The Progressively Changing Songs of Humpback Whales: A Window on the Creative Process in a Wild Animal

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Abstract
Male humpback whales (*Megaptera novaeangliae*) sing long, complex songs in tropical waters during the breeding season. At any one time all the whales in a population sing the same song, which differs significantly from songs of other populations. The song of each population evolves continuously, progressively, and so rapidly that nonreversing changes can be measured from month to month in a singing season. Such changes, which affect the songs at all levels, seem to arise through improvisation and imitation rather than through accident or as conveyors of information. The greatest amount of change appears when singing is most pervasive and the effort of each singer is most intense. A study of humpback songs over thirty-two years in two isolated whale populations provides information about the underlying rules of structure and kinds of changes whales are selecting. Several examples of change within two- and five-year periods are presented. Rhymelike structures occur in songs that contain much thematic material, perhaps serving as a mnemonic device in the context of a rapidly changing oral culture. We speculate that sexual selection is the driving evolutionary force behind song changing.

Some decades ago I was involved in an extensive study of the songs of humpback whales. My focus was on the long, complex, repeating patterns of sounds as phenomena in themselves. Yet as an amateur musician I kept wondering whether what I was hearing might be relevant to a consideration of the biological origins of human music. It was interesting to find "musical" similarities in the creative processes and products of two mammals whose lives are as different from one another as those of whales and humans. Many species that are genetically and behaviorally closer to humans or to whales than they are to one another do not sing at all, yet singing appears in these two species as a complex and flexible social behavior with significance to both singers and listeners.

Humpback whales are intermediate-sized baleen whales, 4 to 5 meters long at birth and reaching 17 meters in length in adulthood. Their Latin name, *Megaptera novaeangliae* ("large-winged New Englanders"), refers to their long white pectoral fins (5 meters long in adulthood) and to the northern center of one of their migration routes. In fact most if not all major ocean basins contain humpback whales. They feed in high latitudes during the summer months and migrate to tropical or semitropical waters, where some breed and others, having gestated for eleven to twelve months, give birth. North Pacific humpback whales summer in Alaskan waters and winter in a number of tropical areas, including the Hawaiian and Reveillagigedo Islands. North Atlantic wintering grounds include Bermuda and several Caribbean banks.

During the roughly five months of their stay in the tropics, male humpback whales sing songs that function in maintaining floating territories
and dominance hierarchies, aspects of male competition during the season of courtship (Tyack 1981; Darling 1983). It seems likely that the songs also attract females, but this remains a matter of speculation, for although human observers have spent thousands of hours in the vicinity of humpback whales, nobody has yet observed them mating. The whales' acoustic behavior is easier to document, as sound travels well under water, and under calm conditions a song is powerful enough to be audible over thousands of square kilometers in favorable conditions (Christopher Clark, personal communication). If one has a hydrophone and a taperecorder, one can spend a day in a boat from which the only view of whales is an occasional distant spout, and come home with excellent recordings of their acoustic displays.

Over the course of fifteen years I examined more than 600 whale songs with a number of colleagues, including Roger Payne, Peter Tyack, Linda Guinee, and Jan Heyman-Levine. We and others, particularly Frank Watlington, recorded the songs over thirty-two years from whales in North Atlantic and the North Pacific humpback populations. We summarized most aspects of our comparisons of the songs in three papers (Payne, Tyack, and Payne 1983; Payne and Payne 1985; Guinee and Payne 1988) that give further details supporting the material I summarize, and here that are also the source of all the illustrations.

Humpback whales' songs are long, highly structured sequences of sound that repeat hour after hour, often without a pause, even when the singer surfaces to breathe. They vary in length, usually lasting between eight and sixteen minutes (range 5 to 35 minutes). Each song includes an extraordinary assortment of notes, or units. These vary in frequency between 30 and 4000 Hz, and in length between 0.15 and 8 seconds; in harmonic structure they range from pure tones to tone bursts, and they show much variety in contour. Figure 9.1 shows how these units are organized into repeating groups or phrases. All the phrases of one sort are grouped together and constitute a theme. A song contains ten or fewer themes that proceed in an invariant order and repeat, often without a pause. A series of songs uninterrupted by a pause of more than a minute is a cycle. The longest song cycle on record lasted 21 hours (Howard Winn, personal communication).

The most flexible aspect of humpback song structure has to do with the number of phrases in each theme. This varies even in the successive songs of a single whale. We refer to songs in which the same kind of material appears in the same sequence as "the same," even if they differ in length due to different amounts of phrase repetition.

It is not easy to record whale songs for study, because one rarely hears a whale singing alone. Usually we heard several or many voices simultaneously, overlapping randomly and sometimes producing the
Figure 9.1
Diagram of hierarchical structure of all humpback whale songs, using a tracing of a spectrogram. Times given are rough indicators. Vertical lines are inserted between phrases. (From Payne, Tyack, and Payne 1983.)
cacophony that New Zealand whale listeners refer to as the barnyard chorus. When we separated out the various voices in such a chorus we discovered all the whales were repeating the same phrases and themes in the same order, but not in synchrony with one another.

When we expanded the study to include whales in more than one population, we discovered that the songs in different populations were similar in structure but quite different in content. When we expanded it to include more than one singing season, we discovered that in each population the songs were continuously and rapidly changing. Thus humpback whale songs were subject to two sources of change: geographical, leading to between-population dialects, and temporal, leading to within-population drift.

On the hunch that the processes involved in drift might reveal something about the innate sources of innovation—perhaps if I were bolder I would use the word “composition”—I devote the rest of the chapter to this phenomenon. Over the course of a few singing seasons, all elements in the song of a humpback whale population change little by little, each at its own rate. Basic units change in frequency, contour, duration, and the ways they are organized to make phrases. Phrases change in the numbers and types of units they contain and in their rhythmic patterning. Themes gradually occupy a larger or smaller percentage of the song on average, for in spite of small-scale variability, there are also large-scale trends in repetition. After some five or ten years, every theme is either much changed as a result of many little changes, or it has become obsolete and dropped out of the song, or both. At the same time, new phrase types have been introduced, imitated, and developed into new themes. Usually new material arises organically in the form of transitional phrases that merge the qualities of phrases in adjacent themes, but from time to time new material seems to arise de novo.

Figure 9.2A and B shows a typical humpback whale song recorded near the Hawaiian Island Maui in March 1977 and another recorded from the same place in March 1978. The changes we measured in each of several hundred songs from those seasons are characterized in these examples. In the earlier year the song had nine themes, one of which was often omitted; in the later year only seven themes were heard. Phrases in the earlier song tended to be shorter than those in the later year, with a different mechanism of phrase lengthening in different themes. Some showed increases in the length of the units, whereas in others the number of units increased.

Figure 9.3 shows the evolution of the phrase structure in one theme in that song (theme 5) over five successive years. In the first subphrase of each phrase we see the splitting of two units into four, the gradual lengthening of these units, and their increased separation in pitch. In the
second subphrase we see an increasing number of grunts over time. As the result of these processes, the whole phrase grew progressively longer throughout the five years. Figure 9.4 presents these changes statistically and shows that they contributed to changes on a larger scale that were simultaneously subject to other changes. The trend for phrase lengthening continued progressively throughout both years, for instance, but phrase repetition decreased in the second year, with the result that the theme tended to be shorter early in the 1978 recording season than it had been in the last months of 1977.

Meanwhile, theme 6 was undergoing a different sort of change that proceeded rapidly enough to be measured on a monthly basis in the singing months of 1977. The replacement of “r’s” (rising units with a sustained final tone) by “j’s” (quick upward-sweeping units) is shown graphically in figure 9.5 and statistically in figure 9.6.

All the other themes were simultaneously changing as well, each in its own way. Changes in theme 7 were based on substitution of phrases rather than of units. We found four common and two uncommon alternate phrase types, which we classified by applying three criteria to the first subphrase (figure 9.7). There was steady progression of alternates (a change at the level of the theme) coupled with the dropping out of the theme (a change at the level of the song; figure 9.8).

Our analysis eventually included all the phrases from all the songs we collected from three decades in North Atlantic and Pacific humpback populations. The results suggest that the whales have an ever-expanding number of ways to modify the structure of their notes, phrases, and themes. Each theme continually changes in its own way and at its own ever-changing rate, apparently as the consequence of decisions (whether conscious or unconscious) that are shared by all the singers. At any given time all the singers seem to agree which themes are stable and which are changing. For those that are changing they agree as to which aspects are changing and which are not, and how and to what extent they are changing.

As biologists we ask, what accounts for and/or drives these rapid changes? A clue to the answer lies in the fact that during the six months on the feeding grounds, when there is very little singing, the song hardly changes: early songs on the breeding grounds are similar to those last heard in the previous season. It is in the middle of the season, when the number of singing whales is largest and the effort of each one is most intense, as reflected by the durations of song sessions, that songs change the most. Thus the changes appear to be not a consequence of between-season forgetting, but a natural, active part of singing—part of a display.

Do these changes contain information about some aspects of the environment that are significant to whales? Probably not, as their timing
Figure 9.2
Tracings of spectrograms of representative songs from March 1977 and 1978. We selected songs that contained all possible themes. In 1977, theme three was rare. Although the sample song shown here omitted it, it was included in the next song sung by that same whale. The star-in-circle symbol in the tracing indicates where theme three was placed when it was sung. The two phrases of theme three shown under the song were produced by the same whale in the song following the one fully traced here. The tracings omit all extraneous sounds (e.g., ocean noise such as ships, other whales, underwater echoes, etc.) as well as harmonics. Pulsive sounds, which on the spectrograms showed dense harmonics, are represented diagrammatically by closely spaced vertical lines, whose spacing does not necessarily reflect the repetition rate of the pulses. (From Payne, Tyack, and Payne 1983.)
Figure 9.3
Sample phrases showing the evolution of theme five over five years. The units changed in frequency, duration, spacing, configuration, and numbers, and the phrases changed duration gradually. (From Payne, Tyack, and Payne 1983.)

(other than of the intensity of the singing itself) does not coincide with natural cycles that affect other aspects of whales' behavior, nor do they repeat. Like improvisation in human music, changes seem to be generated by an internal process, and as in music, the imitation that then occurs reveals listening and learning. Song changing in whales seems to be a clear example of cultural evolution in a nonhuman animal.

Our general understanding of biological forces that drive stylistic changes is that an individual who introduces an innovation gains some advantage from being different. However, an innovation may not be attractive if it is too different from the norm. Human psychology has a term describing the ideal degree of change that an innovation should have if it is to spread and set a new vogue: optimal mismatch. For a novelty to be introduced into a cultural trend, it must have a certain balance of conformity and originality.

With this in mind I found it puzzling that an examination of the songs of the few individual whales we had repeatedly recorded in different months and seasons did not reveal any stylistic leaders. At each interval
Figure 9.4
Some changing parameters of theme five over two singing seasons. Each bar represents a thirty-one-day mean for the parameter being measured (see caption for Figure 9.6).
A: mean number of units per phrase in each song session.
B: mean phrase duration in each song session.
C: mean number of phrases per theme in each song session.
D: mean theme duration in each song session.
E: percentage of song occupied by theme five.
Dashed lines indicate means when a small number of very aberrant songs were included in the calculations. Vertical lines indicate standard errors. (From Payne, Tyack, and Payne 1983.)
we found that each identified singer had changed his song about as much and in about the same ways as all the other singers in the population. Why change so fast and sophisticatedly if everyone else is changing at the same rate and in the same ways? In my opinion, lack of an answer suggests that the scale of our sampling system was inappropriate. Had we managed to collect many songs on a daily basis from more than a few known singers we might have found that leaders do in fact exist, and are imitated so rapidly that their moment of innovation did not show up in our analysis. Then we would have suspected a positive relationship between aspects of their innovation and their success in mating. Biologists have studied a variety of animals in which males indulge in displays that are not in themselves functional: these persist if females prefer to mate with the males who exhibit them.