Open Sci* 2(4):140434. <https://doi.org/10.1098/rsos.140434>
- Mednis A (1991) An acoustic analysis of the 1988 song of the humpback whale, *Megaptera novaeangliae*, off Eastern Australia. *Mem Queensland Museum* 30:323–332
- Medrano L, Salinas M, Salas I, Deguevara PL, Aguayo A, Jacobsen JK, Baker CS (1994) Sex identification of humpback whales, *Megaptera novaeangliae*, on the wintering grounds of the Mexican Pacific Ocean. *Can J Zool* 72:1771–1774
- Mennill DJ, Ratcliffe LM, Boag PT (2002) Female eavesdropping on male song contests in songbirds. *Science* 296:873
- Mercado E III, Perazio CE (2021) Similarities in composition and transformations of songs by humpback whales (*Megaptera novaeangliae*) over time and space. *J Comp Psychol* 135(1):28–50
- Mercado E III, Herman LM, Pack AA (2003) Stereotypical sound patterns in humpback whale songs: usage and function. *Aquat Mamm* 29(1):37–52
- Mikhalev YA (1997) Humpback whales *Megaptera novaeangliae* in the Arabian Sea. *Mar Ecol Prog Ser* 149:13–21
- Minton G, Collins T, Findlay K, Ersts P, Rosenbaum H, Berggren P, Baldwin R (2011) Seasonal distribution, abundance, habitat use and population identity of humpback whales in Oman. *J Cetac Res Manag* 3:185–198
- Mundinger PC (1980) Animal cultures and a general theory of cultural evolution. *Ethol Sociobiol* 1(3):183–223
- Murray A, Cerchio S, McCauley R, Jenner CS, Razafindrakoto Y, Coughran D, McKay S, Rosenbaum H (2012) Minimal similarity in songs suggests limited exchange between humpback whales (*Megaptera novaeangliae*) in the southern Indian Ocean. *Mar Mamm Sci* 28(1):E41–E57. <https://doi.org/10.1111/j.1748-7692.2011.00484.x>
- Murray A, Dunlop RA, Noad MJ, Goldizen AW (2018) Stereotypic and complex phrase types provide structural evidence for a multi-message display in humpback whales (*Megaptera novaeangliae*). *J Acoust Soc Am* 143(2):980–994
- Naguib M, Fichtel C, Todt D (1999) Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proc B R Soc Publ* 266(1419):537–542

- Nielsen R, Mattila DK, Clapham PJ, Palsbøll PJ (2001) Statistical approaches to paternity analysis in natural populations and applications to the North Atlantic humpback whale. *Genetics* 157(4):1673–1682
- Noad MJ, Cato DH, Bryden MM, Jenner M-N, Jenner KCS (2000) Cultural revolution in whale songs: humpbacks have picked up a catchy tune sung by immigrants from a distant ocean. *Nature* 408:537–537. <https://doi.org/10.1038/35046199>
- Norris TF (1995) Effects of boat noise on the singing behavior of humpback whales (*Megaptera novaeangliae*)
- Norris TF, McDonald M, Barlow J (1999) Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. *J Acoust Soc Am* 106(1):506–514
- Owen C, Rendell L, Constantine R, Noad MJ, Allen J, Andrews O, Garrigue C, Michael Poole M, Donnelly D, Hauser N, Garland EC (2019) Migratory convergence facilitates cultural transmission of humpback whale song. *R Soc Open Sci* 6(9):190337. <https://doi.org/10.1098/rsos.190337>
- Payne RB (1979) Song structure, behaviour, and sequence of song types in a population of village indigobirds, *Vidua chalybeata*. *Anim Behav* 27:997–1013
- Payne R (ed) (1983) *Communication and behavior of whales*, vol 76. 1 edn. Westview Press for the American Association for the Advancement of Science, Boulder, Colorado, 643 pp
- Payne RB (1985) Behavioral continuity and change in local song populations of village indigobirds, *Vidua chalybeata*. *Z Tierpsychol* 70:1–44
- Payne R, Guinee LN (1983) Humpback whale (*Megaptera novaeangliae*) songs as an indicator of “stocks”. In: Payne R (ed) *Communication and behavior of whales*, vol 76, 1st edn. Westview Press for the American Association for the Advancement of Science, Boulder, CO, pp 333–358
- Payne RS, McVay S (1971) Songs of humpback whales. *Science* 173(3997):585–597
- Payne K, Payne R (1985) Large scale changes over 19 years in songs of humpback whales in Bermuda. *Z Tierpsychol* 68:89–114
- Payne RB, Thompson WL, Fiala KL, Sweany LL (1981) Local song traditions in indigo buntings: cultural transmission of behavior patterns across generations. *Behaviour* 77(4):199–221
- Payne K, Tyack P, Payne R (1983) Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): a detailed analysis of two seasons in Hawaii. In: Payne R (ed), 1 edn. Westview Press, Boulder, CO, pp 9–57
- Pomilla C, Rosenbaum HC (2005) Against the current: an inter-oceanic whale migration event. *Biol Lett* 1(4):476–479. <https://doi.org/10.1098/rsbl.2005.0351>
- Pomilla C, Amaral AR, Collins T, Minton G, Findlay KP, Leslie MS, Ponnampalam L, Baldwin R, Rosenbaum H (2014) The world’s most isolated and distinct whale population? Humpback whales of the Arabian Sea. *PLoS ONE* 9(12):e114162
- Rasmussen K, Palacios DM, Calambokidis J, Saborío MT, Dalla Rosa L, Secchi ER, Steiger GH, Allen JM, Stone GS (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biol Lett* 3:302–305. <https://doi.org/10.1098/rsbl.2007.0067>
- Reeves RR, Swartz SL, Wetmore SE, Clapham PJ (2001) Historical occurrence and distribution of humpback whales in the eastern and southern Caribbean Sea, based on data from American whaling logbooks. *J Cetac Res Manage* 3(2):117–129
- Rekdahl M, Garland EC, Carvajal GA, King CD, Collins T, Razafindrakoto Y, Rosenbaum H (2018) Culturally transmitted song exchange between humpback whales (*Megaptera novaeangliae*) in the southeast Atlantic and southwest Indian Ocean basins. *R Soc Open Sci* 5(11):172305
- Risch D, Corkeron PJ, Ellison WT, Van Parijs SM (2012) Changes in humpback whale song occurrence in response to an acoustic source 200 km away. *PLoS ONE* 7(1):e29741–e29741. <https://doi.org/10.1371/journal.pone.0029741>
- Ryan JP, Cline DE, Joseph JE, Margolina T, Santora JA, Kudela RM, Chavez FP, Pennington JT, Wahl C, Michisaki E, Benoit-Bird K, Forney KA, Stimpert AK, DeVogelaere A, Black N, Fischer M (2019) Humpback whale song occurrence reflects ecosystem variability in feeding and migratory habitat of the northeast Pacific. *PLoS ONE* e0222456

- Saloma A (2018) Humpback whales (*Megaptera novaeangliae*) mother-calf interactions. Doctoral dissertation, Université Paris Saclay (COMUE), Université d'Antananarivo
- Schevill WE (1964) Underwater sounds of cetaceans. In: Tavolga WN (ed). Pergamon Press Inc., New York, NY, pp 307–316
- Searcy WA, Yasukawa K (1990) Use of the song repertoire in intersexual and intrasexual contexts by male red-winged blackbirds. *Behav Ecol Sociobiol* 27(2):123–128
- Searcy WA, Nowicki S, Hogan C (2000) Song type variants and aggressive context. *Behav Ecol Sociobiol* 48(5):358–363
- Slater PJB, Ince SA (1979) Cultural evolution in chaffinch song. *Behaviour* 71(1–2):146–166
- Smith JN, Goldizen AW, Dunlop RA, Noad MJ (2008) Songs of male humpback whales, *Megaptera novaeangliae*, are involved in intersexual interactions. *Anim Behav* 76(2):467–477. <https://doi.org/10.1016/j.anbehav.2008.02.013>
- Sousa-Lima RS, Clark CW (2008) Modeling the effect of boat traffic on the fluctuation of humpback whale singing activity in the Abrolhos National Marine Park, Brazil. *Can Acoust* 36(1):175–181
- Stafford KM, Lydersen C, Wiig O, Kovacs KM (2018) Extreme diversity in the songs of Spitsbergen's bowhead whales. *Biol Lett* 14(4). <https://doi.org/10.1098/rsbl.2018.0056>
- Stevick PT, Berrow SD, Bérubé M, Bouveret L, Broms F, Jann B, Kennedy A, López Suárez P, Meunier M, Ryan C, Wenzel F (2016) There and back again: multiple and return exchange of humpback whales between breeding habitats separated by an ocean basin. *J Mar Biol Assoc UK* 96(4):885–890. <https://doi.org/10.1017/S0025315416000321>
- Stimpert AK, Peavey LE, Friedlaender AS, Nowacek DP (2012) Humpback whale song and foraging behavior on an Antarctic feeding ground. *PLoS ONE* 7(12):e51214–e51214. <https://doi.org/10.1371/journal.pone.0051214>
- Swingle WM, Barco SG, Pitchford TD, McLellan WA, Pabst DA (1993) Appearance of juvenile humpback whales feeding in the nearshore waters of Virginia. *Mar Mamm Sci* 9(3):309–315
- Tervo OM, Christoffersen MF, Parks SE, Kristensen RM, Madsen PT (2011) Evidence for simultaneous sound production in the bowhead whale (*Balaena mysticetus*). *J Acoust Soc Am* 130(4):2257–2262. <https://doi.org/10.1121/1.3628327>
- Thompson TJ, Winn HE, Perkins PJ (1979) Mysticete sounds. In: Winn HE, Olla BL (eds). Plenum Press, New York, London, pp 403–431
- Todt D, Naguib M (2000) Vocal interactions in birds: the use of song as a model in communication. In: *Advances in the study of behavior*, vol 29, pp 247–296
- Trainer JM (1989) Cultural evolution in song dialects of yellow-rumped caciques in Panama. *Ethology* 80:190–204
- Tsujii K, Akamatsu T, Okamoto R, Mori K, Mitani Y, Umeda N (2018) Change in singing behavior of humpback whales caused by shipping noise. *PLoS ONE* 13(10):e0204112
- Tyack P (1981) Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav Ecol Sociobiol* 8(2):105–116. <https://doi.org/10.1007/BF00300822>
- Tyack PL, Whitehead H (1982) Male competition in large groups of wintering humpback whales. *Behaviour* 83(1/2):132–154
- Van Opzeeland I, Van Parijs S, Kindermann L, Burkhardt E, Boebel O (2013) Calling in the cold: pervasive acoustic presence of humpback whales (*Megaptera novaeangliae*) in Antarctic coastal waters. *PLoS ONE* 8(9):1–7
- Van Waerebeek K, Djiba A, Krakstad J, Samba Ould Bilal A, Bamy I, Almeida AM, Mbye EM (2013) New evidence for a South Atlantic stock of humpback whales wintering on the Northwest African continental shelf. *Afr Zool* 48:177–186
- Vu ET, Risch D, Clark CW, Gaylord S, Hatch LT, Thompson MA, Wiley DN, Van Parijs SM (2012) Humpback whale song occurs extensively on feeding grounds in the western North Atlantic Ocean. *Aquat Biol* 14(2):175–183. <https://doi.org/10.3354/ab00390>
- Whiten A, Caldwell CA, Mesoudi A (2016) Cultural diffusion in humans and other animals. *Curr Opin Psychol* 8:15–21. <https://doi.org/10.1016/j.copsyc.2015.09.002>
- Wiley RH (1991) Lekking in birds and mammals: behavioral and evolutionary issues. In: *Advances in the study of behavior*, vol 20, pp 201–291

- Wilson EO (1975) Sociobiology: the new synthesis. Harvard University Press
- Winn HE, Edel RK, Taruski AG (1975) Population estimate of the humpback whale (*Megaptera novaeangliae*) in the West Indies by visual and acoustic techniques. J Fish Res Board Can 32:499–506
- Winn HE, Thompson TJ, Cummings WC, Hain JHW, Hudnall J, Hays H, Steiner WW (1981) Song of the humpback whale—population comparisons. Behav Ecol Sociobiol 8:41–46
- Zahavi A (1975) Mate selection—a selection for a handicap. J Theor Biol 53(1):205–214
- Zoidis AM, Smultea MA, Frankel AS, Hopkins JL, Day A, McFarland AS, Whitt AD, Fertl D (2008) Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii. J Acoust Soc Am 123(3):1737–1746. <https://doi.org/10.1121/1.2836750>