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Report

Dynamic Horizontal Cultural Transmission of Humpback Whale Song at the Ocean Basin Scale

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Summary

Cultural transmission, the social learning of information or behaviors from conspecifics [1–5], is believed to occur in a number of groups of animals, including primates [1, 6–9], cetaceans [4, 10, 11], and birds [3, 12, 13]. Cultural traits can be passed vertically (from parents to offspring), obliquely (from the previous generation via a nonparent model to younger individuals), or horizontally (between unrelated individuals from similar age classes or within generations) [4]. Male humpback whales (*Megaptera novaeangliae*) have a highly stereotyped, repetitive, and progressively evolving vocal sexual display or "song" [14–17] that functions in sexual selection (through mate attraction and/or male social sorting) [18–20]. All males within a population conform to the current version of the display (song type), and similarities may exist among the songs of populations within an ocean basin [16, 17, 21]. Here we present a striking pattern of horizontal transmission: multiple song types spread rapidly and repeatedly in a unidirectional manner, like cultural ripples, eastward through the populations in the western and central South Pacific over an 11-year period. This is the first documentation of a repeated, dynamic cultural change occurring across multiple populations at such a large geographic scale.

Results and Discussion

Directionality of Song Propagation

Only male humpback whales sing [22], and in each population, they usually show strong conformity to a single song type containing the same themes sung in the same order at any one time [16, 17]. The pattern of the song evolves, sometimes rapidly, within any given population from year to year, but all singers maintain conformity [16, 17]. Song is arranged in a nested hierarchy: it comprises a number of "themes," each of which consists of a number of repeated "phrases." Phrases, in turn, consist of a string of individual sounds or "units" [14].

Here, using multiple populations within the western and central South Pacific Ocean, studied over an 11-year period, we document the rapid and repeated horizontal cultural transmission of multiple song types at the population level. During the breeding season (July–October), this region, stretching from eastern Australia to French Polynesia, contains several breeding groups of humpback whales (see Figure S1 available online). These groups are genetically distinguishable [23], and although interchange does occur, it is at a low level [24–27]. The groups are therefore thought to be either separate populations or populations that form a metapopulation.

Song types were grouped together into song "lineages" if the song was observed to evolve (through changes of units in or addition of units to existing phrases, or the addition and/or deletion of themes) from one song type into another. Each lineage was assigned a color name, and new songs that evolved from old ones within a lineage were assigned similar colors for names. The song types grouped into six different lineages: pink, black/gray, blue, red, yellow, and green. Within lineages, songs were not renamed (e.g., dark red turning to light red) until all of the original themes had been replaced over time as a result of cultural evolution.

Eleven different song types were recorded in the region from 1998 through 2008 (Figure 1). Eight different song types moved in an easterly direction, with four spreading entirely across the region from eastern Australia to French Polynesia (black, blue, dark red, and light red). Only a single song type (light blue) was recorded moving west (from French Polynesia to the Cook Islands). All songs are described in Table S1.

Song Type Evolution and Revolution

The pink song type was present in the central South Pacific populations of the Cook Islands and French Polynesia in 1998. It was the song previously documented off eastern Australia in 1995 and 1996 prior to being replaced by a new song from the western Australian population in 1997 [10], which we called the black song. The black song type was present for two to three years before undergoing changes, including the addition of four new themes, one of which split into three additional themes. Once this split occurred, we called it the gray song type because no themes from the original black song type were retained. This split and loss of the black themes did not occur in eastern Australia (1999) or New Caledonia (2000).

The dark blue song type, which contained none of the black/gray song themes, first appeared in eastern Australia in 2000. The blue song showed some similarities with the dark blue song and is likely to have evolved from it. The blue song type then became the most widely distributed in the region. The blue song had eight themes (Figure 2; Audio S1) and did not change substantially until 2006/2007, although it spread throughout the region during that period. It clearly evolved

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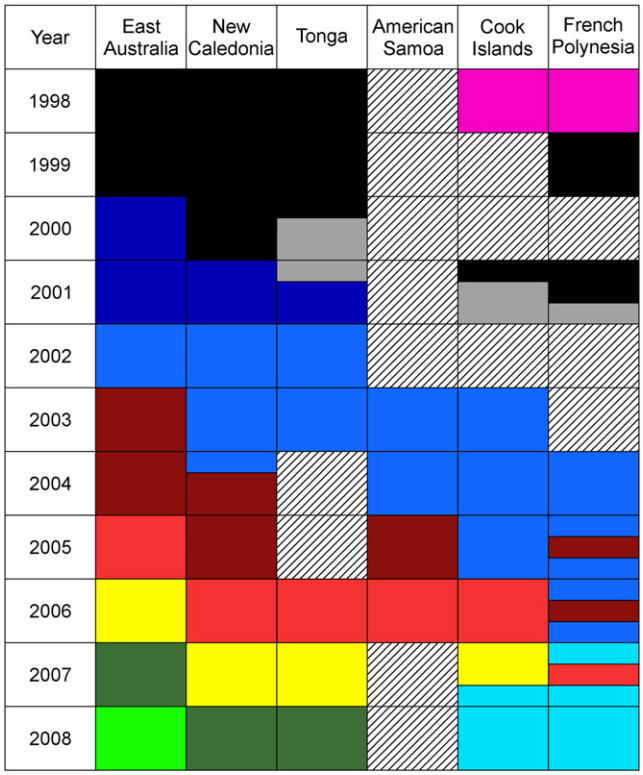

Figure 1. Song Types Identified in the South Pacific Region from 1998 to 2008

Populations are listed from west to east across the region. Each color represents a distinct song type; song type colors are as follows: black, gray, pink, dark blue, blue, light blue, dark red, light red, yellow, dark green, and light green. Two colors within the same year and location indicate that both song types were present. In these cases, the seasons are broken into three periods (early, middle, and late) to indicate when a new song type was recorded. Crosshatching indicates no data available. Descriptions of the typical units used in each theme are provided in Table S1, and sample sizes of the number of singers and the total number of song cycles for each location and year are presented in Table S2.

into the light blue song through the addition and deletion of themes and gradual substitution of units in two themes (Figure S2).

The dark red song type was a simple song with few units in each phrase. It consisted of six themes (Figure 3; Audio S2), and units were added to all themes as it evolved. The light red song contained six themes, three of which had clearly evolved from the original dark red themes (Figure S2). The yellow song type consisted of five new themes, none of which were shared with the light red song. The dark green song type contained four themes, and again, no themes matched those of the previous (yellow) song type. Finally, the light green song type that appeared in eastern Australia (2008) clearly evolved from the dark green song, as evidenced by the evolutionary progression of two themes.

Two types of song change thus occurred in this ocean basin. The first was progressive cultural evolution in which songs changed from one type to another within each population [15, 17, 28]. This type of song change has been clearly documented in other ocean basins, especially in Hawaii in the North Pacific [16], and most notably in a long-term song study from Bermuda in the Caribbean/North Atlantic [17]. Songs of some bird species change or evolve in a progressively cultural way through the accumulation of copying errors over periods of decades [3]; in other cases, rapid and continuous song learning and matching by conspecifics occur [13, 29].

The second type of song change documented in this study involved rapid replacement of a cultural trait, in which a novel song type appeared in each population and rapidly replaced the existing song type [10]. The replacement of the blue song type by the dark red song type in 2003 in the eastern Australian population demonstrates a rapid cultural replacement. This rapid replacement was mirrored in the New Caledonian population in 2004 and American Samoa in 2005. This change from blue to dark red was similar to the only previously documented cultural replacement or "revolution" [10], in which the eastern Australian 1995/1996 song (our pink song type) was rapidly replaced in eastern Australia in 1996/1997 by a novel song from the western Australian population (our black song type). Indeed, the black song type can now be tracked from the western Australian population in 1995 to French Polynesia in 2001, a cultural signal spanning two ocean basins and seven years.

Our study shows that the cultural revolutions from pink to black and from blue to (dark) red were not restricted to eastern Australia but radiated eastward across the region, with the latter occurring in different places at different times over a four-year period. Although these revolutions were clear, the types of changes that occurred from black/gray to (dark) blue, light red to yellow, and yellow to dark green were less clear. We suggest that the change from black/gray to (dark) blue represents a cultural revolution because of the lack of shared themes or any other similarity, although data were limited to the western populations. The yellow song type also could not be linked to either the previous (red) or following (green) lineages. Thus, these transitions may represent either rapid evolutionary changes that have not been well traced or genuine revolutionary changes.

Easterly Cultural Transmission

Regardless of whether the song changes in any one population were evolutionary or revolutionary, it is clear that songs changed and radiated consistently from west to east in a series of "cultural waves." The unidirectionality of the song spread is striking. Most song types were first documented in the eastern Australian population and spread to New Caledonia and Tonga, and then on to American Samoa, the Cook Islands, and finally to French Polynesia. This dynamically changing display produced a patchy checkerboard pattern of song types (behavioral variants or phenotypes).

One possible explanation for the eastward movements of song types is that the eastern Australian population is the largest in the region [25, 30] and its influence on the other populations, whether by emigration of individuals or contact on shared migration routes [24–26, 31] (song only travels effectively for tens of kilometers at most [28]), is thus likely to be greater than the influence of the other populations on the eastern Australian population. However, photoidentification studies of individuals in the region have shown low levels of interchange, mainly between adjacent populations, particularly between eastern Australia and Oceania [26], but without any clear directionality in such movements [27]. Conversely, these long-term photoidentification studies have shown a high level of site fidelity for each population in the region [24–27]. On the one hand, this suggests that song transmission is unlikely to be explained by the movement of individuals from eastern Australia eastward. On the other hand, Noad et al. [10]

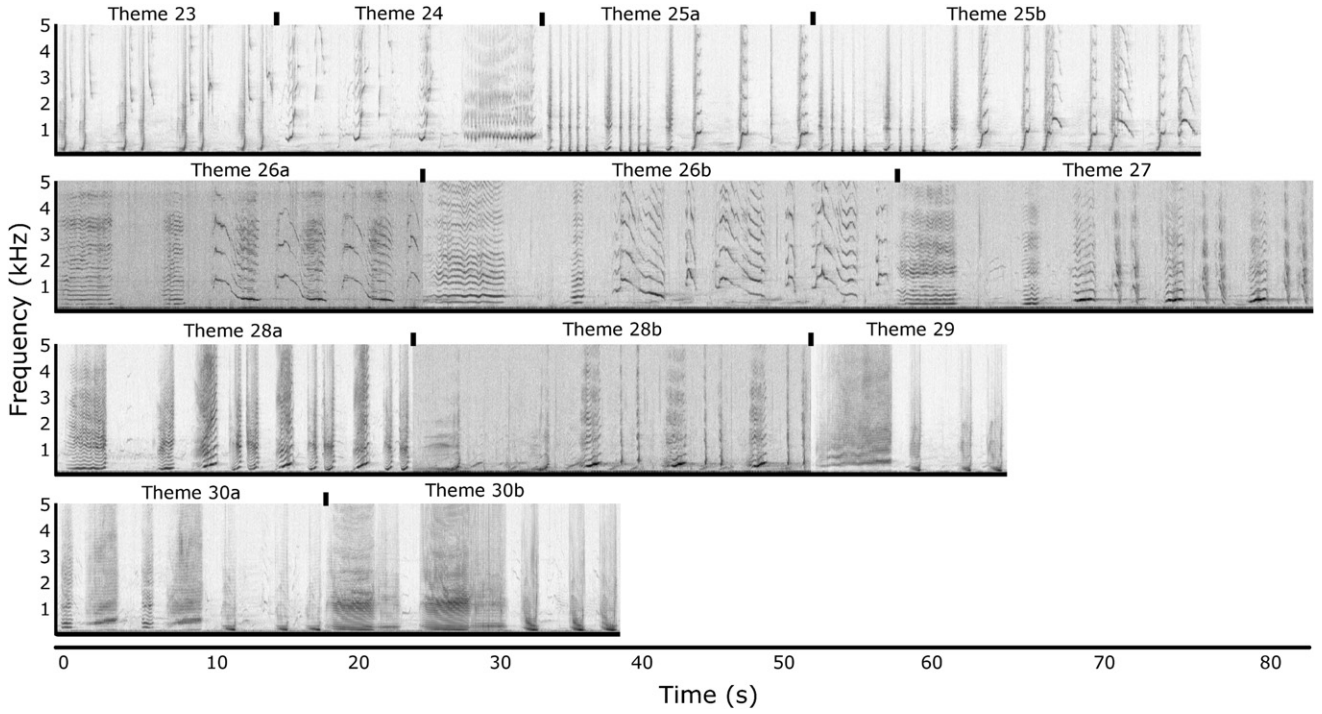

Figure 2. Spectrographs of the Blue Song Type (Themes 23–30)

A representative phrase for each theme is shown. Note that some themes contain "a" and "b" phrases. These were all classified as the blue song (see Figure S2 for the evolutionary progression of theme 29). See also Audio S1.

showed that a song type, introduced at a very low initial prevalence, could then be rapidly adopted by an entire population. If only a few individuals are required to enter a population to induce a song change, then it is possible that previous photoidentification studies would not have had the resolution to capture such events.

The other possible mechanism for song exchange is through shared migratory routes [21, 24, 25, 31]. Unfortunately, we know very little about humpback whales' distribution in the Southern Ocean or their migratory paths to and from their breeding grounds. Although the mechanisms of transmission via social learning in humpback whales are unclear, Noad et al. [10] showed that the majority of singers in the eastern Australian population changed their song completely from one type to another within two to three months, suggesting that individual males change their songs rapidly. If this is the case, migratory routes would not need to overlap extensively, because minimal contact may be all that is required for song learning.

Certainly, the rapid speed at which song types spread from one population to the next with high fidelity precludes a genetic explanation for this phenomenon. This is not to say that there is no underlying genetic basis for song, but that the observed pattern of song types spreading among populations in the region is clearly indicative of cultural transmission. An ecological basis for this pattern is also unlikely. Humpback

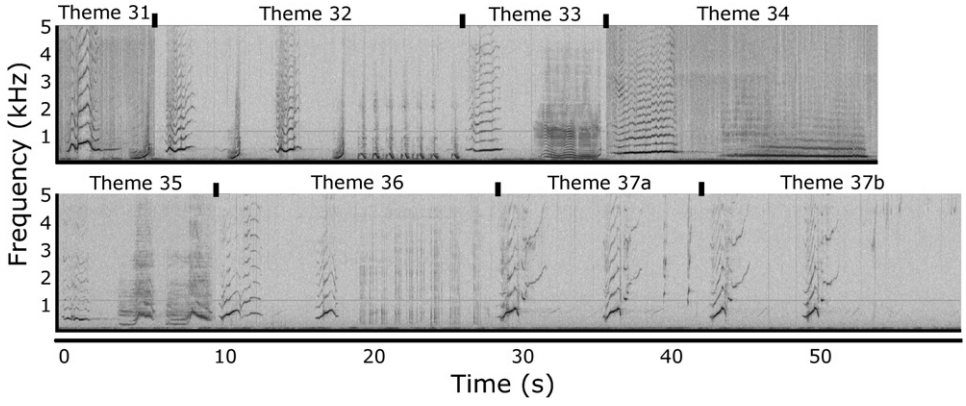

Figure 3. Spectrographs of the Dark Red Song Type (Themes 31–37)

A representative phrase for each theme is shown. Note that theme 37 contains "a" and "b" phrases. These were all classified as the dark red song (see Figure S2 for the evolutionary progression of themes 36 and 37b). See also Audio S2.

whales in different populations and hemispheres often sing vastly different versions of the display even when breeding areas may have similar ecologies (e.g., islands formed by seamounts) [21], whereas in this study, the same song was used by populations with breeding grounds with entirely different ecologies (e.g., eastern Australian shallow shelf waters versus islands formed by seamounts).

Conclusions

The example of cultural transmission of behavior we have presented here provides a clear pattern of complete population-wide changes that were replicated in multiple populations over a vast geographic region. The level and rate of change is unparalleled in any other nonhuman animal and thus involves culturally driven change at a vast scale. In addition, at least one of the song types studied here was transmitted between two different ocean basins [10]. The vocal linkage between the Indian and South Pacific Ocean basins raises the question of how far a single song type can be horizontally transmitted. Investigating the underlying mechanisms of song evolution may yield powerful insights into the transmission of cultural traits and the evolution of culture and plasticity in sexually selected traits. Humpback whale song is unique because intense conformism to the current (song) norm is coupled with high plasticity in the trait [32]. Why both plasticity and conformity might be selected, how these interact with sexual selection, and how cultural evolution influences both are intriguing questions in need of attention.

Experimental Procedures

All methods are explained in detail in Supplemental Experimental Procedures.

Field Locations and Data Collection

The six main field sites corresponded to the known major migration and breeding grounds within the western and central South Pacific region (Figure S1). Songs were recorded using a variety of hydrophones suspended from boats by multiple researchers across the region from 1998 to 2008.

Song Unit Transcription

Songs were viewed as spectrographs, and all units in a song session were transcribed by human classifiers based on the visual and aural qualities of the sound as in multiple other published humpback whale song studies [10, 14–17, 21, 28]. Each unit sound type was assigned a name. A subset of units (400) was quantitatively measured, and a discriminant function analysis with cross-validation was undertaken. This correctly classified 80% of sounds, ensuring consistent categorization [33].

Defining Songs and Song Types

A song was defined as any complete cycle of themes with no repetition of a theme [17]. We assessed the similarity of songs and grouped all songs of the same type together through the matching of the content and sequence of themes. We identified 67 themes that were assigned to 11 song types. Three naive observers correctly classified over 94% of themes in a blind test of the reliability of our classification procedure.

Differences between song types were usually striking; example spectrographs of the distinctly different blue and dark red song types are shown in Figure 2 and Figure 3, respectively. Evolution of song types occurs through progressive change to units (shown in Figure S2 for both song types), phrase composition, and the insertion or omission of themes [15–17, 28]. Evolutionary changes in themes are easily recognized by observing changes at particular positions in the song and illustrate the connection between the themes and thus the song types.

Each song type was assigned a color name. If the song evolved into a new song (where all the original themes had evolved into new themes or disappeared), it was named a different shade of the original song's color (e.g., dark green changed to light green) to show that they were distinct but related; otherwise, a clearly different color was assigned to the new song. The typical units used in each theme and sample sizes are described in Table S1 and Table S2, respectively.

Supplemental Information

Supplemental Information includes two figures, two tables, Supplemental Experimental Procedures, Acknowledgments, and two audio files and can be found with this article online at doi:10.1016/j.cub.2011.03.019.

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