Chapter 8
Culture and Social Learning in Baleen Whales

Ellen C. Garland and Emma L. Carroll

Abstract Culture, the sharing of behaviors or information within a community acquired through some form of social learning from conspecifics, represents a "second inheritance system". This assertion, while still controversial, is a clear indication that culture and the study of social learning in animals is no longer a taboo subject. Some of the strongest evidence for culture in animals has come from the study of cetaceans; while the focus has typically been on the odontocetes (mainly sperm whales, killer whales, and bottlenose dolphins), baleen whales provide important, unique, and robust evidence for cultural processes. Baleen whales undertake a myriad of behaviors across a variety of contexts. Some of these behaviors have been investigated with a cultural lens and have clearly shown maternally directed (and thus culturally transmitted) site fidelity to breeding, feeding and migratory routes, dynamic cultural transmission of song, and social transmission of novel feeding techniques. Undertaking cultural studies in large, free-ranging cetaceans requires multiyear, long-term datasets with enough detail to track changes; such datasets are rare and take decades to accumulate. However, we are now seeing a number of such datasets come to light, and the results are spectacular. Here, we first provide an overview of culture and its transmission; we then highlight some of the clearest examples of baleen whale culture to date, concluding with research considerations. Culture and its influence on the lives of cetaceans can no longer be ignored as, to paraphrase some of the pioneers in the cetacean culture field, it is now clear that culture rules their [cetaceans'] lives.

Keywords Animal culture · Social learning · Cultural processes · Song · Migration · Feeding · Vocal learning · Isotopes

E. C. Garland (✉)
Centre for Social Learning & Cognitive Evolution, and Sea Mammal Research Unit, School of Biology, University of St. Andrews, St. Andrews, Fife KY16 8LB, UK
e-mail: ecg5@st-andrews.ac.uk

E. L. Carroll
School of Biological Sciences, University of Auckland, Waipapa Taumata Rau, Auckland 1010, New Zealand

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_8

8.1 Culture and Social Learning

To be human is to be cultural. Cultural traditions have shaped human societies (Ramsey 2013); this concept has led to heated debate about the existence of culture in animals (see Laland and Janik 2006; Whiten et al. 2017; Whiten 2021). Since evidence for social learning of behavioral variants and their subsequent social transmission have come to light in species from fruit flies (*Drosophila melanogaster*; Danchin et al. 2018) to southern right whales (*Eubalaena australis*; Valenzuela et al. 2009), such arguments are diminishing. Culture and its transmission have been extensively investigated in our nearest cousins, the great apes, in particular chimpanzees (*Pan troglodytes*; Whiten et al. 1999, 2007). A wide body of research illustrates the broad-scale patchwork of behavioral variants across populations and controlled experiments demonstrate the social learning and transmission of behaviors (including tool use; Whiten et al. 2007, 2017; Whiten 2017). These have set the stage for understanding animal culture.

The term "culture" is defined in a broad sense as "shared behavior or information within a community acquired through some form of social learning from conspecifics" (Rendell and Whitehead 2001; Fragaszy and Perry 2003). The term "culture" can at times be used interchangeably in the peer-review literature with the term "tradition" (Whiten 2017). The important step when asserting that a behavior is cultural is the transmission process (i.e., social learning) and subsequent diffusion of the behavior from the innovator through a population. Animals are able to innovate or invent behaviors de novo (e.g., exploit a new resource), but it is the learning of this innovation *from another* individual and the diffusion, spread, sharing, or transmission of the behavior through a population that is of interest here. This is what is meant by culture.

Influences such as genetics or ecology contribute to behavior, and these factors may explain behavioral differences between and among populations. To establish that a behavior is culturally transmitted, the so-called exclusion method involves an examination of the plausibility of other influences or confounding factors. This method has received both praise and criticism (Laland and Janik 2006; Krützen et al. 2007). For example, in the late 1990s, variation in chimpanzee behavior across Africa was described. After exclusion of ecological explanations, 39 different behavioral patterns were reported as cultural (Whiten et al. 1999). The method of exclusion is useful to create a broad-brush examination that should be refined in future analyses. A general criticism of this method is that behaviors do not develop in isolation but as an interaction between environmental experience and a genetic blue-print or predisposition (Laland and Janik 2006). The animal culture field is now moving beyond the method of exclusion toward approaches evaluating the magnitude of each potential causal factor on the development of a specific behavior (Laland and Janik 2006; Allen et al. 2013; Whitehead et al. 2019).

A potentially confounding issue when designating behaviors as having a cultural basis is the pathway of transmission. Vertical transmission is from parent to offspring (e.g., mother to calf), oblique transmission is from a non-parent model to the next generation (e.g., juvenile learning the song of an unrelated adult male), and horizontal transmission is transmission within a cohort (e.g., learning a new feeding technique from your peers) (Whitehead et al. 2019). The direction of information flow is important, especially when attempting to distinguish vertical cultural transmission from underlying genetic explanations. For example, in Shark Bay , Western Australia, a subset of the bottlenose dolphin (*Tursiops* sp.) population forages for food using marine sponges (Krutzen et al. 2005; Sargeant and Mann 2009). "Sponging" is habitat specific and is vertically transmitted from mother to calf (Krutzen et al. 2005; Kopps et al. 2014). Sponging was initially identified in a single matriline (Krutzen et al. 2005), raising concerns of the genetic influence on the purported cultural behavior. However, a second sponging matriline has been identified in Shark Bay indicating this is a more widespread foraging tactic (Kopps et al. 2014) and most likely culturally transmitted.

Here, we highlight some of the studies that have provided evidence for cultural processes in baleen whales. These include studies of migration, foraging, acoustic communication, and breeding behaviors. Cultural processes can be investigated using approaches such as molecular genetics, isotopes, acoustics, and telemetry tags. We do not cover all of the different social learning mechanisms or delve deeply into discussions of conformity (see Laland 2008). The goal of this chapter is to provide readers with the biological concept and framework of culture, and perhaps inspire readers to take a look into interpretations of their own data through a cultural lens.

8.2 Culture in Cetaceans

The past two decades have seen an explosion in cetacean culture studies. From an initial synthesis by Rendell and Whitehead (2001) through to recent work with a diverse number of species and behavioral contexts [reviewed in Whitehead and Rendell (2015)], a clear conclusion has emerged: Culture is important to cetaceans. Four genera have been the focus of most cultural studies: the sperm whale (*Physeter macrocephalus*), killer whale (*Orcinus orca*), bottlenose dolphin and humpback whale (*Megaptera novaeangliae*). Vocal clans, ecotypes, sponging and song are part of these species, respectively. These are examples of cultures that have shaped communities and species. We urge readers to explore studies on this subject, some of which are presented by species in Book 1 of this series (Würsig 2019). Here, we note two examples of odontocete culture, before focusing on baleen whales.

Killer whales can be divided into ecotypes strongly associated with diet (foraging specialization; Ford et al. 1998; Foote et al. 2016). Pods are composed of a number of related matrilines, and each pod has a pod-specific acoustic repertoire (dialect; Ford 1991). Subtle acoustic call differences are shared among members of a pod, and some call types are also shared among pods within an area, creating "acoustic clans" (Ford 1991; Miller et al. 2000; Yurk et al. 2002). These clan "dialects" undergo cultural drift and evolve (Filatova and Miller 2015); call changes can be horizontally transmitted among matrilines (Deecke et al. 2000); and calves learn their repertoires from their mothers (i.e., vertical transmission; Filatova et al. 2015). Multiple cultural processes are therefore at work. Dialects provide vocal markers not only of pods, but also of ecotypes. Like dialects, feeding specializations are vertically transmitted within the matriline; such conditions may promote gene–culture coevolution and potentially, speciation (see Foote et al. 2016; Ford 2019). Sperm whales also provide an excellent example of gene–culture coevolution, where feeding specializations and vocal dialects interact and are culturally transmitted (see Cantor et al. 2019).

Bottlenose dolphins produce patterns of frequency-modulated sounds called "signature whistles" that encode individual identity (Caldwell and Caldwell 1965; Janik et al. 2006). Bottlenose dolphins copy one another's signature whistles as a means of addressing specific social companions, in effect addressing a conspecific by using their "name" (Janik 2000; King and Janik 2013). This ability is rare in non-human animals (King and Janik 2013). Bottlenose dolphins are also able to label objects with novel learned whistle patterns (Richards et al. 1984). Thus, vocal learning abilities of bottlenose dolphins are exceptional among mammals and hint at underlying complex cognitive abilities (Janik 2009).

Tool-using culture has been documented in a subset of wild bottlenose dolphins in Shark Bay, West Coast Australia (Krutzen et al. 2005; Sargeant and Mann 2009; Connor et al. 2019; Mann 2019; Wild et al. 2019a). Individuals place marine sponges over their rostra to probe the sediment for fish in deep-water channels (Mann and Sargeant 2003; Krutzen et al. 2005). Sponging behavior is passed vertically from mother to calf (Krutzen et al. 2005, 2014), although mainly female calves acquire sponging behavior, as male offspring of sponging mothers tend to not show sponging in later life (Mann and Sargeant 2003; Krutzen et al. 2005). Initially, a single matriline was discovered to sponge (Krutzen et al. 2005); but subsequently, a second sponging matriline was identified, indicating that sponging is not a unique foraging tactic (Kopps et al. 2014), and unlikely to be confounded by genetic inheritance factors (Laland and Janik 2006). The importance of social learning on the diffusion of sponging was more recently investigated using network-based diffusion analysis, which accounts for ecological and genetic factors (Wild et al. 2019a). Results support previous findings that sponging is vertically socially transmitted from mother to (primarily female) offspring (Wild et al. 2019a). The behavioral proclivity of sponging therefore represents a clear example of tool-use culture in a marine mammal (Krutzen et al. 2005; Krützen et al. 2014).

8.3 Evidence for Culture in Baleen Whales

We focus here on two species that provide case studies for culture in baleen whales: southern right whales and humpback whales. But, we acknowledge that there are many other potential examples of cetacean culture yet to be discovered.

8.3.1 Migratory Culture in Southern Right Whales

As with other baleen whales, southern right whales move between offshore high latitude summer foraging grounds and sheltered coastal wintering grounds. Long-term studies that used photographs of natural markings (photo-ID) and unique genetic profiles to identify individual whales have shown that females demonstrate long-term fidelity to their wintering grounds (Bannister 2001; Rowntree et al. 2001; Carroll et al. 2016). Females calve in these preferred wintering grounds and migrate with their calves to preferred foraging grounds. These mother behaviors provide a way for offspring to learn their mothers' migratory traditions in their first year of life. The cultural transmission of migratory preferences, or migratory culture, has profound implications for genetic structure and connectivity across the species' migratory network. Such behavior is believed to contribute to significant genetic differentiation between wintering grounds, particularly evident in maternally inherited mitochondrial DNA (mtDNA; Patenaude et al. 2007; Carroll et al. 2015, 2018). Such a pattern is found in other baleen whales, demonstrating how molecular methods allow us to understand the behavioral lives of whales (Chap. 6).

Correlations between mtDNA, a proxy for maternal lineage or tradition, and stable isotope data, a proxy for foraging grounds, have yielded interesting results. The first study was conducted using 131 southern right whales from the Argentine wintering ground, primarily including females with calves (Valenzuela et al. 2009). The study showed there was a non-random association between maternal lineage, as indicated by mtDNA version or haplotype, and foraging ground, as indicated by stable isotope data (Fig. 8.1). Whales with the same mtDNA haplotype were more likely than expected by chance to have more similar isotope profiles. This work was confirmed and expanded based on 78 whales sampled on the Australian wintering ground (Carroll et al. 2015). Whales that shared mtDNA haplotype and were more genetically related were also more likely to have more similar isotope profiles. The simplest explanation for this finding is maternally directed learning of foraging grounds, such that related animals are foraging in isotopically similar locations.

Migratory culture also plays a role in the recovery of southern right whales following the decline of whaling and could be a key determinant of their response to climate change. Once numbering perhaps 100,000 throughout the Southern Ocean, the species declined to possibly less than 400 individuals around 1920 (Jackson et al. 2008). Today, the species shows patchy recovery: For example, few whales occur around mainland New Zealand and the east Australian wintering grounds, compared with the strongly recovering populations in the New Zealand sub-Antarctic Islands and in southwest Australia (Carroll et al. 2011, 2015). It is likely that when whales that inhabited a region were extirpated, the memory of that area as a good migratory destination was also lost. This loss of "cultural memory", exacerbated by the loss of adjacent populations and low abundance, means it is unlikely that previously inhabited areas will be recolonized on a timeframe relevant to management (i.e., decades; Clapham et al. 2008).

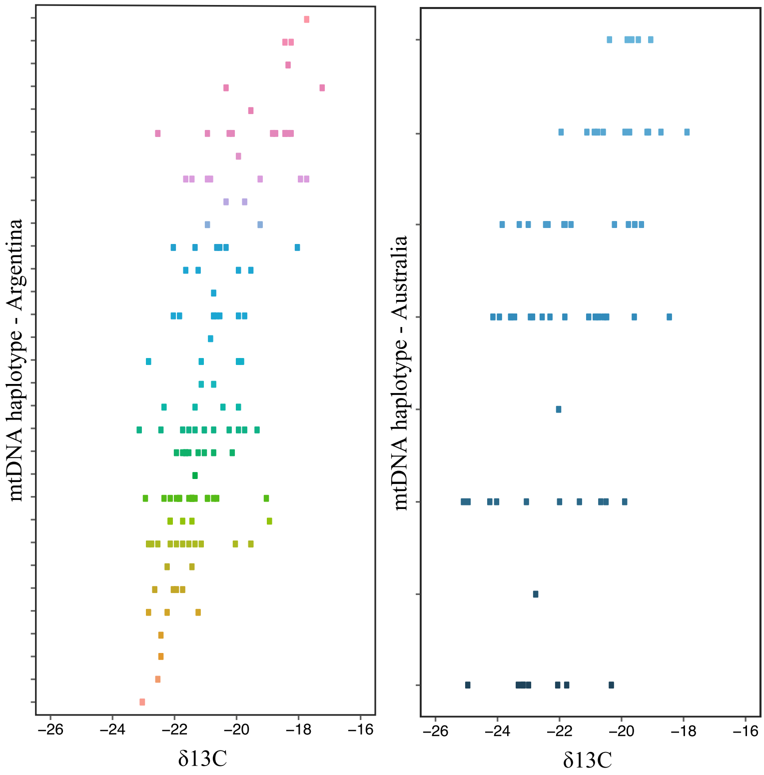

Fig. 8.1 Empirical evidence for southern right whale migratory culture: correlation between foraging ground, as shown by δ13C value, and maternal lineage, as indicated by mtDNA version or haplotype for southern right whales sampled on wintering grounds. Data are plotted independently for the Argentine wintering ground, with each square representing an individual whale [left panel, data from Valenzuela et al. (2009)] and the Australian wintering ground [right panel, data from Carroll et al. (2015)]

Southern right whale recovery also depends on their ability to adjust to changes in prey distribution. The vertical transmission of migratory culture has likely been beneficial on long time scales as it provides useful information on foraging and nursery habitats in an often visually featureless and vast sea (Whitehead 2010). Indeed, there is evidence that the recovery of southern right whales has been very dependent on environmental conditions at their feeding grounds. The reproductive success of southern right whales on their wintering grounds in Argentina and Brazil has been correlated with oceanographic conditions and krill availability at their South Georgia foraging ground, respectively (Leaper et al. 2006; Seyboth et al. 2016). However, in an era of climate change, these cultural traditions can become detrimental if they are too fixed to respond to rapid resource shifts due to climate change or other anthropogenic activities (Keith and Bull 2017). Such problems are called ecological or evolutionary traps, entailing a behavior that originally increased fitness (e.g., fidelity to rich feeding ground) but then became a hindrance in the face of rapid environmental change (e.g., changes in distribution of food resources due to climate variation and/or anthropogenic activities; Schlaepfer et al. 2002; Keith and Bull 2017). Encouragingly, there is evidence that at least some baleen whale species can behaviorally adapt to such shifts. For example, humpback whales in the Gulf of St. Lawrence, Canada, have altered the timing of their migratory journeys to coincide with earlier prey availability (Ramp et al. 2015). However, humpback whales may be uniquely plastic in their foraging behaviors (see next section), and we do not know if southern right whale culture is too conservative to cope with shifting prey resources under rapid climate change conditions.

8.3.2 Feeding Traditions and Song Culture in Humpback Whales

Humpback whales have multiple independently evolving cultural traditions within a population. These include the social learning of feeding tactics (Allen et al. 2013), maternally directed site fidelity to breeding grounds, feeding grounds and migratory routes (Baker et al. 1990), and the evolution and revolution of song displays (Payne and Payne 1985; Noad et al. 2000; Garland et al. 2011). We focus on two different behavioral contexts—song culture and feeding tactics—as migratory culture has been covered in the previous section and may be considered broadly similar between the two genera.

In 1980, a humpback whale in the Gulf of Maine population on the east coast of North America performed an innovative modification to their feeding technique, termed “lobtail feeding” (Allen et al. 2013). Humpback whales commonly forage by “bubble-net feeding”, where a bubble stream is produced below and around a school of prey followed by lunging through the bubbles (Chap. 5). The lobtail feeding technique is a modification of the original bubble-net feeding behavioral sequence by adding a series of tail slaps to start the sequence (Weinrich et al. 1992). Researchers observed an increase in the feeding technique over a 27-year period, suggesting social transmission of the innovation through the population. However, its emergence coincided with the crash of one prey species, herring (*Clupea harengus*), and a switch in prey to sand lance (*Ammodytes americanus*), suggesting an ecological factor (Allen et al. 2013).

The spread of a behavioral innovation can be investigated by apportioning the relative influence of multiple factors (i.e., ecological, social, and genetic) using network-based diffusion analysis (NBDA). Allen et al. (2013) employed NBDA to analyze the spread of the lobtail feeding innovation. Results strongly indicated that social transmission was responsible for the spread as support for models including social transmission were six to 23 orders of magnitude greater than for models without social transmission (Allen et al. 2013). While there was clearly an ecological driver to initiate the innovation (i.e., change in prey abundance resulting in a switch in prey), the *spread* of the innovation through the population was overwhelmingly driven by social transmission. Modeling approaches such as NBDA assist researchers in examining multiple drivers for a behavior while not removing the behavior out of the environmental context. The NBDA method has drawbacks; for example, it includes the need for large (e.g., hundreds to thousands of sightings) datasets to have the power to tease out relative effects of different drivers. Furthermore, application of NBDA to population-wide, stable cultural traditions may be limited in situations where social transmission could have historically occurred between populations.

Let us now investigate song culture and dynamics. Male humpback whales sing a long, complex, stereotyped, and hierarchically structured vocal display termed "song" (Payne and McVay 1971; Herman and Tavolga 1980), which functions in sexual selection to attract a mate and/or mediate male–male interactions (Herman 2017). Most males within a population sing a similar song at any time; that is, they sing songs which share similar themes, phrases, and units, as well as the same arrangement of song components. Thus, there is strong cultural conformity to the current arrangement (version) of the song display in male humpback whales (Payne et al. 1983; Payne and Payne 1985). Songs also evolve through time (Payne and Payne 1985); males within the population incorporate changes into their own song to maintain the observed cultural conformity. Further information on general humpback whale song can be found in Chap. 11, while humpback whale social communication is explored in Chap. 10.

Over the last two decades, some striking song dynamics have been discovered in the South Pacific. Noad et al. (2000) discovered that over a two-year period, song from the west Australian population replaced the existing song of the east Australian population. This rapid and complete change was termed by the authors a "song revolution" to distinguish it from the common and traditional perspective of a gradual "song evolution" process. More recent studies have shown that song transmission from the west into the east Australian population is relatively frequent and represents the transfer of multiple song types between the Indian and South Pacific Ocean basins (Rekdahl 2012; Allen et al. 2018).

Payne and Guinee (1983) hypothesized three different mechanisms to allow songs to be shared among populations. First, song sharing could occur on shared feeding grounds and/or on shared or partially shared migratory routes. Second, males may share song by visiting more than one wintering ground in consecutive years. And finally, song sharing may occur by males visiting more than one wintering ground within a breeding season. Since the Australian continent separates east and west Australian breeding grounds, song transmission between the two breeding grounds was suggested to occur either through males switching breeding grounds between seasons and/or through males from the different breeding grounds occurring on the same feeding ground in the same season (Noad et al. 2000). Models of humpback whale song revolutions test which of these scenarios are most likely to initiate a song revolution (Lamoni 2018). To successfully mirror the west–east transmission pattern with song revolution data, the model required a song memory to ensure that singers did not revert back to their old song. This suggests that a cognitive capacity is required to concurrently remember the previous seasons' songs and the current song, similar to songbirds (McGregor and Avery 1986). Such capacity is likely essential to not only remember previous songs, but also to rapidly learn the ever-changing, complex and culturally driven song display.

The introduction of a substantial amount of novel material (i.e., when a new song type is introduced) requires rapid learning to reproduce the observed pattern. Garland et al. (2017) investigated how humpback whales learn a new song type by examining instances of song hybridization, where we recorded a whale thought to be in the process of learning a new song during a song revolution. Songs were segmented and then learned as whole themes, akin to how some songbirds learn song and human infants learn language in segments (Garland et al. 2017). The position in the song where a singer switched from "old" to "new" song themes was not random. Garland et al. (2017) uncovered a "*switch when similar rule*": Singers smoothly transitioned from old to new song themes at the location in each song where the similarity in unit type and arrangement was highest.

Garland et al. (2017) confirmed that song structure and syntax are important to humpback whales. To further investigate song learning, Allen et al. (2018) investigated song complexity in the east Australian population over 13 consecutive years. Song complexity increased during periods without revolutions, but decreased after revolutions, leading to oscillations in the long-term pattern of song complexity. Allen et al. (2018) suggested that relative complexity of songs in song revolutions may represent an upper limit to song learning (Allen et al. 2018), while the degree of structural complexity and syntax in the song may facilitate rapid learning of novel material (Allen et al. 2019). How memory, vocal complexity, speed of learning, song structure, and syntax interact is unknown, but the integration of these components is likely to yield intriguing results.

Garland et al. (2011) documented a striking pattern where multiple song types spread from the east Australian population eastward through the populations of the South Pacific, causing multiple song revolutions in a series of cultural waves (Fig. 8.2). Song types typically took two years to spread from east Australia, located in the western South Pacific, across to French Polynesia, in the central South Pacific, approximately 6000 km away. The new, revolutionary songs replaced the current song in each population as they spread. This pattern created a checkerboard of behavioral phenotypes at the decadal scale (Fig. 8.2). Garland et al. (2011) also traced Noad et al.'s (2000) original cultural revolution as it transited across the Pacific, representing a cultural signal that spanned two ocean basins and seven years.

Subsequent work demonstrated that song revolutions rapidly and repeatedly transit exclusively east across the South Pacific region, and song-type differences can be used to identify populations (Garland et al. 2011, 2012, 2013b, 2015, 2017; Owen et al. 2019). Why songs spread in an easterly direction remains elusive; one hypothesis is that this directionality is due to differences in population sizes across the region (Garland et al. 2011). South Pacific humpback whale song transmission remains the best example to date of repeated, population-wide, horizontal cultural transmission in which behavioral variants are passed among populations of a non-human animal. While human behavior (e.g., fashion trends) remains the best analogy for this cultural process, we suspect that another baleen whale, the bowhead whale

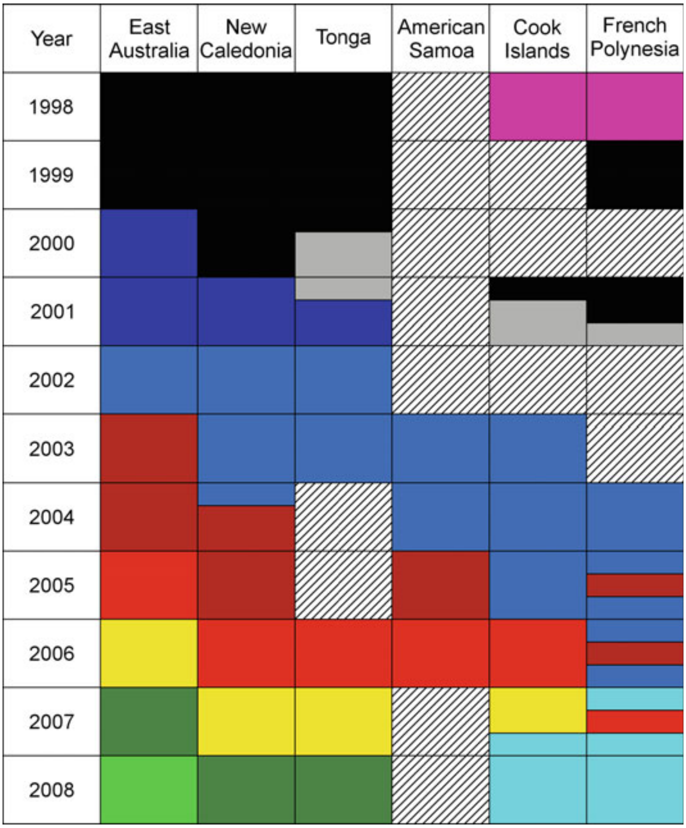

Fig. 8.2 Humpback whale song types identified in the South Pacific region from 1998 to 2008 (from Garland et al., 2011). Populations are listed from west to east across the region. Each color represents a distinct song type; song-type colors are as follows: black, gray, pink, dark blue, blue, light blue, dark red, light red, yellow, dark green, and light green. Two colors within the same year and location indicate that both song types were present. In these cases, the seasons are broken into three periods (early, middle, and late) to indicate when a new song type was recorded. Crosshatching indicates no data available. Reprinted from Current Biology, 21, Garland et al., Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale, 687–691, 2011, with permission from Elsevier

(*Balaena mysticetus*), may also be a prime candidate for future discoveries of song culture. We know significantly less about bowhead whale song than humpbacks (see Chap. 12); however, bowhead whale song is complex, changes rapidly, possibly evolves, and may be individual or group specific. These features hint that this display may have a cultural component.

8.4 Conclusions and Future Directions

By acting as a "second inheritance system" (Whiten 2017), culture provides an important and understudied aspect of animal behavior. Culture plays an important part in the lives of cetaceans (Whitehead and Rendell 2015). Here, we have presented an overview of evidence for cultural processes in baleen whales. But, why do we care and why should you? One important answer is that a significant number of cetacean populations are impacted by human activities and require conservation management and interventions. There are real population consequences arising from ignoring culture when considering outcomes (Brakes et al. 2019, 2021). As the climate changes, the ability of baleen whale populations to be behaviorally plastic and respond to change may be limited by culture. Maternally directed migratory culture in southern right whales, for example, may result in an inflexibility to change feeding areas (Keith and Bull 2017), further exacerbating a slow recovery or blocking it. Alternatively, cultural traditions may provide a buffer to environmental extremes through exploiting a different foraging niche (Gruber et al. 2019), as recently documented in Shark Bay bottlenose dolphins (Wild et al. 2019b). For example, during an extreme marine heatwave, individual bottlenose dolphins that sponge-fed were less impacted in terms of survival than non-sponge-feeders (Wild et al. 2019b). Wild et al. (2019b) suggest that spongers were buffered against the cascading effects of habitat loss following the heatwave by having access to a less severely affected foraging niche. However, long-term population viability will be impacted if conditions do not improve, as reproduction was equally impacted for both groups (Wild et al. 2019b).

The undertaking of cultural studies of free-ranging cetaceans requires multiyear and long-term datasets with enough detail to track changes. Such datasets are rare and take decades to accumulate. A number of long-term datasets are coming to fruition; we urge readers to think about what data they hold and whether re-examining these data through a cultural lens might yield interesting results. The next decade will be an exciting time for cetacean research, especially relative to considerations of culture. It appears that each time a researcher investigates their behavioral data in detail, a new example of cetacean culture is discovered. Examples of cultural traditions from cetaceans are pivotal to our understanding of culture in animals and are having an impact on the fields of animal culture and their conservation (Brakes et al. 2019, 2021).

Acknowledgements We thank Christopher Clark, Bernd Würsig, and Andrew Whiten for their comments on this chapter. We thank Luciano Valenzuela for providing raw data for Fig. 8.1. E.C.G. is supported by a Royal Society University Research Fellowship, and E.L.C. is supported by a Royal Society of New Zealand Rutherford Discovery Fellowship. This chapter stems from many extended discussions on a Friday evening commuter train between St. Andrews and Edinburgh; we therefore thank our respective favorite brands of whisky for fueling these lively discussions.

References

Allen J, Weinrich M, Hoppitt W, Rendell L (2013) Network-based diffusion analysis reveals cultural transmission of Lobtail feeding in humpback whales. Science 340:485–488. https://doi.org/10.1126/science.1231976

Allen JA, Garland EC, Dunlop RA, Noad MJ (2018) Cultural revolutions reduce complexity in the songs of humpback whales. Proc R Soc B Biol Sci 285:20182088. https://doi.org/10.1098/rspb.2018.2088

Allen JA, Garland EC, Dunlop RA, Noad MJ (2019) Network analysis reveals underlying syntactic features in a vocally learnt mammalian display, humpback whale song. Proc R Soc B Biol Sci 286:20192014. https://doi.org/10.1098/rspb.2019.2014

Baker CS, Palumbi SR, Lambertsen RH et al (1990) Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature 344:238–240

Bannister JL (2001) Status of southern right whales (*Eubalaena australis*) off Australia. J Cetacean Res Manag Spec Issue 2:103–110

Brakes P, Dall SRX, Aplin LM et al (2019) Animal cultures matter for conservation. Science 363:1032–1034. https://doi.org/10.1126/science.aaw3557

Brakes P, Carroll EL, Dall SRX et al (2021) A deepening understanding of animal culture suggests lessons for conservation. Proc R Soc B Biol Sci 288:20202718. https://doi.org/10.1098/rspb.2020.2718

Caldwell MC, Caldwell DK (1965) Individualized whistle contours in bottle-nosed Dolphins (*Tursiops truncatus*). Nature 207:434–435. https://doi.org/10.1038/207434a0

Cantor M, Gero S, Whitehead H, Rendell L (2019) Sperm Whale: the largest toothed creature on earth. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer, pp 261–280

Carroll E, Patenaude N, Alexander A et al (2011) Population structure and individual movement of southern right whales around New Zealand and Australia. Mar Ecol Prog Ser 432:257–268. https://doi.org/10.3354/meps09145

Carroll EL, Baker CS, Watson M et al (2015) Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. Sci Rep 5:16182

Carroll EL, Fewster RM, Childerhouse SJ et al (2016) First direct evidence for natal wintering ground fidelity and estimate of juvenile survival in the New Zealand southern right whale *Eubalaena australis*. PLoS ONE. https://doi.org/10.1371/journal.pone.0146590

Carroll EL, Bruford MW, DeWoody JA et al (2018) Genetic and genomic monitoring with minimally invasive sampling methods. Evol Appl 11:1094–1119. https://doi.org/10.1111/eva.12600

Clapham P, Aguilar A, Hatch LT (2008) Determining spatial and temporal scales for management of cetaceans: lessons from whaling. Mar Mammal Sci 24:183–201

Connor RC, Sakai M, Morisaka T, Allen SJ (2019) The Indo-Pacific Bottlenose Dolphin (*Tursiops aduncus*). In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer, pp 345–368

Danchin E, Nöbel S, Pocheville A et al (2018) Cultural flies: conformist social learning in fruitflies predicts long-lasting mate-choice traditions. Science 362:1025–1030. https://doi.org/10.1126/science.aat1590

Deecke VB, Ford JKB, Spong P (2000) Dialect change in resident killer whales: implications for vocal learning and cultural transmission. Anim Behav 60:629–638. https://doi.org/10.1006/anbe.2000.1454

Filatova OA, Miller PJO (2015) An agent-based model of dialect evolution in killer whales. J Theor Biol 373:82–91. https://doi.org/10.1016/j.jtbi.2015.03.020

Filatova OA, Samarra FIP, Deecke VB et al (2015) Cultural evolution of killer whale calls: background, mechanisms and consequences. Behaviour 152:2001–2038. https://doi.org/10.1163/1568539X-00003317

Foote AD, Vijay N, Avila-Arcos M et al (2016) Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. Nat Commun 7:11693. https://doi.org/10.1101/040295

Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can J Zool 69:1454–1483

Ford JKB (2019) Killer Whales: behavior, social organization, and ecology of the Oceans' Apex Predators. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer, pp 239–259

Ford JKB, Ellis GM, Barrett-Lennard LG et al (1998) Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Can J Zool 76:1456–1471. https://doi.org/10.1139/z98-089

Fragaszy DM, Perry S (2003) Preface. In: Fragaszy DM, Perry S (eds) The biology of traditions: models and evidence. Cambridge University Press, Cambridge, pp xiii–xvi

Garland EC, Goldizen AW, Rekdahl ML et al (2011) Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Curr Biol 21:687–691. https://doi.org/10.1016/j.cub.2011.03.019

Garland EC, Lilley MS, Goldizen AW et al (2012) Improved versions of the Levenshtein distance method for comparing sequence information in animals' vocalisations: tests using humpback whale song. Behaviour 149:1413–1441. https://doi.org/10.1163/1568539X-00003032

Garland EC, Gedamke J, Rekdahl ML et al (2013a) Humpback whale song on the Southern Ocean feeding grounds: implications for cultural transmission. PLoS ONE 8:e79422. https://doi.org/10.1371/journal.pone.0079422

Garland EC, Noad MJ, Goldizen AW et al (2013b) Quantifying humpback whale song sequences to understand the dynamics of song exchange at the ocean basin scale. J Acoust Soc Am 133:560–569. https://doi.org/10.1121/1.4770232

Garland EC, Goldizen AW, Lilley MS et al (2015) Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. Conserv Biol 29:1198–1207. https://doi.org/10.1111/cobi.12492

Garland EC, Rendell L, Lamoni L et al (2017) Song hybridization events during revolutionary song change provide insights into cultural transmission in humpback whales. Proc Natl Acad Sci U S A 114:7822–7829. https://doi.org/10.1073/pnas.1621072114

Gruber T, Luncz L, Mörchen J et al (2019) Cultural change in animals: a flexible behavioural adaptation to human disturbance. Palgrave Commun 5:1–9. https://doi.org/10.1057/s41599-019-0271-4

Herman LM (2017) The multiple functions of male song within the humpback whale (*Megaptera novaeangliae*) mating system: review, evaluation, and synthesis. Biol Rev 92:1795–1818. https://doi.org/10.1111/brv.12309

Herman LM, Tavolga WN (1980) The communication system of cetaceans. In: Herman LM (ed) Cetacean behaviour: mechanisms and functions. Wiley, New York, pp 149–209

Jackson JA, Patenaude NJ, Carroll EL, Baker CS (2008) How few whales were there after whaling? Inference from contemporary mtDNA diversity. Mol Ecol. https://doi.org/10.1111/j.1365-294X.2007.03497.x

Janik VM (2000) Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289:1355–1357. https://doi.org/10.1126/science.289.5483.1355

Janik VM (2009) Acoustic communication in delphinids. Adv Study Behav 40:123–157. https://doi.org/10.1016/S0065-3454(09)40004-4

Janik VM, Sayigh LS, Wells RS (2006) Signature whistle shape conveys identity information to bottlenose dolphins. Proc Natl Acad Sci U S A 103:8293–8297. https://doi.org/10.1073/pnas.0509918103

Keith SA, Bull JW (2017) Animal culture impacts species' capacity to realise climate-driven range shifts. Ecography (cop) 40:296–304. https://doi.org/10.1111/ecog.02481

King SL, Janik VM (2013) Bottlenose dolphins can use learned vocal labels to address each other. Proc Natl Acad Sci U S A 110:13216–13221. https://doi.org/10.1073/pnas

Kopps AM, Krützen M, Allen SJ et al (2014) Characterizing the socially transmitted foraging tactic "sponging" by bottlenose dolphins (*Tursiops* sp.) in the western gulf of Shark Bay, Western Australia. Mar Mammal Sci 30:847–863. https://doi.org/10.1111/mms.12089

Krutzen M, Mann J, Heithaus MR et al (2005) Cultural transmission of tool use in bottlenose dolphins. Proc Natl Acad Sci U S A 102:8939–8943. https://doi.org/10.1073/pnas.0500232102

Krützen M, van Schaik C, Whiten A (2007) The animal cultures debate: response to Laland and Janik. Trends Ecol Evol 22:6. https://doi.org/10.1016/j.tree.2006.10.011

Krützen M, Sina K, MacLeod CD et al (2014) Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (*Tursiops* sp.) provides access to a novel foraging niche. Proc R Soc B 281:20140374. https://doi.org/10.1098/rspb.2014.0374

Laland KN (2008) Animal cultures. Curr Biol 18:366–370. https://doi.org/10.1016/j.cub.2008.02.049

Laland KN, Janik VM (2006) The animal cultures debate. Trends Ecol Evol 21:542–547. https://doi.org/10.1016/j.tree.2006.06.005

Lamoni L (2018) The role of individual behaviour in the collective cultural evolution of humpback whale songs. PhD thesis University of St, Andrews, UK. 198 p

Leaper R, Cooke J, Trathan P et al (2006) Global climate drives southern right whale (*Eubalaena australis*) population dynamics. Biol Lett 2:289–292. https://doi.org/10.1098/rsbl.2005.0431

Mann J (2019) Maternal care and offspring development in odontocetes. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer, pp 95–116

Mann J, Sargeant B (2003) Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In: Fragaszy DM, Perry S (eds) The biology of traditions: models and evidence. Cambridge University Press, Cambridge, pp 236–266

McGregor PK, Avery MI (1986) The Unsung Songs of Great Tits (*Parus major*)—learning neighbors songs for discrimination. Behav Ecol Sociobiol 18:311–316

Miller PJO, Bain DE (2000) Within-pod variation in the sound production of a pod of killer whales, Orcinus orca. Anim Behav 60:617–628. https://doi.org/10.1006/anbe.2000.1503

Noad M, Cato DH, Bryden MM et al (2000) Cultural revoultion in whale songs. Nature 408:537

Owen C, Rendell L, Constantine R et al (2019) Migratory convergence facilitates cultural transmission of humpback whale song. R Soc Open Sci 6:190337. https://doi.org/10.1098/rsos.190337

Patenaude NJ, Portway VA, Schaeff CM et al (2007) Mitochondrial DNA diversity and population structure among southern right whales (*Eubalaena australis*). J Hered 98:147–157. https://doi.org/10.1093/jhered/esm005

Payne K, Payne RS (1985) Large scale changes over 19 years in songs of humpback whales in Bermuda. Z Tierpsychol 68:89–114. https://doi.org/10.1111/j.1439-0310.1985.tb00118.x

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) Communication and behavior of Whales. Westview Press Inc., Boulder, CO, pp 9–57

Payne R, Guinee LN (1983) Humpback whale (*Megaptera novaeangliae*) songs as an indicator of 'stocks.' In: Payne R (ed) Communication and behavior of Whales. Westview Press Inc., Boulder, CO, pp 333–358

Payne RS, McVay S (1971) Songs of Humpback Whales. Science 173:585–597

Ramp C, Delarue J, Palsbøll PJ et al (2015) Adapting to a warmer ocean—seasonal shift of baleen whale movements over three decades. PLoS ONE 10:1–15. https://doi.org/10.1371/journal.pone.0121374

Ramsey G (2013) Culture in humans and other animals. Biol Philos 28:457–479. https://doi.org/10.1007/s10539-012-9347-x

Rekdahl ML (2012) Humpback whale vocal communication: use and stability of social calls and revolutions in the songs of east Australian whales. PhD thesis. The University of Queensland, Brisbane, Australia. 174 p

Rendell L, Whitehead H (2001) Culture in whales and dolphins. Behav Brain Sci 24:309–382

Richards DG, Wolz JP, Herman LM (1984) Vocal mimicry of computer-generated sounds and vocal labelling of objects by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. J Comp Psychol 98:10–28

Rowntree VJ, Payne R, Schell D (2001) Changing patterns of habitat use by southern right whales (*Eubalaena australis*) on their nursery ground at Península Valdés, Argentina, and in their long-range movements. J Cetacean Res Manag Spec Issue 2:133–143

Sargeant BL, Mann J (2009) From social learning to culture: Intrapopulation variation in bottlenose dolphins. In: The question of animal culture, pp 152–173

Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. Trends Ecol Evol 17:474–480. https://doi.org/10.1016/S0169-5347(02)02580-6

Seyboth E, Groch KR, Dalla Rosa L et al (2016) Southern right whale (*Eubalaena australis*) reproductive success is influenced by Krill (*Euphausia superba*) density and climate. Sci Rep 6:1–8. https://doi.org/10.1038/srep28205

Valenzuela LO, Sironi M, Rowntree VJ, Seger J (2009) Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). Mol Ecol 18:782–791. https://doi.org/10.1111/j.1365-294X.2008.04069.x

Weinrich MT, Schilling MR, Belt CR (1992) Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae.* Anim Behav 44:1059–1072. https://doi.org/10.1016/S0003-3472(05)80318-5

Whitehead H (2010) Conserving and managing animals that learn socially and share cultures. Learn Behav 38:329–336. https://doi.org/10.3758/LB.38.3.329

Whitehead H, Rendell L (2015) The cultural lives of whales and dolphins. The University of Chicago Press, Chicago

Whitehead H, Laland KN, Rendell L et al (2019) The reach of gene–culture coevolution in animals. Nat Commun. https://doi.org/10.1038/s41467-019-10293-y

Whiten A (2017) A second inheritance system: the extension of biology through culture. Interface Focus 7:160142

Whiten A (2021) The burgeoning reach of animal culture. Science

Whiten A, Goodall J, McGrew WC et al (1999) Cultures in chimpanzees. Nature 399:682–685

Whiten A, Spiteri A, Horner V et al (2007) Transmission of multiple traditions within and between chimpanzee groups. Curr Biol 17:1038–1043. https://doi.org/10.1016/j.cub.2007.05.031

Whiten A, Ayala FJ, Feldman MWD, Laland KN (2017) The extension of biology through culture. Proc Natl Acad Sci 114:7775–7781

Wild S, Allen SJ, Krützen M et al (2019a) Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. Biol Lett 15:20190227. https://doi.org/10.1098/rsbl.2019.0227

Wild S, Krützen M, Rankin RW et al (2019b) Long-term decline in survival and reproduction of dolphins following a marine heatwave. Curr Biol 29:R239–R240. https://doi.org/10.1016/j.cub.2019.02.047

Würsig B (2019) Ethology and behavioral ecology of odontocetes: concluding remarks. In: Würsig B (ed) Ethology and behavioral ecology of odontocetes. Springer, pp 483–494

Yurk H, Barrett-Lennard L, Ford JKB, Matkin CO (2002) Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. Anim Behav 63:1103–1119