



Gene–culture coevolution in whales and dolphins

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Whales and dolphins (Cetacea) have excellent social learning skills as well as a long and strong mother–calf bond. These features produce stable cultures, and, in some species, sympatric groups with different cultures. There is evidence and speculation that this cultural transmission of behavior has affected gene distributions. Culture seems to have driven killer whales into distinct ecotypes, which may be incipient species or subspecies. There are ecotype-specific signals of selection in functional genes that correspond to cultural foraging behavior and habitat use by the different ecotypes. The five species of whale with matrilineal social systems have remarkably low diversity of mtDNA. Cultural hitchhiking, the transmission of functionally neutral genes in parallel with selective cultural traits, is a plausible hypothesis for this low diversity, especially in sperm whales. In killer whales the ecotype divisions, together with founding bottlenecks, selection, and cultural hitchhiking, likely explain the low mtDNA diversity. Several cetacean species show habitat-specific distributions of mtDNA haplotypes, probably the result of mother–offspring cultural transmission of migration routes or destinations. In bottlenose dolphins, remarkable small-scale differences in haplotype distribution result from maternal cultural transmission of foraging methods, and large-scale redistributions of sperm whale cultural clans in the Pacific have likely changed mitochondrial genetic geography. With the acceleration of genomics new results should come fast, but understanding gene–culture coevolution will be hampered by the measured pace of research on the socio-cultural side of cetacean biology.

gene–culture coevolution | Cetacea | cultural hitchhiking

Evolution is dependent on inheritance. Although the transmission of genes is primary, it is not the only mode of inheritance. As recently articulated in the extended evolutionary synthesis, inheritance extends beyond genes to include epigenetic inheritance, physiological inheritance, ecological inheritance, social transmission, and cultural inheritance, all of which can lead to heritability of phenotype (1). From the perspective of modern humans, cultural inheritance, which directly determines much of our own behavior as well as indirectly determining how we affect the global environment, has particular salience (2).

Culture, as an inheritance system, can be defined as behavior or information shared within a community that is acquired from conspecifics through some form of social learning (3), i.e., learning that is influenced by observation of, or interaction with, another animal or its products (4). Social learning comes in a range of forms including imitation, emulation, teaching, and local enhancement (5), all of which can promote behavioral similarity between learner and model. Culture may include a wide range of behavior, including foraging methods, vocalizations, diet selection, social behavior, movement, habitat use, social structure, and play (e.g., refs. 3 and 6); potentially higher-level attributes of culture, e.g., conservative cultures, exploratory cultures, or pacific cultures (refs. 3, 7, and 8), also can affect a range of behavior. Cultures may be stable over many generations or transitory fads. The learning is often from parent to offspring in the former and from peer to peer in the latter (9).

The different modes of inheritance do not act wholly independently. Phenotypic assimilation by one mode of inheritance may influence the transmission of traits by another mode. Genes produce the basic organismal phenotype, and this genetic phenotype

places major constraints on the other modes of inheritance. Circumstances in which other inheritance mechanisms control the inheritance of genes are much less obvious but can have great evolutionary significance (10). Thus, there has been particular interest in gene–culture coevolution (11–13).

Theoreticians started to model potential interactions between genes and culture in the 1970s (14), and there has been much empirical and theoretical work since then (11, 13, 15, 16). However, gene–culture coevolution has rarely been formally defined. For the perspective of this article, I consider cases in which culture—i.e., group-specific social learning—affects the distribution of DNA found in a population. That is, we can reasonably suppose that the distribution of genes in a population would be different if individuals were not transmitting cultural information through social learning. Gene–culture coevolution includes very specific selective processes in which a particular cultural practice affects the evolution of a particular gene or genes. The most famous example is the coevolution of dairy farming and the lactase gene, allowing adult humans in dairy-farming cultures to digest milk products (17). However, gene–culture coevolution can also include general processes. If culture is driving significant parts of a species' behavior, then this influence may constrain genetic evolution. For instance if cultural processes isolate groups and give them distinctive behavior, then this isolation may initiate or promote the course of speciation or reduce the diversity of genes that are transmitted in parallel with the cultural traits (18–20). Under this concept of gene–culture coevolution there will be circumstances in which the available information may not be definitive. Scenarios including or excluding culture may both be consistent with results.

Gene–culture coevolution has been considered almost entirely from the perspective of *Homo sapiens*, and the great majority of research has been aimed at the hypothesis that there are specific genes whose distribution has been affected by human cultural practices (11, 13, 15). Two of the best-documented cases are the dairy farming–lactase relationship mentioned above and a scenario relating human activities, such as clear-cutting of forests, with malaria incidence, and sickle cell anemia. Different cultural practices in different parts of the world that increase susceptibility to malaria are correlated with higher allele frequencies of the HbS variant of normal adult hemoglobin that in heterozygotes confers protection against malaria infection but in homozygotes results in sickle cell anemia (21, 22).

Population genomics has been able to highlight areas of DNA subject to selection, give an approximate date for selective sweeps, and provide links to functionality. The recent expansion of the genomic enterprise has revealed a great sway of recent selection on the genomes of modern humans, particularly in

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populations derived following migration out of Africa (23). It has been hypothesized that an accelerated rate of adapted substitutions over the last 40,000 y is linked to cultural innovations and consequent demographic group selection (24). These findings led authors to propose gene–culture coevolution as the dominant form of evolution in recent human history, because of the speed at which genetic change has taken place and correlation with the occupation of new niches and the establishment of new cultures (10, 13). However, a temporal correlation, and even a plausible scenario linking a particular selective gene to a cultural trait, does not demonstrate culture as causal to genetic change. Demographic history can be a vital factor in driving the genetic variation of contemporary populations. For instance, population bottlenecks can cause founder effects in both genes and culture, leading to correlations between specific genes and specific cultures that are not the result of gene–culture coevolution. There are, in fact, relatively few cases in which human culture has been irrefutably shown to have caused genetic change (13). That is not to say that gene–culture coevolution is rare, and indeed the overall temporal correlation between the recent explosion in the scope of human culture and an extremely accelerated rate of selection on genes seems to point toward a major effect. However, in most instances it is very difficult to provide a compelling empirical case that the interaction between culture and genetics is causal.

Even harder to substantiate are the proposals for more general effects of culture on patterns of human genetics. For instance, models have shown that the remarkably low levels of human genetic diversity could result from culturally mediated population structure (25) or from selectively important cultures being transmitted in parallel with neutral genes (26). However, there is no strong empirical evidence for either of these processes.

Although culture is clearly present in other species, it is dwarfed in almost all respects by its impact on modern humans (27–29). Thus, given the difficulties of demonstrating gene–culture coevolution in by far the most cultural species, there has been little effort to look elsewhere. However, gene–culture coevolution can theoretically operate in simple cultural systems (14), and there may be attributes of nonhuman species that could accentuate the effects of culture on genes or make them more discernible.

Birds offer one candidate taxon for nonhuman gene–culture coevolution. In oscine species, birdsong is largely a socially learned population phenomenon and thus represents culture (30). For instance, populations of the sharp-beaked Galápagos ground finch (*Geospiza difficilis*) have socially learned songs with an important role in mating but respond fully only to songs from their own island population (31). Thus, Grant and Grant suggest that cultural transmission is driving speciation (31). However, some other studies have found little evidence of links between cultural and genetic evolution in birds (e.g., ref. 32).

Of all nonhuman species, culture seems particularly prevalent and significant among Cetacea (3). The cetaceans include about 89 species of whales and dolphins, ranging in size from 1 to 30 m. They use a range of habitat from large rivers to the deep ocean, in polar, temperate, and tropical waters. They eat a wide range of marine animals, from copepods to large whales. Cetaceans are divided into the mysticetes or baleen whales that filter feed on schools of prey using baleen, and the odontocetes that use echolocation to locate and track single prey.

Although cetaceans are not easy to study, there is good evidence for cultural transmission in song, migrations, foraging behavior, social conventions, cooperative associations with humans, and play (3). Almost all cetacean species whose behavior has been much studied show possibly, or likely, culturally acquired behavior (3). For gene–culture coevolution, culture needs to be quite stable—fads need not apply—and to affect fitness directly or indirectly. When social groups with distinct cultures

live sympatrically and these groups have differential reproductive success, then gene–culture coevolution can be driven powerfully by group selection (3, 27). Stable, sympatric social groups with distinctive cultures are the hallmark of two large odontocete species with matrilineal social systems, the killer whale (*Orcinus orca*) and the sperm whale (*Physeter macrocephalus*) (3). In these species, females, typically, and males, sometimes, spend their lives grouped with their mothers while both are alive, forming stable social units of about 10 animals. The social units are themselves elements of higher-level matrilineally based social tiers such as clans, communities, and ecotypes. Distinctive behavior, which is believed to be generally culturally transmitted, maps onto the different elements of the social tiers (3). This socio-cultural relationship sets up conditions in which gene–culture coevolution could lead to neutral or functional genes being found in different elements of the social system or to more general effects such as speciation or reductions in genetic diversity.

Here I examine four general hypotheses for gene–culture coevolution in whales and dolphins: (i) that culture has led to incipient speciation of killer whale ecotypes; (ii) that culture has driven the evolution of functional genes in killer whales; (iii) that low levels of mtDNA diversity in five species of matrilineal odontocete result from cultural hitchhiking; and (iv) that geographical patterns of mtDNA result from cultural behavior. As with gene–culture coevolution in humans, evidence is not always conclusive, and I will consider alternative mechanisms for the observed patterns.

Ecotype Radiations in Killer Whales?

Although killer whales as a species have an extremely diverse diet, ranging from herring to the largest whales, each killer whale is typically a member of an ecotype, and most ecotypes are extremely specialized in what they eat and often in how they catch it. Ecotypes are distinctive in a range of other behaviors, as well as morphology (20). In each of the North Pacific, North Atlantic, and Antarctic two or more ecotypes, each with a few hundred to a few thousand animals, are sympatric but socially isolated (20). Best known are the three North Pacific ecotypes: a salmon-eating specialist ecotype known as “residents,” a mammal-eating specialist or “transient” ecotype, and an “offshore” ecotype, which feeds upon sharks (20). All three ecotypes cluster in distinct mitochondrial and nuclear genome clades (33, 34) that diverged a few hundred thousand years ago (35). We have less complete information for the Antarctic, but there appear to be five ecotypes respectively specializing on minke whales (*Balaenoptera acutorostrata*) (ecotype A), seals (ecotype B1), penguins (ecotype B2), and fish (ecotype C and perhaps ecotype D) (20). These Antarctic ecotypes seem to have diverged more recently than those in the North Pacific, and ecotypes B1, B2, and C, at least, are part of a distinct and relatively shallow Antarctic clade (34, 35). The distinctions between the ecotypes have led Morin et al. to suggest that they should be considered separate species or subspecies (36), but this proposal has not been formally implemented.

Since the initial discovery of killer whale ecotypes, scientists have speculated about how they may have arisen. Although some issues are disputed, a consensus hypothesis about the fundamentals of ecotype formation has grown. This culturally driven ecological speciation scenario has been articulated most clearly by Riesch et al. (20), with support from more recent genomic studies (35). Ecological speciation needs (i) an ecological source of divergent selection; (ii) a form of reproductive isolation; and (iii) a mechanism linking divergent selection to reproductive isolation (37). The killer whale scenario is especially interesting because culture seems to play a key role in all three components.

Within the best-studied killer whale ecotypes there is evidence that different matrilineal social units can have distinctive ways of

life. For instance, the AT1 transient matriline of Prince William Sound, Alaska has particular ways of capturing fast-swimming Dall's porpoises, *Phocoenoides dalli* (38). Such foraging methods are almost certainly socially learned, primarily within matrilineal units. As these foraging methodologies become more efficient through cultural selection, they will tend to become more specialized, so that matrilineal, or groups of socially connected matrilineal, develop new ways of life. These matrilineal units are thought to be the progenitors of the ecotypes (20). In concordance with this scenario, new genomic studies indicate that ecotypes started with small populations of related animals (35).

The second and third conditions of ecological speciation, the emergence of reproductive isolation between ecotypes, are key to the population structure of killer whales. Riesch et al. consider four mechanisms through which cultural divergence could lead to reproductive isolation among ecotypes (20). Most directly, cultural xenophobia could restrict mating patterns. Vocal dialects, which are socially learned and thus culture, are good candidates (20). These dialects appear to set barriers to mating with close associates, and, in accordance with a paradigm of mating only with animals whose vocalizations are similar but not too similar, also might prevent mating between proto-ecotypes (20). Secondly, the cultural specializations that come to define ecotypes would likely make between-ecotype dispersal difficult and often functionally impossible. Killer whales are culturally conservative (7); thus, for instance, adopting the specialized, collaborative behavior of a seal-eater might be very hard for a postweaning salmon-eater, who had already absorbed the conformist ways of her own lineage. Third, genetic drift within ecotypes could lead to postzygotic infertility or reduced fitness of hybrids. Such drift is particularly likely given the generally small sizes, and even smaller founding bottlenecks, of the ecotypes (20, 35). Riesch et al.'s (20) final mechanism promoting reproductive isolation among ecotypes is the selection on functional genes by different cultural practices. New genomic studies have found strong evidence for this selection (35), and this evidence is described in the next section.

Although ecological speciation driven by cultural specialization is the favored hypothesis for ecotype formation and is consistent with what is known of the behavior, ecology, genetics, and genomics of killer whales, the hypothesis is not proven. An alternative hypothesis is that nonecological cultural divergence might have predated the ecological specializations (20). For instance, proto-ecotypes could have been based on vocalization patterns of groups of killer whales that had similar diets, and then, once isolated, these groups could have begun to specialize ecologically. It is hard to envisage an alternative ecotype-generating scenario that does not have a cultural component.

Gene–Culture Coevolution of Functional Genes

We have evidence that culture has influenced the evolution of functional genes in killer whales, and killer whale ecotypes provide the substrate for these inferences. In fewer than 10,000 generations, killer whales have radiated from a single ancestral lineage to colonize regions from the Arctic to the Antarctic and all waters in between (34, 35). Until humans reached Antarctica, killer whales were the most widely distributed mammals and likely were subject to a diverse range of selective pressures associated with different habitats. The stable cultural traditions of killer whale ecotypes provide a rare and attractive system for investigating gene–culture coevolution in functional genes. However, as with most genomically derived putative linkages between genes and culture in humans (10), there is no definitive proof that cultural practice has affected selection pressure on the identified genes.

Genomic studies have looked at two particular contrasts: between fish-eating and mammal-eating ecotypes and between temperate and Antarctic ecotypes. Because diet in killer whales

is almost certainly socially learned, and the ecotypes themselves likely arise from this cultural process (see previous section), the first contrast can reasonably be deemed cultural; the second is less directly so, but culture likely underpins almost all behavioral differences between ecotypes. Niche construction is the modification of the environment by an organism, so that the changes influence natural selection (39). In their review of gene–culture coevolution, Laland et al. (10) emphasized that the defining characteristic of niche construction is the modification of selection pressures and that this modification could be achieved through processes such as migration, dispersal, and habitat selection. Niche construction then provides a link between the cultures of killer whale ecotypes and their habitats.

Recent population genomic studies comparing the fish-eating resident and mammal-eating transient ecotypes of the North Pacific found a signature consistent with selection on genes associated with diet (35, 40). The regions of the genome that most differentiated members of the resident ecotype contained genes associated with digestive tract formation during developmental stages and carboxylic ester hydrolase activity, including the hydrolysis of long-chain fatty acid esters (35). A signature of selection on the *CBS* gene, which has a role in the methionine cycle, was found in the mammal-eating transient ecotype. Interestingly, a signature of selection on a different set of genes that play a key role in the methionine cycle was also found in the predominantly mammal-eating B1 ecotype from the Antarctic (35). Methionine is an essential amino acid that cannot be produced by the body and must be obtained through dietary intake of protein (41). Foote et al. (35) hypothesized that the more sporadic intake of large amounts of dietary protein by mammal-eating killer whales may exert selection pressures on the methionine cycle different from those experienced with a more temporally consistent intake of protein by fish-eating killer whales. Similar to the parallel examples of lactose tolerance and malaria resistance in different human populations, the signatures of selection on the same pathway in two independently derived mammal-eating ecotypes supports the notion that selection may be associated with culturally acquired ecological niches.

Although the killer whales in the North Pacific inhabit relatively temperate waters, those found in Antarctic waters arguably inhabit the most extreme environment of this species' range. The three Antarctic ecotypes included in a recent population genomics study share a recent common ancestor (34, 35). Targets of selection along the evolutionary branch to this ancestral Antarctic population includes genes associated with adipose tissue development; interestingly, the same process has been under selection in the polar bear, *Ursus maritimus*, compared with the brown bear, *Ursus arctos*, and are suggestive of a link to adaptation to a colder climate (42).

The *FAM83H* gene, which regulates the keratin cytoskeleton, including that in epithelial cells (43), is one of the genes most differentiated in the Antarctic and North Pacific ecotypes, containing four fixed nonsynonymous substitutions in the Antarctic ecotypes (35). Antarctic killer whales are thought to have a slow regeneration of skin cells because of the thermal constraints of allowing blood to circulate to the outer epithelial cells (44). This slow skin regeneration is evidenced from the build-up of diatoms, giving Antarctic killer whales a yellowish hue compared with North Pacific killer whales (45). Genes associated with skin regeneration, such as *FAM83H*, therefore may be under selection because of this thermal constraint. Just as human cultural practices frequently buffer selective pressures from harsh environments (10), Antarctic killer whales seem to use behavioral adaptation to mitigate the impact of the Antarctic climate upon skin regeneration. Satellite tagging has revealed that these whales make regular round trips to warm subtropical waters; when they return they have lost the yellow hue of their diatom film, indicating they have regenerated the outer epithelial cells (44).

Several phenotypic distinctions between ecotypes appear functional, given the ecotypes' different cultural behaviors, and are likely genetically based, but the candidate genes for these distinctions have not yet been identified. Most obviously, ecotypes that eat mammals are generally larger than those that eat fish (20). This difference in size could be related to the nutritional values and availability of the different foods, but it also may have a genetic component. In the North Pacific, mammal-eating transients seem to have more robust mouth parts than fish-eating residents (20). The type B1 Antarctic killer whales use a particularly extreme form of coordination, synchronous fluke beats, to create waves that knock seals off ice flows (46). They also have relatively larger white eye-patches than other ecotypes. Are these large eye-patches coincidence or the result of gene-culture coevolution?

Cultural Hitchhiking in Matrilineal Whales

This section summarizes information in ref. 47. As molecular genetics was applied to cetacean species during the 1990s, an unexpected pattern appeared. The four whale species known to have matrilineal social systems, the killer whale, sperm whale, and two pilot whale species (*Globicephala macrorhynchus* and *Globicephala melas*), possessed much lower diversities of the control region of their mtDNA than other cetacean species with comparable population sizes or latitudinal ranges (19). In the nearly two decades since then, many additional estimates of cetacean control region diversity have been published, for other species (including another presumed matrilineal species, the false killer whale, *Pseudorca crassidens*), with larger and more geographically dispersed samples, and greater coverage of the genome (47). The pattern still holds (Fig. 1). The range-wide mtDNA diversities in the matrilineal species are $\sim 29.8\%$ of that of nonmatrilineal species with similar latitudinal ranges (47). For regional estimates the ratio is 16.6%.

Low genetic diversity usually invokes discussion of bottlenecks and selection. Both these default mechanisms have been used to explain the low mtDNA diversity of the matrilineal species of Cetacea (48–53). However, neither bottlenecks nor selection link the remarkably low diversity of the species to their matrilineal social systems. Furthermore, contrary to expectations from bottlenecks, the diversity of nuclear microsatellites is not obviously reduced in the matrilineal whales (although this result may be partially explained by the greater effective population size and higher mutation rates of microsatellites compared with mtDNA) (47). In sperm whales, Alexander et al. (48) found no evidence for selection in the control region relative to other regions of the

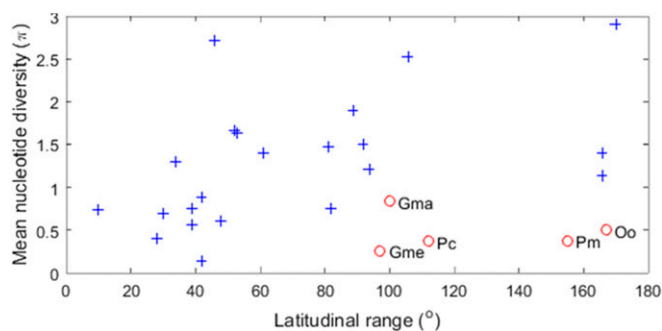


Fig. 1. Mean mtDNA nucleotide diversity (across estimates for a species with $n > 100$ covering $>25\%$ of the species' range or at least one ocean basin) against the latitudinal range of cetacean species. Nonmatrilineal species are indicated by a plus sign, and matrilineal species are indicated by circles. Gma, short-finned pilot whale; Gme, long-finned pilot whale; Oo, killer whale; Pc, false killer whale; Pm, sperm whale. Adapted from ref. 47.

mitochondrial genome, but this finding does not exclude a selective sweep originating in these other regions.

More satisfying than bottlenecks or selection are scenarios postulating important demographic processes operating primarily at the level of the matrilineal group, thus reducing the effective population size to something like the number of groups and thus lowering the expected genetic diversity (54–56). However, agent-based models found no realistic circumstances in which the demography of matrilineal groups could reduce genetic diversity, unless fitness differentials between groups were heritable (57). If there is a heritable component to fitness within matrilineal groups, then the conditions for reduced genetic diversity become much relaxed (57). This heritability could happen with selection on the mitochondrial genome, for instance in response to mitochondrial disease or deep diving (47, 48), but there is no need for a species to have a matrilineal social system for selection on genes to reduce mtDNA diversity, so this explanation is unsatisfying.

The heritable component to fitness does not need to be genetic; it just needs to be transmitted matrilineally. Killer and sperm whales are well known for their matrilineally transmitted cultures (3). Cultural hitchhiking is the hypothesis that these matrilineally transmitted cultures, with fitness differentials, have reduced diversity of the mitochondrial genes that are being transmitted in parallel (19). Thus cultural hitchhiking is a form of gene-culture coevolution. Agent-based models have shown that cultural hitchhiking can work in circumstances that seem realistic for the matrilineal whales (57) but do not necessarily imply that cultural hitchhiking is behind their low mtDNA diversity.

However, it is most parsimonious to assume that a factor common to the matrilineal species has led to reduced diversity. Because that factor does not seem to be the direct influence of matrilineality itself (57), I suspect that it is culture. Matrilineal social systems are particularly good substrates for the evolution of stable, group-specific cultures (3), and stable, group-specific cultures are the prerequisite for cultural hitchhiking (57). However, culture may affect genetic diversity through different paths in different species (18), as illustrated by the two best-known matrilineal species, sperm and killer whales.

Female and immature sperm whales use tropical and subtropical waters, where they live in matrilineally based social units (58). These units, in turn, are members of coda clans (59). The coda clans have distinctive dialects, movements, microhabitat use, and social behavior, as well as differential reproductive success (59–62). The clans are sympatric but do not associate with one another; they show no differences in nuclear microsatellites but do have distinct mtDNA haplotype distributions (63, 64). Thus, sperm whales fit the classic cultural hitchhiking scenario well, with clans being the cultural groups under selection, and cultural hitchhiking is the most parsimonious explanation for their low mitochondrial diversity. A selective sweep in the mitochondrial genome is also consistent with available results on sperm whales (48) but does not obviously provide a link with matrilineality.

Although killer whales are also matrilineal, their subdivision into ecotypes adds a layer of additional possible drivers of low genetic diversity. Population subdivision itself tends to reduce genetic diversity (65). The highly specialized ways of life of many of the ecotypes may make them particularly vulnerable to extirpation, removing characteristic mtDNA haplotypes in the process, and thus reducing diversity (65). The ecotypes have very different culturally transmitted behavior—one of the conditions for cultural hitchhiking—but their lifestyles are so different that it is hard to see how they would often be in competition (however, see ref. 66 for a scenario of indirect competition between ecotypes), so cultural hitchhiking at the ecotype level seems an incomplete explanation. Processes that reduce diversity within ecotypes would also affect the overall diversity of killer whales.

Genomic studies give strong support for bottleneck effects during the founding of ecotypes, as well as selection driven by ecotype-specific cultural traits (35, 67). Cultural hitchhiking also could operate on socio-cultural groups within ecotypes, such as the communities of resident ecotype killer whales (68). However, at this time, our evidence for a cultural factor behind the low mtDNA diversity of killer whales lies primarily in its role in setting up the ecotypes and driving selection within them (see previous sections). In this respect, the killer whale situation corresponds quite closely to Premo and Hublin's (25) suggestion that culturally transmitted barriers to mating and dispersal may have set up conditions for the reduction in human genetic diversity through bottlenecks and selection.

We know much less about the three other matrilineal species: the short-finned pilot whale, the long-finned pilot whale, and the false killer whale. Although the evidence for matrilineal social systems is quite good (69–71), we have not identified suitable socio-cultural groups on which cultural hitchhiking might operate, nor do we know whether such groups are barriers to mating, as with the killer whale ecotypes, or, alternatively, share nuclear genes through male dispersal, as with sperm whale coda clans. For these species we also have little idea as to what important matrilineally based cultural traits either provide selection differential or define population structure. However, the low mtDNA diversity in these matrilineal species is unlikely to be a coincidence; culture is probably involved in some way.

Culture and the Geographical Distribution of Genes

The geography of the genes of *H. sapiens* has been thoroughly redistributed by culture. Both the neutral genes characteristic of northern Europeans and some functional ones (e.g., those for blond hair) are much more widely dispersed than would have been expected a millennium ago. This dispersal is a result of their linkage to the knowledge of oceanic navigation and weapons technology, as well as a drive to explore, all culturally acquired. In several cases the geographical distribution of cetacean genes has a strong cultural imprint. This geographical pattern happens most obviously when migration routes are learned matrilineally, and so migratory destinations may have distinctive mtDNA haplotype distributions. However, there are also more complex situations in which the link between geography and culture is not as direct.

Most beluga whale (*Delphinapterus leucas*) populations make seasonal migrations between shallow summering areas, where the young are born, and deeper-water wintering grounds. The young belugas are presumed to learn these migration routes from their mothers and repeat them sufficiently faithfully that summering grounds that were emptied by intense whaling remain almost unoccupied several generations later, even though they border the migration routes of other belugas whose summering grounds were not intensely whaled. So strong are these matrilineal cultural traditions that a population of belugas summering in western Hudson Bay, Canada, has mtDNA haplotypes traced to a Pacific refugium during the Wisconsin glaciation, whereas those summering in eastern Hudson Bay have an almost entirely different distribution of haplotypes that are presumed to derive from an Atlantic refugium (72). This distinction has been maintained over several thousand generations even though there are no physical barriers between the summering grounds and the migration routes and wintering grounds of the two populations, where the animals mate, overlap so that there is mating between them (73).

Baleen whales also show geographical genetic structure in mtDNA resulting from maternal learning of migration destinations. For instance, humpback whales (*Megaptera novaeangliae*) in the North Atlantic and North Pacific consistently use particular summer feeding grounds in temperate latitudes but breed in common tropical wintering areas. Calves use the same summering grounds as their mothers, but not necessarily their fathers, setting up mtDNA haplotype distinctions among feeding

grounds (74). The wintering grounds of southern right whales (*Eubalaena australis*) have distinct mtDNA haplotype distributions, presumably because of maternal migratory fidelity, and Carroll et al.'s (75) analysis of gene distributions and stable isotopes suggests that the migratory cultures also affect genetic structure on feeding grounds.

Such cases of cultural migration routes and habitat use may not be uncommon among animal species such as birds and ungulates, although many traditional migrations are insufficiently faithful to set up clear genetic patterning (76). Such patterns can also be found without culture, for instance salmon using chemical traces to home to their native streams, and so set up clear geographical genetic distinctions. Using senses alone to home to native areas consistently is an alternative explanation for the geographical patterns of mtDNA in cetaceans. However, given the social nature of these species, and especially the long mother–calf relationship that typically includes several migrations, the cultural explanation is more parsimonious.

Geographical patterns of gene distributions can also be driven by cultural inheritance of traits that are not themselves about migration but affect habitat use secondarily. The population of bottlenose dolphins (*Tursiops* spp.) in western Shark Bay, Australia, shows very pronounced distributional differences for three main mtDNA haplotypes over scales of a few kilometers (Fig. 2). There are no barriers to movement between the primary ranges of the different haplotypes, and individuals could move between these ranges in less than an hour. Kopps et al. (77) relate the geographical patterns of mtDNA to foraging methods learned from the mother. One particular foraging type, “sponging,” in which a sponge is used as a tool to forage in relatively deep waters, is known to be learned almost entirely from the mother (78, 79), and in Kopps et al.'s (77) sample is restricted to just one haplotype characteristic of the deeper waters (haplotype E in Fig. 2).

As illustrated by human colonization, culture can potentially affect the dynamics of gene distributions. Sperm whale populations are subdivided into cultural coda clans that are matrilineally based,

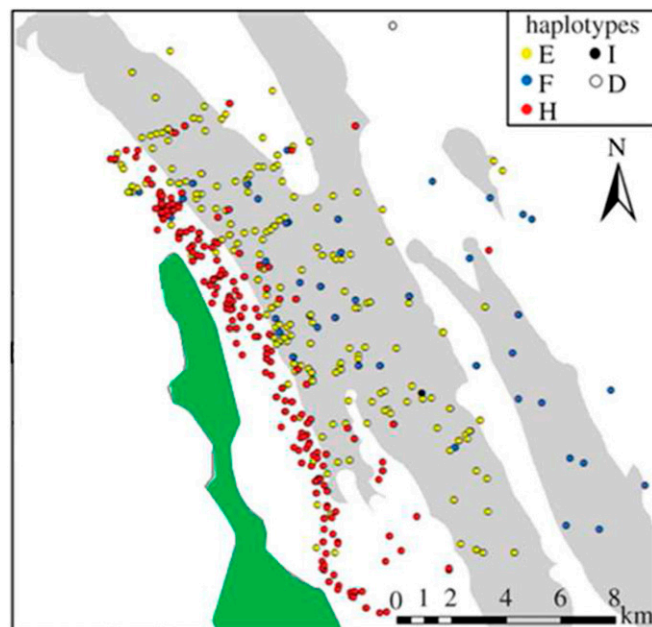


Fig. 2. Segregation of bottlenose dolphin haplotypes by habitat in western Shark Bay, Australia. Survey colors represent haplotypes of dolphins. Each sighting of a sampled dolphin was plotted. Green represents land, white represents shallow water (< 10 m), and gray represents deeper water (≥ 10 m). Adapted from ref. 77.

show distinct mtDNA haplotype distributions, and are often sympatric (59, 64). Between 1985 and 1995 there were two principal cultural coda clans off the Galápagos Islands, but in 2013 and

2014 these had been replaced by two different clans previously primarily found elsewhere in the Pacific (80). It seems that clan membership was a primary factor governing the movements of the

Table 1. Potential cases of gene–culture coevolution in whales and dolphins

Effect	Species	Brief description	Noncultural mechanisms/comments	Strength of evidence for gene–culture coevolution	Ref.
Speciation					
Ecotype radiations	Killer whale	A deep division of killer whales into ecotypes driven by foraging cultures	Perhaps other cultural behavior initiated ecotype formation	Strong	(20)
Gene-culture coevolution of functional genes					
Genes related to digestive tract	Killer whale	Differ between mammal-eating and fish-eating ecotypes		Possible	(35)
Genes related to methionine cycle	Killer whale	Differ between mammal-eating and fish-eating ecotypes	Independent contrasts in North Pacific and Antarctic	Strong	(35)
Genes related to adipose tissue development	Killer whale	Differ between Antarctic and temperate ecotypes	Cultural role not direct	Possible	(35)
Genes related to skin regeneration	Killer whale	Differ between Antarctic and temperate ecotypes	Cultural role not direct	Possible	(35)
Size	Killer whale	Differences between mammal-eating, fish-eating and bird-eating ecotypes	No genes identified; could be environmental	Weak	(20)
Robustness of mouth parts	Killer whale	Differ between mammal-eating and fish-eating ecotypes	No genes identified; preliminary study	Weak	(20)
Coloration	Killer whale	Most enlarged white eye-patch in ecotype that uses most coordinated behavior	No genes identified	Weak	(20)
Cultural hitchhiking in matrilineal whales					
Low mtDNA diversity	Sperm whale	mtDNA has hitchhiked on selective cultural traits transmitted in parallel	Clans are strong candidate for cultural groups; could be caused by selective sweep in mtDNA or bottleneck (less supported)	Possible	(57)
Low mtDNA diversity	Killer whale	Ecotype population structure, plus additional cultural effects, bottlenecks and/or selection have reduced diversity	Culture very likely to have role(s); several possible routes; not necessarily classic cultural hitchhiking	Strong	(57)
Low mtDNA diversity	Pilot, false killer whales	mtDNA has hitchhiked on selective cultural traits transmitted in parallel	Little evidence other than correlation between matrilineal social system and low mtDNA diversity	Weak	(57)
Culture and gene geography					
Distinctive mtDNA distributions of summering areas	Beluga whale	Belugas follow their mothers on first migrations	Born in summer, could be purely environmental sensing, but unlikely	Strong	(72)
Distinctive mtDNA distributions of summering areas	Humpback whale	Humpbacks follow their mothers on first migrations	Born in winter, so, because first visit to summering grounds is with mother, this is social learning	Strong	(74)
Distinctive mtDNA distributions of wintering areas	Southern right whale	Right whales follow their mothers on first migrations	As born in winter, could be purely environmental sensing, but unlikely	Strong	(75)
Distinctive mtDNA distributions at small scales	Bottlenose dolphin	Dolphins learn specialized feeding techniques from their mothers, leading to habitat selection	Social learning of some foraging techniques well established	Strong	(77)
Change in mtDNA distribution caused by cultural clan redistribution	Sperm whale	Clans redistributed themselves over 30 y, changing mtDNA distribution	Genetic change inferred; redistribution could have been independent of clan membership, but unlikely	Possible	(80)

sperms, and so the changes in their mitochondrial gene distributions (80). Thus, culture can have an important role in structuring the geographical dynamics of a population and, consequently, its genes.

Discussion

Given the difficulty of studying whale and dolphin behavior, there is a remarkable amount of evidence for cetacean culture (3). Some of this culture has driven gene evolution. The extent and nature of gene–culture coevolution in cetaceans is very uncertain, as it is in humans (13). Table 1 summarizes the ideas and evidence. Although the strength of evidence is variable (Table 1), culture seems to have driven the evolution of both neutral and functional cetacean genes in several quite different ways. In all cases, socially learned behavior affects how individuals interact with their environment or with each other and thus affects the transmission patterns or selection pressures on genes. Included is the relatively prosaic mechanism of young animals faithfully following their mothers on their first migrations and using these learned migrations for the rest of their lives to set up mtDNA distinctions between geographical habitats. However, there is also evidence for unusual processes: culture driving ecological speciation and cultural hitchhiking reducing genetic diversity.

There are strong parallels with what is known regarding human gene–culture coevolution and evidence for the evolution of functional genes in different killer whale ecotypes with distinct cultural behavior (35). However, the clear phylogenetic and cultural divisions between killer whale ecotypes make it easier, in some respects, to pin down gene–culture coevolution in these species than in the messier trajectory of human evolutionary history.

In 1996 Feldman and Laland (11) suggested that social learning was rarely stable enough in nonhumans to support long-standing cultural traditions upon which selection could act. Documenting cultural stability over generations is not easy in nonhumans. However, there is archaeological evidence for over 4,000 y of a particular type of nut-cracking by chimpanzees (*Pan troglodytes*) at one site in west Africa (81). Faithful transmission of cultures over many generations is implied by many of the patterns in cetacean genetics documented in Table 1. Examples include the strong mtDNA differences between beluga whales on different summering grounds and the linkage of functional genes with ecotype behavior in killer whales.

Although evidence for culture is present across the range of cetacean species whose behavior has been studied (3), there is considerable variation in how that culture is expressed. One constant, however, is a strong mother–calf bond, lasting at least many months and often much longer. This relationship is an excellent conduit for social learning, and stable cultures (3). Migration routes, dialects, and foraging strategies are often learned from the mother and so are transmitted in parallel with mtDNA, potentially leading to gene–culture coevolution. However in some of the larger odontocetes the matrilineal influence is much stronger. Females, and sometimes males, typically spend their lives with their mothers and other maternal relatives. Not only does this association increase the potential learning period and number of models, but the behavior within these matrilineal social units may become very stereotyped, through processes such as conformism and symbolic marking (82). These factors increase the range of ways culture can affect genes, especially the matrilineally transmitted mitochondrial genes. So there is a

particular emphasis on killer whales, sperm whales, and the other matrilineal odontocetes. When matrilineal social structures with distinct and stable cultures cease exchanging mates, then nuclear genes become targets for gene–culture coevolution. Killer whales are the only species in which we know that sympatric matrilineal groups become reproductively isolated, and it is no coincidence that killer whales feature so prominently in Table 1. However, there may be other cetacean species in which mating barriers, either physical or social, between groups with different cultures could allow gene–culture coevolution on nuclear genes.

Some of the processes discussed here, particularly the cultural inheritance of migration routes driving the geography of genes, may be present in other nonhuman species. In species such as chimpanzees that have important stable foraging cultures (6, 81) the evolution of functional genes might be driven by culture; for instance a group that uses a particular tool might evolve senses or musculature to make better use of it. In birds, culturally inherited songs can demarcate social relationships and mating opportunities, perhaps promoting speciation (31). However, this process is somewhat different from the culturally driven ecological speciation of killer whales, and the killer whale scenario is likely rare (20) and maybe unique. Cultural hitchhiking producing low genetic diversity may also be rare, because it requires quite stable groups of relatives with quite stable functionally important cultures producing consistent fitness differentials; cultural hitchhiking works much more efficiently if the cultural groups are sympatric (26, 57).

This review has focused on culture causing differences in genes within species. However, when cultural transmission becomes important, there may be species-wide selection for characteristics that make this transmission more effective. Humans as well as some species of Cetacea have remarkably large brains, as well as menopause. There have been suggestions that both traits could be adaptive in complex cultural systems (3, 83).

The prospects for our understanding of gene–culture coevolution in cetaceans, as well as other nonhumans, are good, but uneven. On the gene side, recent progress in sequencing technology has allowed the transition from targeting candidate genes to conducting genome-wide or whole-genome comparisons. This advance makes finding gene–culture coevolution much more likely, because studies are not limited to identifying genetic variants associated with a particular cultural behavior a priori. As costs go down and expertise builds, genomic studies are being used increasingly on cetaceans and are being deployed with added depth and scope (84). In contrast, studies of cetacean social structure and culture are naturally slow and painstaking and are not getting any cheaper. Some shortcuts are being used, such as inferring diet through stable isotopes and automated processing of recordings of vocalizations, but we also require much more detailed observation at sea. For major progress in understanding gene–culture coevolution, the socio-cultural side needs innovation, commitment, and investment.

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