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# The Humpback's New Songs: Diverse and Convergent Evidence Against Vocal Culture via Copying in Humpback Whales

**Eduardo Mercado III**

Department of Psychology, University at Buffalo, The State University of New York

Email: emiii@buffalo.edu

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**Abstract –** Singing humpback whales constantly modify their songs over hours, days, months, and years, throughout their adult lives. Intriguingly, humpbacks appear to vary songs in concert, with most singers in a population producing similar songs at any given time. The convergent vocal dynamics of singing humpbacks have convinced many that songs are vocal customs, passed from singer to singer through vocal imitation. This interpretation has recently been challenged, however, by the discovery that singers not in acoustic contact may sing highly similar songs, and also appear to change their songs along similar trajectories. How could singers that cannot hear each other culturally conform? Here, it is argued that the changes humpback whales make to songs are inconsistent with either communal copying or competitive improvisation. Instead, singers appear to be continuously morphing the acoustic properties of songs in predictable ways both within and across songs, even in the absence of cross-population interactions. There is no direct evidence that singing humpback whales learn songs by copying other singers. The fact that groups of singers change songs in similar ways is not evidence of vocal imitation, cultural transmission, or cultural evolution. So called "cultural revolutions" in humpback whale songs, which have been touted as the clearest and most impressive evidence of culture in any nonhuman animal, actually provide evidence against vocal culture in humpback whales. Vocal complexity and convergence can arise through mechanisms other than cultural transmission via vocal imitation, and in the case of humpback whales, genetic predispositions and ecological conditions may be more relevant to determining how singers collectively change songs over time.

**Keywords –** Acoustic communication, Cetacean, Mysticete, Cultural transmission, Bioacoustics

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

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Lyn, H., & Mercado III, E. (2022). What counts as evidence for or against vocal culture in humpback whales? *Animal Behavior and Cognition, 9*(2), 213-216. https://doi.org/10.26451/abc.09.02.05.2022

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Interest in animal cultures has increased significantly over the last few decades, especially with respect to vocal cultures, broadly defined as vocal behavior patterns shared by members of a local population that arise through social learning (see also Aplin, 2019; Fehér & Tchernichovski, 2013; Hyland Bruno et al., 2021). Some of the best evidence of vocal culture comes from spoken languages and vocal music (Benetti & Costa-Giomi, 2020; Loewenstein, 2019), notable for their uniqueness and geographic-

specific forms in humans (Deacon, 1997). In fact, the only other mammals that show comparable vocal plasticity to humans are whales and dolphins (Janik, 2014; Mercado et al., 2014). Amongst cetaceans, the vocal prowess of humpback whales (*Megaptera novaeangliae*) is frequently singled out as one of the clearest examples of vocal culture in a nonhuman species (Botting et al., 2017; Rendell & Whitehead, 2001; Tyack, 2019). For instance, Whiten (2019, p. 34) suggested that "whale songs are clearly culturally transmitted because songs change, sometimes quite dramatically, over periods of years, yet new song types spread across large populations, thus implicating social learning." Whiten defines cultural transmission as "the various processes of social learning through which individuals may acquire traditions by learning from existing practitioners (p. 28)," implying that humpback whale songs are vocal customs learned from other singers. In the case of singing humpback whales, the specific social learning process through which songs are hypothesized to be culturally transmitted involves "high fidelity copying" (Garland & McGregor, 2020), commonly referred to as vocal imitation (Mercado et al., 2014).

What evidence has convinced scientists that humpback whales modify their songs to match those they hear conspecifics producing? Data presented as support for this hypothesis come from analyses of recorded songs showing that: (1) the structure of songs changes relatively rapidly within populations, with all singers making the same changes (Guinee et al., 1983; Payne & Payne, 1985; Payne et al., 1983); (2) songs produced by adjacent populations change along the same trajectories, suggesting that songs may spread from one population to another (Garland, Gedamke, et al., 2013; Garland et al., 2011; Rekdahl et al., 2018); and (3) songs produced by culturally unconnected populations often differ (Winn et al., 1981). In principle, such variations could provide strong circumstantial evidence for vocal culture in humpback whales. However, the ways that singing humpbacks vary their songs actually compel the opposite inference: that vocal imitation and cultural transmission play little role in song evolution (see Table 1). To understand why this is so, it is important to understand exactly how humpback whales vary their songs over time. Precisely characterizing singers' vocal variations is crucial to evaluating the potential role of vocal imitation in the dynamics of whale songs, as well as the likelihood that songs are cultural products.

**Table 1**

*The Case Against the Vocal Culture Hypothesis in Humpback Whales*

| Prediction | Counterevidence |
|---|---|
| Song evolution will follow different trajectories in isolated groups of singers | Isolated singers show similar trajectories of change (Cerchio et al., 2001; Darling & Sousa-Lima, 2005) |
| Introduction of novel songs will lead to copying | Playbacks of songs from isolated populations do not lead to copying by singers (Darling et al., 2012); No instances of competing novel songs |
| Song differences will grow with increasing temporal and/or geographic separation | Singers separated by continents and decades may converge on the same complex themes/songs (Mercado & Perazio, 2021b); acoustic changes across months/years match those present within songs (Mercado & Perazio, 2021a; Payne et al., 1983) |
| Singers from isolated populations will have distinctive local vocal customs | Singers from isolated populations produce acoustically matching themes (Mercado, 2016; Mercado et al., 2003) |

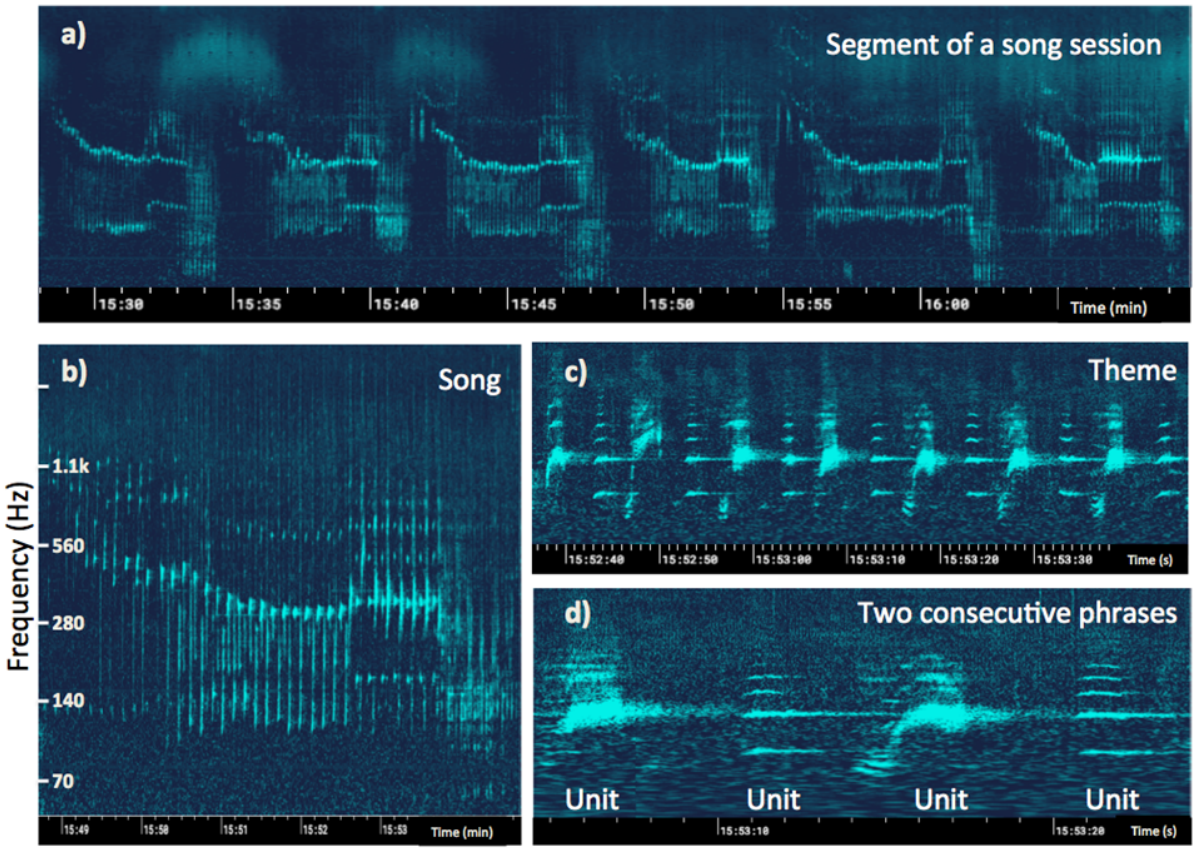
*Note.* The vocal culture hypothesis claims that yearly changes in humpback whale songs are the result of a cultural transmission process in which singers attempt to copy high quality, innovative songs that they have recently heard (i.e., singing humpback whales are socially learning how to produce new songs by vocally imitating existing practitioners).

## How Humpback Whale Songs Vary

Sound sequences produced by humpbacks have "a rather musical quality" (Schreiber, 1952, p. 116). Payne and McVay (1971) argued that because elements of the sequences were repeated in a fixed order (see Figure 1), cycles within the sequences qualified as songs. Winn and colleagues (1970, 1978) were the first to transcribe songs symbolically, replacing individual sounds or units with descriptive labels (e.g., "moans," "cries", and "whoops"). This approach simplifies comparisons of songs across singers, over time, and across species (Eriksen et al., 2005; Garland, Noad, et al., 2013; Kershenbaum & Garland, 2015). For example, the whale song phrase "moan, moan, cry, cry, whoop, whoop, whoop," shares features with the refrain "It's a small world after all," such as the number and pacing of discriminable sounds with harmonic structure. Themes within songs typically consist of repeated phrases (Figure 1c).

**Figure 1**

*Structural Regularities Produced by a Singing Humpback Whale in Hawaii*




*Note.* (a) Spectrogram of six consecutive songs sampled from a song session produced by a single whale off the coast of Hawaii in 2015 reveals cross-song similarities and differences. (b) The fourth song in this sample illustrates how the singer gradually morphed acoustic properties of units while progressing through a song; units appear as vertical bands. (c) Repeating unit sequences (or "phrases") within this song define a theme. In this example, the repeated phrase consists of two units. (d) Repeated phrases share many acoustic features, but also can show systematic variations along multiple acoustic dimensions. Changes to songs within and across years typically involve modifications to units, phrases, and/or themes. Spectrographic images captured from https://patternradio.withgoogle.com/

Winn and Winn (1978; 1985) suggested that: (1) the repertoire of units used by humpbacks was fixed; (2) singers rearranged units to construct songs (see also Garland & McGregor, 2020; Helweg et al., 1992); and (3) songs partially differed in content each year. The yearly variations they identified, later

confirmed by other researchers (Payne & Payne, 1985; Payne et al., 1983), included changes in the units within songs, the number of unit repetitions, and the patterns of units within phrases, with the rate and degree of song change varying substantially across years (Cato, 1991; Payne & Payne, 1985). Progressive (i.e., gradual) changes in song phrases across years constitute the "cultural evolution" of humpback songs (Payne et al., 1983). For instance, if humpbacks sang the phrase "It's a small world after all" in 1963, they might replace this with "It's a small, small world" in 1964, then with "It's a crazy, crazy world," in 1965, and so on, such that by 1984, the phrase became "What's love got to do with it?" Observations of collective, progressive changes in phrases and themes across years are what originally led researchers to propose that humpback whale songs are cultural phenomena (Payne & Payne, 1985).

Past portrayals of humpback whale songs as constantly evolving, communally approved jingles have captured the imagination of both scientists and laypeople. These descriptions provide only a caricature of how humpback whales actually change songs, however, one that obscures key aspects of song dynamics relevant to evaluating claims of vocal culture. Units are not words or musical notes and a huge variety of units sound like "cries" or "moans" (Mercado & Perazio, 2021a). Similarly, phrases are not verses or sentences. Transcribing recordings into symbol sequences discards much of the variation that singing whales are producing, including variations in rhythm, timing, and pitch patterns. Even the demarcation of "songs" within the streams of sounds produced by humpback whales is problematic, because singers typically do not pause while singing, making designations of the beginning or end of a song arbitrary, like identifying the "first horse" on a carousel. When the acoustic changes that singing humpback whales make to their songs over time are taken into account, a different picture of how singers modify their songs emerges.

Acoustic analyses of humpback whale songs show that the changes singers make to units and phrases across years are comparable to the changes they make within and across consecutive songs (Mercado, 2021; Mercado & Perazio, 2021a; Payne et al., 1983). Those transformations involve: (1) the compression/expansion of unit durations; (2) shifts in unit frequency content and frequency modulation; and (3) increases/decreases in the number of unit/phrase repetitions. In short, songs evolve over time (both within and across days) as singers systematically morph units, phrases, and rhythms (Mercado & Perazio, 2021a). If changes in humpback whale songs depend on the local vocal actions of individuals, then trajectories of change within local groups should differ depending on the specific individuals within each group. Contra this prediction, all studies that have examined trajectories of acoustic change in songs have found similar trajectories of change, even across groups that are not in acoustic contact (Cerchio et al., 2001; Darling & Sousa-Lima, 2005; Garland & McGregor, 2020). Acoustically isolated groups of singers morph units and phrases along similar trajectories at both shorter and longer time scales, implying that the vocal idiosyncrasies (or innovations) of local singers are not strongly determining how songs evolve. Although cetologists acknowledge that some changes to songs may follow an innate template (Cerchio et al., 2001; Garland & McGregor, 2020), they continue to hypothesize that singing humpback whales rapidly learn to produce novel songs by changing their own song to match songs they are hearing (McLoughlin et al., 2018; Zandberg et al., 2021), because of a "sexually selected drive for novelty" (Zandberg et al., 2021, p. 2).

The widespread assumption that singing humpback whales vocally imitate competitors' songs to maintain or enhance their own reproductive fitness has sparked comparisons to song learning by birds (Cholewiak et al., 2018; Cholewiak et al., 2013; Garland & McGregor, 2020; Garland et al., 2017; Parsons et al., 2008), and grounded past portrayals of humpback songs as vocal customs (Payne et al., 1983; Payne, 1985). Humpback whale songs evolve in ways that bird songs do not, however, and cross-species differences argue strongly against the possibility that vocal imitation of novel songs or song elements contributes significantly to yearly changes in the songs of whales.

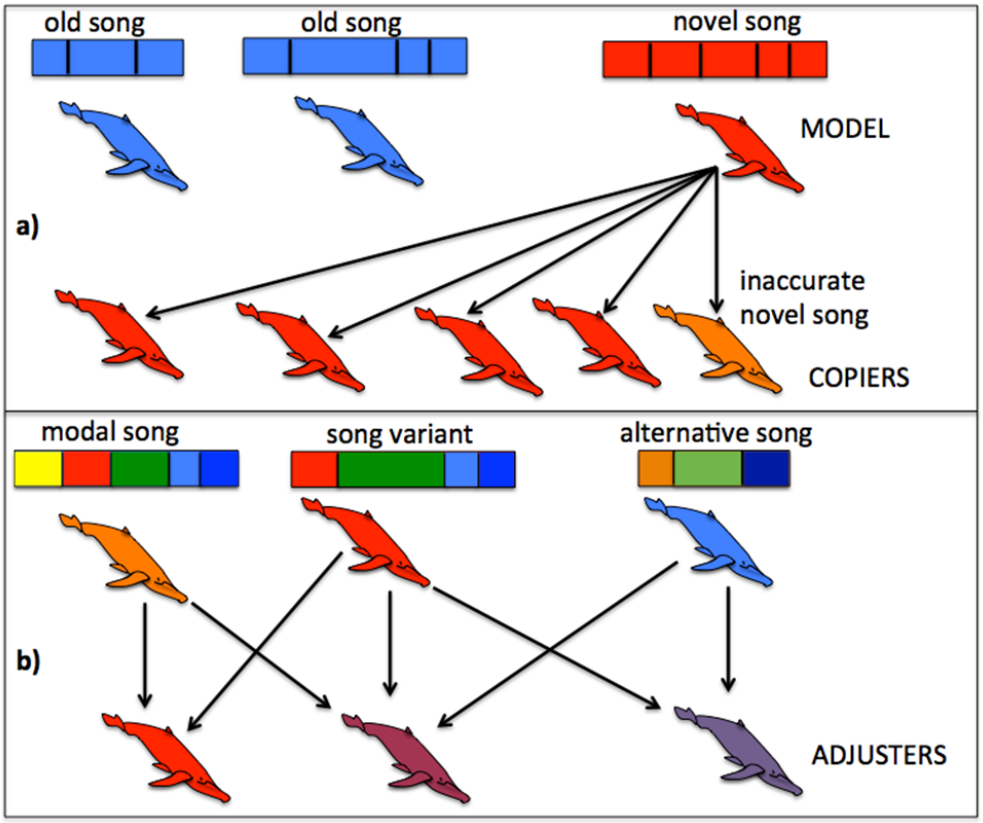
## Do Singers Learn Songs by Imitating Other Singers?

The consensus explanation for why humpback whales constantly and collectively change their songs over time is that singers are competing for mates and in-style songs are sexier (Cerchio et al., 2001;

Garland et al., 2022; Payne, 2000), or better local badges (Darling et al., 2006, 2012). According to this view (Figure 2a), songs change when singers improvise, imitate improvisers, or inaccurately imitate other singers (Garland et al., 2022; Garland & McGregor, 2020; McLoughlin et al., 2018; Payne, 2000). If singers are prone to copying novel songs, then exposing them to successful songs from other populations should elicit imitations (e.g., see Noad et al., 2000). In a playback study examining humpbacks' responses to familiar and unfamiliar songs, however, 71% of singers exposed to foreign songs swam away from the simulated immigrant, and no singers imitated the novel song (Darling et al., 2012). Actively avoiding innovative crooners (and thereby degrading auditory reception of their songs) is an odd reaction for singers that are supposedly attempting to memorize and/or evaluate the intricacies of any novel song features that they encounter.

**Figure 2**

*Proposed Processes that May Drive Concerted Changes in Humpback Whale Songs*




*Note.* (a) Recordings of singers within a population at any given time show that most are singing similar songs, a finding that is often cited as evidence that singers culturally conform to the most popular and innovative song variant. For change to occur in songs over time, it is usually assumed that one singer must introduce some modification to its song, either by improvising or making a copying error, after which all other singers vocally imitate that change, thereby maintaining conformity. Song change is thus viewed as being akin to fashion trends in humans. Singers are presumed to be able to memorize and reproduce all features of any new song or phrase they hear, and the one singer that directs all changes within a population is assumed to be the sexiest singer (the model). (b) Although singers in a population produce songs that are similarly structured, intra-individual acoustic variability in songs is comparable to inter-individual variability (i.e., individuals are not just repeating the "same" song, see Figure 1a). Cross-singer similarities could result from intrinsic constraints on song features (e.g., phrase templates, shown here as predictable shifts in the color spectrum) rather than from social conformity. If singers adjust song properties in response to similar ecological factors (including the vocal actions of audible conspecifics) following similar rules, then all singers within a population are likely to change their songs along similar trajectories (just as flocks of starlings converge in their movements when they murmurate), without requiring singers to either memorize other whales' songs or to learn to reproduce them through vocal imitation. In this alternative scenario, one influencer whale does not drive all song changes. Instead, all singers independently adjust their songs in reaction to similar ongoing events, leading to collective changes within a population.

Dramatic changes in song properties (called "cultural revolutions") are often cited as incontrovertible evidence of vocal culture in humpback whales (Botting et al., 2017; Garland & McGregor, 2020; Tyack, 2008; Whitehead & Rendell, 2014). Noad and colleagues (2000) noted that whales in the east Australian population began singing songs that matched those produced by the west population in earlier years, leading these researchers to speculate that east coast singers at some point heard and copied a small number of vagabond westerners, ultimately causing the western song to go viral. Later, Garland and colleagues (2011) reported that this same popular song spread easterly to populations throughout the South Pacific. They discovered that this kind of rapid song transformation was not a unique event. Instead, "cultural waves" of songs appeared to spread in this way every year for a decade, always moving from west-to-east. The most recent analyses of Australian songs show revolutions occurring every other year on average (Allen et al., 2018). This surfeit of "revolutions" (~50 over 15 years) has expanded speculations about when cross-population song sharing happens, with it now assumed to occur in feeding grounds or during migrations when singers from different populations are more likely to come into acoustic contact (Owen et al., 2019; Warren et al., 2020; Zandberg et al., 2021).

Garland and colleagues (2020, 2017, 2018) proposed that cultural revolutions in songs occur when a single singer innovates or hears singers from another population, whereas cultural evolution (more gradual change) results from copying errors. While intuitively appealing, this explanation immediately runs into problems accounting for observed song changes. First, if innovations drive cultural revolutions, then waves that spread unidirectionally across populations imply either that only western Australian singers are innovative or that improvisers not from west Australia are always ignored. Second, if more than one sexually fit singer in any population of humpbacks improvises or makes a provocative error, then this should lead to competing song/phrase types within that population. Fifty years of recordings have yet to reveal any evidence that such song battles occur in any population. Given that there may be thousands of singers in a population, it is highly implausible that only one whale would improvise novel songs or make popular mistakes.

Even if one is willing to accept that there might be a single innovator, invader, or errant imitator directing song changes in each population of humpbacks (and that singers can accurately predict which innovations/errors females will find attractive, etc.), the hypothetical "telephone game" proposed to drive song evolution/revolutions does not (and cannot) account for how singing humpbacks actually change their songs. In particular, if songs change through an accumulation of copying errors and/or imitated innovations, then regressions to phrases or songs produced in the past should be rare. On the contrary, many phrase "types" are abandoned only to reappear at a later date (Mercado et al., 2003; Winn & Winn, 1978), and several are shared by acoustically-isolated populations (Mercado, 2021; Mercado & Perazio, 2021b; Winn & Winn, 1985). Singers are not irreversibly (or arbitrarily) changing phrase structure. Instead, singers appear to renovate, refurbish, and re-use a fixed repertoire of phrases by flexibly adjusting the timing, duration, frequency content, and timbre of the units within those phrases.

The recent discovery that singing humpbacks located in different oceans produced the same complex song provides strong evidence against claims that singers are continuously imitating faddish song styles (Mercado & Perazio, 2021b). The vocal culture hypothesis predicts that the changes singing humpback whales make to songs are irreversible (Guinee & Payne, 1988), and lead to completely novel arrangements of units (Garland et al., 2022; Garland & McGregor, 2020). The chances that two innovative populations of imitative singers randomly converged on the same patterns and timing of 100+ acoustically complex units after centuries of independent cultural transmission are infinitesimal given that singers annually vary their unit repertoires and arrangements of units.

Evidence of continuous, unidirectional waves of "cultural revolutions" not only challenges claims that humpbacks innovate and imitate songs, it also calls into question past reports of song dialects across populations. Ever since Winn and colleagues (1978, 1981) first described singers as using dialects, researchers have cited cross-population song differences as further support for vocal culture in humpback whales (Darling et al., 2019; Darling & Sousa-Lima, 2005; Helweg et al., 1998; Payne & Guinee, 1983; Winn et al., 1981). Garland and colleagues' (2011, 2018) analyses show, however, that such population

differences between songs recorded in the same year can arise when the emergence of a "song type" in one population is delayed relative to its appearance in other populations. Consequently, differences in songs across humpback populations in a given year do not provide evidence either that singers adhere to local dialects or that they learn songs by listening to fellow singers. The fact that humpback whales from different populations typically do not produce the same songs in the same year simply shows that singers' transformations of songs are not globally synchronized.

## A New Perspective

There is no question that vocal imitation can contribute to vocal cultures in some species (e.g., Fehér & Tchernichovski, 2013; Hyland Bruno et al., 2021). Although singing humpback whales undoubtedly change their songs extensively within their lifespans (Guinee et al., 1983), and may respond flexibly to other singers (Cholewiak et al., 2018; Guazzo et al., 2020), or to other sound sources (Cerchio et al., 2014; Fristrup et al., 2003; Miller et al., 2000), there is no direct evidence that: (1) hypothetical wandering minstrels inspire other singers to follow their lead (Noad et al., 2000); (2) singers vocally imitate any song features; or (3) song dialects are present or relevant to humpback whales. The fact that humpbacks collectively change their songs in interesting ways over time similarly provides no direct evidence that either vocal imitation or cultural transmission contributes to those variations (see also Sperber, 2000). In contrast, the finding that culturally unconnected singers recorded in Hawaii and Puerto Rico converged on the same song form (Mercado & Perazio, 2021b) provides compelling evidence that cultural transmission is not necessary for "song sharing" to occur.

Cultural evolution was originally proposed to explain humpbacks' song variations because researchers could not conceive of any way that genes, the environment, or individual learning could lead to rapid synchronous changes within populations (Payne et al., 1983). Comparative studies over the past forty years have, however, revealed numerous ways that genetics, ecological factors, and asocial learning can cause groups of animals to collectively change their actions across multiple time scales (Laland & Evans, 2017; Laland et al., 2009; Whiten, 2019). For example, individual, innate reactions to local conditions can lead to convergent changes within a group, as is seen in schooling fish (Hemelrijk & Hildenbrandt, 2012; Parrish et al., 2002), howling wolves (Mazzini et al., 2013), murmurating birds (Hemelrijk & Hildenbrandt, 2011; Storms et al., 2019), and other complex adaptive systems (Carmichael & Hadzikadi, 2019). Such reactions can be coordinated within groups in ways that lead to systematic changes in behavior within and across generations without requiring individuals to imitate or learn the actions of others (Mercado, 2021; Sumpter, 2006). Recently, some have argued that any within-group behavioral conformity should be considered cultural (Neadle et al., 2017; Whitehead & Rendell, 2014), as long as the actions of individuals are influenced by those of conspecifics (e.g., increasing in frequency over time within the group). By this criterion, vocal contagion among crying babies on an airplane is a cultural phenomenon. Describing changing whale songs as an extraordinary cultural phenomenon (Garland & McGregor, 2020; Zandberg et al., 2021) achieves little scientifically if all this means is that humpback whales collectively change their songs in intriguing ways.

Green and colleagues (2011) proposed that rather than copying the songs of conspecifics, singing humpbacks might instead interactively adjust song elements (Figure 2b). For instance, singers producing songs at the same time in a particular locale might adjust properties of their songs to reduce mutual interference (see also Cholewiak et al., 2018), in a process similar to that employed by groups of echolocating bats (Jones & Conner, 2019). According to the coordinated adjustment hypothesis, cumulative changes to songs are driven by ecological factors (specifically, variations in the perceived soundscape) rather than by innovation or vocal imitation. One advantage of this hypothesis is that it can be directly tested by virtually introducing multiple lone singers to each other (e.g., by using two-way radio broadcasts transmitted with underwater speakers). The coordinated adjustment hypothesis predicts that bringing lone singers into acoustic contact should provoke them to change elements of their songs in ways that reduce possible interference. Developing hypotheses that can be experimentally tested is critical for identifying the

mechanisms that lead humpback whales to change their songs (Bandini et al., 2020; Mercado & Delong, 2001).

Researchers in the field of marine mammal science are wholly convinced that humpback whales routinely learn how to sing new songs by imitating other singers. As one reviewer put it, "It is difficult to review any paper that seriously disputes song copying in humpback whales. Where does one start? The evidence for song copying is overwhelming." As someone who accepted the vocal culture hypothesis for over two decades, I can understand why whale researchers might view any challenge to this interpretation as incredible. The job of scientists, however, is to go where the evidence leads, with a willingness to abandon failed hypotheses and a commitment to search for simpler explanations. To do otherwise is to follow in the footsteps of the Emperor's subjects from Hans Christian Anderson's famous fable, *The Emperor's New Clothes*, effectively ignoring the evidence and seeing what isn't there.

> *Once upon a time, winged denizens of the deep lured listeners to their intellective doom with their wondrous warbling.*
> *Everyone in the universities said, "Oh, how cultured are the songs of these creatures! And behold the complex weaving!"*
> *"But I don't see any culture," a little psychologist said.*
> *The scientists shivered, for they suspected he was right. But they thought, "The science has to go on." So they published more proudly than ever, as their colleagues held high the culture that wasn't there at all.*[1]

**Conflict of Interest:** I declare that I have no financial conflicts of interest with the content of this article.

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[1] Adapted from Hans Christian Anderson's "The Emperor's New Clothes"

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