

8.1. Japanese scientist Toshio Kasuya has made important discoveries about whale societies and exposed illegal practices of the Japanese whaling industry. He has eloquently highlighted the implications of whale and dolphin culture. Here he is searching for Irrawaddy dolphins on the Ayeyarwady River, Burma. Photograph courtesy of Toshio Kasuya.

Not all the evidence for cetacean culture is equal. Looking again at the evidence we have presented in the previous chapters, where we didn't include anything that we didn't think was at least plausibly culture, we can split it up into three categories based on how sure we can be that culture is actually the underlying explanation—definitely, likely, or plausibly.

Definitely Culture The best evidence for culture—by our definition—in the cetaceans is the song of the humpback whale, and it comes not from experiment but careful observation. It is Exhibit A in the case against the dogmatic view that

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only experiments can inform us about nonhuman culture. Scientists have documented how the song changes in both evolutionary and revolutionary mode within the lifespan of individuals. There is no way even the most outlandish scenarios can explain this pattern with genetics alone. Even some of the more hard-nosed critics of animal culture do not dispute this.11 There is no realistic way all the males in an ocean basin could sing the same song and have it evolve over months and years without them listening to each others' songs and adjusting their own accordingly. We can't be sure about the precise mechanisms involved-we think it's most likely down to vocal learning, where individuals acquire new songs and themes from hearing them sung by others. However, it is theoretically feasible that humpbacks are born with innate vocabularies of song units, and their production is triggered by hearing them produced by others. These are interesting questions but irrelevant to the central one at hand here. Irrespective of which mechanism is at play, the song changes rely on humpbacks hearing each other. Thus there is social learning, and the behavior is communal, so we have culture by our definition. The other baleen whale songs in which the form of the song used by all singing whales changes systematically over time-scales much shorter than population turnover, those of bowheads and blue whales, although less well known, must also be culture by the same reasoning.

The key thing about humpback song is that it changes greatly within the lifespan of individuals. There are other examples where behavior changes rapidly, so by similar logic, arbitrary normative behavior spreading quickly through populations, such as the dead-salmon-pushing fad of the killer whales and the tailwalking that Billie the dolphin introduced into her population, must also be culture, albeit relatively ephemeral and so perhaps unlikely to have persistent effects. Similarly, the details of how lobtail feeding has spread through the population of humpback whales in the Gulf of Maine are incompatible with scenarios that do not involve some level of social learning, although changing ecological conditions probably made such behavior more advantageous and therefore also more likely to be uncovered through individual learning—modeling of the spread of lobtail feeding indicates that both processes played a role.12

Finally, we know enough now to be certain that the pulsed-call dialects of killer whales are cultural. We have evidence of how calls vary between pods, clans, and *communities*.13 Scientists have tracked how specific calls accumulate gradual small changes over time and how these changes occur in parallel in pods that associate a lot with each other.14 If you move a young killer whale into a tank with adults that use a different dialect, it acquires

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that dialect.15 There is no room to doubt the cultural nature of killer whale communication.

Likely Culture The other vocal and nonvocal behavior we have described in the large matrilineal whales are almost certainly culture. It is possible to devise scenarios that are theoretically feasible but unlikely in practice in which genetics or individual learning and environmental variation explain the characteristic movement patterns of sperm whales or the beach rubbing by one community of killer whales but not others. However, it is much, much more likely that the sperm and killer whales learn this behavior, probably mostly from their mothers.

We have described in chapter 6 the diversity of foraging strategies that killer whales use in different parts of the world, including herding herring, intentional stranding on beaches, and washing seals off ice floes. Sometimes different strategies co-occur in the same region, such as the fish and mammal eating ecotypes (the residents and transients) of the Northeastern Pacific. We can, though, detect genetic differences between these populations, which could lead to doubt about the role of culture and leads us to placing these behaviors in the "likely" category. However, we also know that, when tested, captive killer whales have proven impressively proficient at copying each other's behavior, even behaviors never seen before. Hence, remembering Morgan's caveat, we have independent evidence that killer whales are quite capable of cultural transmission, and this makes it very likely that this process has an important role in explaining behavioral variation in the wild.

When it comes to sperm whales, we again have strong evidence of different dialects and different habitat use between groups of whales that occupy the same area in the eastern tropical Pacific. Here, we have looked for genetic differences that could play a meaningful role in generating this variation in behavior when it comes through the female line, by analyzing DNA from naturally sloughed skin. We could not detect them. It seems implausible that this variation could be generated and maintained without cultural transmission playing a significant role. However, an element of doubt lies in the fact that we have only properly tested the genetics of the maternal lineages. It is theoretically feasible that sex-linked genes passed down the paternal line could produce these patterns if male sperm whales only mated with females from the same vocal clan they were born into, something we don't have the data to properly look at yet. It seems rather unlikely, however, since males leave both the tropics and the groups they were born into

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for ten years or more before returning to look for mating opportunities and, when on mating grounds, rove around between different groups of females. The presence of such paternal genes specific to clans would also completely contradict the results of a preliminary study that found absolutely no difference between clans in genes passed down through both parents.16 It would be astonishing were such genes to be identified. Nonetheless, because we cannot rule them out, we must accept an element of doubt.

It is rather harder to pin down the foraging specializations of the bottlenose dolphins, from solitary pursuits like sponging to genuinely unique phenomena like cooperative fishing. For instance, we know now that the use of sponges is carried out in particular places by particular matrilines, so both environment and genetics could reasonably have a role (although this needn't exclude a role for culture). The technicalities of the genetic studies of sponging mean that a small element of doubt must remain. We know that in one part of Shark Bay, all the sponging dolphins bar one have the same mitochondrial genotype passed down the maternal line, whereas in another part of the bay, most of the spongers have a different genotype. In some cases the difference between the genotypes associated with sponging and not sponging are as small as a single nucleotide substitution. This is a bit like swapping a single letter in a word—although it is a small change, in the right place it can make a big difference. However, the parts of the mitochondrial DNA that have been studied-the "hypervariable regions"-are thought to be noncoding, in that they have no role in producing the respiratory enzymes vital for life. Where scientists have looked at areas of the mitochondrial DNA that do code, they find no evidence that specific sequences are associated with the sponging behavior.17 This means the window in which noncultural explanations must operate is really quite small, with the only plausible genetic explanation relying on complex additive interactions between genes that somehow occur only in specific matrilines that are also different in different places. Nonetheless, the window exists, so we must retain a degree of uncertainty. Less certain, because they are less studied, the human-dolphin fishing cooperatives nonetheless seem very likely to us to have to contain some cultural element for them to have persisted in subsets of the local populations over multiple generations, although environmental conditions-the presence of fish and human fishers-are clearly important, and genetics might also have a role. Provisioning and begging also look pretty cultural. In both Shark Bay and Cockburn Bay, Western Australia, the pattern by which dolphins acquire the habit of obtaining fish from humans seems to follow the path of the dolphins' social network.

If we knew nothing else about dolphin learning abilities we might have

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placed these behaviors in a more tentative category. However, as with the killer whales, we can add to this the experimental results showing that dolphins can copy each other. Granted, none of the wild behaviors have been specifically tested in this way, so they can be individually criticized as unproven. What we do have, though, when the evidence is considered as a whole, is a combination of incredibly diverse behavior in the wild and evidence for sophisticated social learning abilities in captivity. On balance, the evidence in this picture tilts heavily toward a cultural explanation for dolphin behavioral diversity, although because they have been less studied, we will place some specific examples in the "plausible" category below.

We also place the songs of the minke and fin whales in the likely culture category. In the songs of these species we do not have the definitive "progression over time" evidence that seals the cultural argument for humpback, bowhead, and blue whale songs. But these songs do vary spatially, and while it is theoretically possible to come up with genetic or environmental scenarios that cause the spatial variation, they have little plausibility. The songs within particular regions are highly stereotyped, while those of different regions are quite distinct. Neither the whales' environment nor their genetic variation follows this pattern. Instead, they follow more gradual clines.18

Finally, another area where the evidence makes it very likely culture is playing a role is in the seasonal migration movements of a number of species. We know this because of photo identification and genetic studies that reveal patterns of matrilineal segregation across feeding grounds— whales consistently use their mothers' migration destinations, not those of their fathers. The simplest explanation is cultural transmission of migration routes from mother to calf. So we can put the migration behaviors of right and humpback whales in this category, too. We don't think the urge to migrate is itself necessarily culturally transmitted—this is easily explained with genetics alone—but the specific routes, as well as specific summer and winter grounds, are most likely learned by young during the first migrations of their lives as they follow their mothers. A similar process appears to occur in populations of beluga whales.

Plausibly Culture Behavioral variation between communities or areas suggests where to look for culture but doesn't prove that the variation is explained by social learning. While we might strongly suspect the origin of some behavior is cultural, with an absence of other evidence we are limited in the strength of conclu

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sions we can draw. Note that this is not the same as evidence of absence of culture. We think that the reason we have to consider these cases as merely plausible is that they have not been investigated to any great degree. We are not aware of any case in cetacean research where a scientist looking at how behavior develops has produced evidence that is not consistent with a large role for culture, but consistency is not confirmation. So in this section we place some behaviors that we have noted in previous chapters because their complexity and/or their cooperative nature suggest to us that culture is playing a role but about which we know little more than their initial description. These include the ways bottlenose dolphins process cuttlefish and engage in various cooperative feeding techniques like mud-ring feeding and working in groups to chase fish onto mud banks. We would also include in this category the various foraging techniques of humpback whales (apart from lobtail feeding where the case for culture is good), bottlenose dolphin dialects, and the migrations of dusky dolphins along the New Zealand coast, as well as those of Antarctic killer whales to Brazil and back.

A Whale without Culture? One obvious way to assess the importance of culture in the life of an animal is to ask the reverse question—what happens when the opportunity to acquire culture is restricted? This can be done experimentally if you remove any potential sources of social learning by raising individuals in isolation. Another related approach is to change the nature of the culture available to acquire, by transferring young or eggs into a context in which the social information available is different from that offered by their natural parents, termed cross-fostering. If individuals raised in isolation do not develop the behavior being studied, then we might conclude that some kind of social learning is necessary. Such isolated rearing has been an important part of our understanding the role of cultural transmission in the development of birdsong.19 Similarly, if cross-fostered individuals develop behavior more similar to their adoptive parents or social group than that of their biological parents or the social group they were born into, then again it seems that social learning has a big role to play. This approach has been used to great effect by the Norwegian scientist Tore Slagsvold to show that social learning plays an important role in how foraging develops in small forest birds.20

It is also obvious though that there are some problems with these approaches, which is why they haven't been as widely used in studies of mammals. Raising individuals in isolation requires hand rearing by humans. In some species, this is straightforward, but in others it is notoriously diffi-

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