

## What Counts as Evidence For or Against Vocal Culture in Humpback Whales?

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**Abstract** – The debate concerning the mechanisms that drive population-level song evolution in humpback whales rests on evidence that social learning mechanisms contribute to variations in song elements. In the following dialogue, Eduardo Mercado addresses points raised in support of claims that song evolution in humpbacks arises from social learning, and Heidi Lyn further challenges the idea that recent evidence argues against this interpretation.

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**Related Articles** – This article is part of an Opposing Viewpoints series on the topic of vocal culture in whales. See also:

Mercado III, E. (2022). The humpback's new songs: Diverse and convergent evidence against vocal culture via copying in humpback whales. *Animal Behavior and Cognition*, 9(2), 196-206. https://doi.org/10.26451/abc.09.02.03.2022

Lyn, H. (2022). Cultural confusion: Parsimony, social learning, and humpback whales. *Animal Behavior and Cognition*, 9(2), 207-212. https://doi.org/10.26451/abc.09.02.04.2022

**Heidi Lyn:** Many studies of social learning and culture in animals have emerged over the last couple of decades. Much of this work has focused on primates, but there is also good evidence that cetaceans share comparable cognitive mechanisms for learning from each other. Even if you think that social learning is a more complex faculty than asocial learning, your own research suggests that humpback whales are constantly changing their songs together as a group, so it is a bit surprising that you are now arguing that social learning is not contributing to those changes.

**Eduardo Mercado:** I want to point out that I never said that social learning was a more complex faculty; that was done by other researchers. Also, I am convinced that whales and dolphins can socially learn, including learning vocal actions from observing others produce sounds. In principle, humpback whales could use this ability to construct and produce songs. For decades, I thought that singers were learning new song content by copying conspecifics. Accumulating evidence, however, has forced me to abandon that interpretation.

**HL:** Excellent point – I concede that I used their points as a way to refute a pervasive idea in the field, and that I may have over-interpreted your statement for that purpose. OK, so whales and dolphins do socially learn, but just not in this instance? You seem to view social learning explanations as unwarranted simply because there are possible alternative non-social explanations for some features of song evolution in humpback whales. You acknowledge that humpbacks have the ability to vocally learn, and that other systems that look very similar do seem to be culturally learned, so wouldn't it make more sense to assume that vocal learning is contributing to song evolution? (I am not going to argue for cultural transmission here, btw. I agree thoroughly that the cultural claim has not been proven at all.)

**EM:** Vocal learning may contribute to singers' capacities to construct and use songs, as may individual learning. The evidence of common phrase structure and sequencing across isolated populations, however, argues against either of these mechanisms contributing much to determining how singers change the structural properties of songs, phrases, or units.

**HL:** Why do you think that's the case? Because we see one population with a similar song to another population? That doesn't preclude either social or individual learning from being present. I think you overstate the strength of your data as an argument against social mechanisms being present. I agree that your data require explanation, but it seems to me your findings could be explained by biological constraints and preferences that guide humpback whale song evolution, similar to those found in most vocal systems, which can still easily be incorporated into a socially-learned paradigm.

**EM:** I tend to agree with the position of Tennie and colleagues (2020) that if isolated groups are independently discovering or constructing the same action sequences, then imitation of others is not necessary for the acquisition of those sequences. If biological constraints and individual preferences can explain how humpback whale songs evolve over time, then what is left for the copying hypothesis (or the vocal culture hypothesis) to explain? The vocal culture hypothesis specifically predicts that singing humpback whales from isolated populations should not converge on songs that are structurally identical, for the same reasons that make it unlikely that two geographically isolated groups of humans would converge on identical costumes for religious ceremonies.

**HL:** I think that the likelihood of biological constraints on vocalizations make that probability much higher than you're assuming. While identical religious garb may never appear across cultures, I'm sure there are some similarities and that is without any biological constraints. More importantly, though, I'm not sure that I agree that biological constraints and preferences can completely explain the changes in humpback whale song. I was only arguing that they would drastically increase the possibility that one population (or more) over the entire history of humpback whales eventually created a similar song to another population four decades apart. It seems that you are suggesting that all changes that have ever been seen in humpback whale song are explainable by non-social phenomenon, but I haven't seen evidence of that. Because the data show that songs spread throughout a population and the population sings that same song over time, isn't social transmission the simplest explanation for how songs spread across populations?

**EM:** Do songs spread? What we know is that they change. Sometimes they change simultaneously in geographically separated groups. Other times the changes occur sequentially in adjacent groups. The simplest explanation that can account for both phenomena is that singers change their songs along predictable trajectories. Of course, this explanation does not identify why humpbacks change their songs over time.

**HL:** If all singers are simply following fixed rules of song change rather than learning from each other, then why are the cultural waves in humpback whale songs discovered by Garland and colleagues always occurring west-to-east? That seems more like a smoking gun for culture than any of the evidence you suggest rules out cultural mechanisms.

**EM:** The unidirectional changes in songs observed off of Australia are an oddity for both interpretations. If changes in whale songs follow a predictable trajectory, then all that is necessary to produce waves of change are some ecological factors (e.g., length of migration) that systematically slow progress along that trajectory for some groups relative to others. Given that such "waves" have only been observed near Australia, probably those factors are geographical.

**HL:** Or they are social? Garland has published at least one paper showing an individual whale from the "novel" population singing his song on the way north, and by the migration south, the population had switched to predominantly singing the new song (Garland et al., 2013). And the "waves" of change encompass the populations out toward Tonga. Regardless of what aspects of the new song they picked up or why they chose to switch, this still seems indicative of social change.

**EM:** The cultural transmission explanation does not predict unidirectional waves or geographic uniqueness of wave-like spreading of songs, which is why Garland and colleagues have introduced auxiliary hypotheses to account for these features (e.g., whales from smaller populations mainly copy novel songs produced by singers from larger populations, Zandberg et al., 2021; Garland et al., 2021). Such ad hoc hypotheses run the risk of making the vocal culture hypothesis unfalsifiable (Popper, 1962). Garland's data do not show that singers are picking up any new features of songs by hearing novel songs. The data show that the songs changed along the same trajectory in multiple groups of whales.

**HL:** Here, I think we're discussing two different forms of vocal learning. Janik and Slater (2000) talked about production learning (as in, learning new call types) and context learning (as in rearranging known call types or using them in new contexts). I would absolutely buy that humpbacks might have a system where the calls themselves are biologically pre-determined, but their arrangement is modified over time by a social system. Wouldn't that fit all of the data?

**EM:** I've yet to see any evidence of either of these forms of vocal learning in humpback whales. Singing humpbacks are using different sets of sounds every year and morph sounds continuously within these sets, so there are no stable "call types." The most recent analyses of songs suggest that it is the patterns within songs that are more stable/innate, not the sound repertoire (so the opposite of the system you're envisioning). The vocal learning model you're describing can only explain song evolution and convergence if you assume there is a single innovative whale in each ocean driving the changes across multiple populations, and that singers that cannot hear each other will nevertheless change their songs to include innovations that they have never encountered. I find both of those assumptions to be implausible.

**HL:** Are you arguing that vocal learning plays no role in the changes that singing humpback whales are making to their songs? If not, then what role do you think vocal learning plays?

**EM:** I am arguing that there are mechanisms other than vocal imitation and cultural transmission that can better account for the changes that adult humpback whales make to songs that are worth investigating. I expect that vocal learning does play an important role in the acoustic behavior of humpback whales. Adults are changing the repertoire of units that they use within songs all the time, so at a minimum vocal learning should determine how effectively they can do that. However, the fact that a species can vocally learn does not mean that as adults they will copy others' songs. For instance, black-capped chickadees produce songs with a simple, predictable structure as adults, but nevertheless depend on vocal learning mechanisms during development to produce those stereotypical songs (Kroodsma et al., 1995). Humpback whales may similarly depend on vocal learning mechanisms, even if they never copy the features of any songs that they encounter as adults. What I believe counts as evidence against cultural learning in humpback whales are instances in which singers change songs along similar, predictable trajectories without having ever been in acoustic contact. Evidence for cultural learning could come from

playbacks that evoke copying behavior from singers and that ultimately spreads to other whales not originally exposed to those playbacks.

**Conflict of Interest:** We, the authors, declare that we have no financial conflicts of interest with the content of this article.

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