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1. Progressive Changes in the Songs of Humpback Whales *(Megaptera novaeangliae)*: A Detailed Analysis of Two Seasons in Hawaii

Abstract

Previous studies have shown that humpback whales sing long, complex songs which are shared by all animals on the same calving ground but which change with time. The present study analyzes in detail the process by which the rapid and synchronous changes throughout two singing seasons in Hawaii occurred. For purposes of statistical analysis, each season is divided into six equal periods. 151 songs from 1976-77 and 159 songs from 1977-78 are dissected and compared in terms of the duration, number, frequency, spacing, and configuration of units, phrases, themes, and songs. The mean results from all measurements in each period are compared to those from other periods, revealing dramatic monthly evolution following set rules of change. Substitution, omission, and addition occur at different rates in different themes, but at any one time all songs are similar.

The mechanism by which the whales achieve this, and the adaptive significance of such an elaborate feature of a display remains unclear. Little change occurs between the form of songs at the end of one singing season and the start of the next (six months later), discrediting the theory that forgetfulness during the months on the feeding grounds (where singing rarely occurs) might be the main source of song change. Major trends of song change in one year do not repeat in the next, thus the changes may be thought of as primarily cultural rather than being linked to natural rhythms or periodic phenomena. A classification of all animal songs based on how variety is introduced is proposed, in which humpback whales fill a missing link between some birds that increase their repertoires all their lives by mimicry, and human beings, who create songs *de novo*, without confining

themselves to the reworking of existing material, as humpbacks do.

Introduction

While on their breeding grounds, humpback whales (*Megaptera novaeangliae*) show an unusual vocal behavior: they sing long and complex songs (Payne 1968, 1970; Payne and McVay 1971; and Winn, Perkins, and Poulter 1971). Humpback whales in different oceans sing different songs (Payne 1978) even though at any one time and in any one area, all individuals sing similar songs (Payne 1978; Winn and Winn 1978; Payne and Payne in press). However, whales in each broad area of ocean (perhaps even over entire oceans) change their songs together over time (Winn and Winn 1978; Payne and Guinee 1983).

Large scale progressive changes were observed in humpback songs from Bermuda in a sample containing 13 of the 18 years between 1957 and 1975 (Payne and Payne in press). In all but one year, the songs were collected only in April and May. At any given moment, all singing whales sang the same version of their song, but after a year or more, that version had disappeared and was replaced by a new version. As time went on, the song became increasingly different from the earliest version recorded. The extent of the changes from one year to the next varied, but in times of rapid change, it only took a few years for every part of the song to be altered beyond recognition.

It is inconceivable that such rapid and complete turnover of the song material could reflect genetic changes. Guinee, Chu, and Dorsey (1983) show that the explanation is not to be found in a turnover of individuals, for the songs of individuals change just as the songs of the group do. New variations in the song must be transmitted by learning. The progressive changes in whale song can thus be seen as a form of cultural evolution, in the sense that the song is a learned trait which evolves.

When we started the research reported here, we were testing a simple hypothesis for what caused the observed progressive changes. Our own experience and that of others indicates that during the summer months when the whales are on their feeding grounds, singing is extremely rare (pers. comm. with P. Beamish, E. Guthrie, D. McSweeney, J. Perkins, W. Schevill, W. Watkins and H. Whitehead). We know of only three recordings of more than a few isolated sounds from feeding grounds (McSweeney and Payne in prep). It therefore seemed reasonable that the whales might forget some details of their complex song during their almost silent summers. Upon returning to their breeding grounds in the following winter, they might piece together a new song out of whatever they remembered. The result would be a

modified version of the old song, which would hold throughout the singing season. Through this mechanism, humpback song would evolve from year to year.

The Hawaiian Islands provide ideal conditions to test this hypothesis while examining the process of song change. Because there are humpbacks in Hawaiian waters for six months during the singing season, one can record throughout the time. Further, the waters on the lee side of the Hawaiian Islands allow recording from small boats during most days of the season.

Our first Hawaiian recordings were made in the 1975-76 singing season. In 1976-77, we recorded throughout the full season, and we have continued making season-long samples each year through the 1981-82 season. This paper reports the results of detailed analysis of recordings from the first two complete singing seasons (1976-77 and 1977-78).

It provides evidence that the changes in song are not simply due to forgetfulness between singing seasons. Most changes did not occur between seasons. Instead, they occurred during the time when the whales were singing, developing their songs methodically in measurable steps. Furthermore, the types of change varied from season to season, and so could not be attributed to repeating seasonal factors.

We know of no other animal where whole populations introduce such complex, rapid and non-reversing changes into their vocal displays, abandoning old forms and replacing them with new. It is not clear what selective advantage would be obtained by changing songs continuously.

Materials and Methods

All but two of the humpback song sessions discussed in this paper were recorded off the leeward coast of Maui in the Hawaiian Islands (the two exceptions were recorded approximately 150 km away, near the big island of Hawaii). Humpbacks are sighted in the Hawaiian Islands from mid-November to mid-May. Singing is heard sporadically, becomes almost continuous, and dies out again during those six months, in the shallow waters bounded by the four islands of Maui, Kahoolawe, Lanai, and Molokai. We made recordings in daylight from a 16' motorboat using several tape recorder and hydrophone combinations, in all cases with a frequency response uniform within 5 db for frequencies between 50 and 10,000 Hertz. In order to avoid recording in the same area on consecutive days, we left our base in Lahaina, Maui each day on a different bearing. We would periodically listen for song until we got a good enough signal-to-noise ratio from one singer to record its song

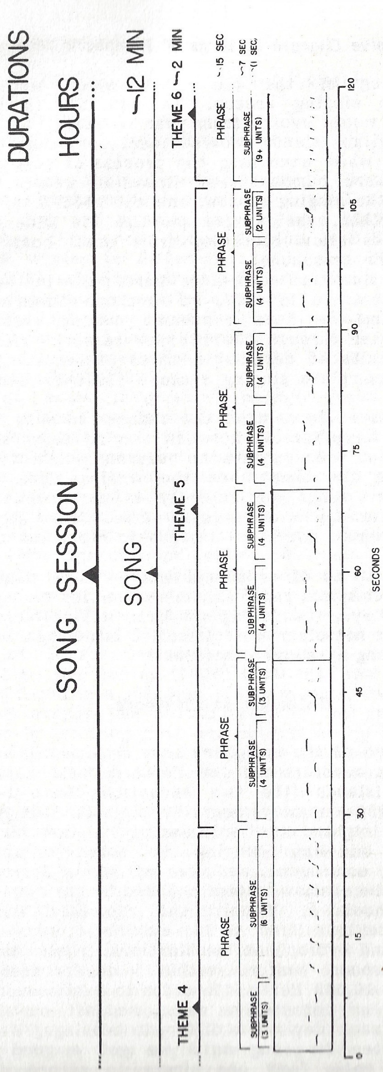

Figure 1. Diagram of hierarchical structure of all humpback whale songs, using a tracing of a spectrogram to illustrate. Times given are rough indicators.

without interference from other singers or from ambient ocean noise.

During the 1976-77 season (19 December 1976 to 18 May 1977), 111 hours of recordings were made. During the 1977-78 season (25 November 1977 to 27 April 1978), 121 hours of recordings were made. In order to obtain these recordings, observers spent over 1000 hours in boats actively searching for, observing, photographing (for identification of individuals) and recording humpbacks.

Upon return from the field, spectrograms of all good recordings were made using a Spectral Dynamics SD-301C real time analyzer, a Tektronix 604 monitor oscilloscope, and a 35mm Nihon Kohden oscilloscope camera. Frequency was displayed on the y-axis of the oscilloscope. The sweep was held stationary and the film (actually a continuous strip of 35 mm photographic paper) was moved parallel to the x-axis at a rate of 0.5 cm per second. The sampling rate was once per 10 msec and sound intensity at each point of the frequency spectrum was roughly indicated by modulating the intensity of the electron beam. This spectrum intensity was logarithmic. Frequency display was linear; the analysis range was from 40 - 2500 Hz; and the effective bandwidth was 10 Hz.

The resulting reels of photographic paper were developed, cut into strips 60 cm long and mounted in sequence on large sheets of paper, each sheet displaying from 2 to 6 songs. Songs that were incompletely recorded (due to temporary electronic or mechanical disturbances or the need to change tape) were not included in the analyzed songs. However, complete themes and their component phrases from these song fragments were counted when tallies of total themes and phrases were being considered. (Terminology is explained in Figure 1). A total of 151 complete songs from 1976-77 and 159 complete songs from 1977-78 made up the final sample of analyzed songs. Twelve sessions contained aberrant songs. The study of these songs was carried out by Frumhoff (1983).

The duration of songs, themes, and phrases was measured directly from the strips of photographic paper (spectrograms) with a ruler or with dial calipers when unit durations were being considered. A set of fixed definitions of different categories of units, phrases, and themes was made. This allowed us to make an objective analysis of any song; to make counts of specific elements of which it was composed; and to subject the results to statistical tests.

All themes and phrases and many individual units in each song were categorized both by inspection and by measurements of the spectrograms. Only a few examples of each type of change which we discovered will be presented in this paper. Over 5000 hours were spent making and analyzing the spectrograms.

Table 1. Distribution of sample of analyzed songs. "Periods" are consecutive portions of the singing season 31 days long. Periods having the same number occur at the same time each year.

	1976-77			1977-78		
	# Ses-sions	# Songs	# Songs/Session	# Ses-sions	# Songs	# Songs/Session
PERIOD I (Nov 14 - Dec 14)	-	-	No Data	7	20	1,8,2,1,4,2,2
PERIOD II (Dec 15 - Feb 14)	4	23	5,4,11,3	9	28	1,1,7,1,2,12,1,1,2
PERIOD III (Jan 15 - Feb 14)	9	36	3,2,5,6,4,6,2,4,4	10	45	5,4,3,6,10,5,1,5,1,5
PERIOD IV (Feb 15 - Mar 17)	12	45	1,4,3,2,6,4,1,6,1,11,1,5	5	19	1,4,2,8,4
PERIOD V (Mar 18 - Apr 17)	4	19	7,7,2,3	15	47	5,1,1,5,2,4,5,1,2,2,5,3,1,7,3
PERIOD VI (Apr 18 - May 18)	11	28	4,3,3,2,4,2,2,1,1,5,1	-	-	No Data
TOTAL	40	151		46	159	
TOTAL (BOTH YEARS)	310 Songs 86 Song Sessions					

In order to analyze statistically the changes that we measured, we divided each singing season into six, 31-day time periods. The placement of the six successive periods within the 1976-77 singing season was adjusted so as to distribute recording days (see Table 1 for the number of songs recorded each day) as evenly as possible within each period. This same distribution of periods gave a good fit to the days on which we recorded during the 1977-78 singing season. As a result, periods indicated by the same number in different years cover exactly the same days of the year. Table 1 gives the starting and ending dates of the six periods. It should be noted that we failed to get any recordings in all of the first period (Period I) of the 1976-77 season and during most of the last period (Period VI) of the 1977-78 season. In other years, a few whale songs have been heard and recorded in Hawaii both earlier and later than the time encompassed by our six periods, but the great majority of the singing occurs within them.

Mean values of several parameters of themes and songs were calculated for each of the six time periods. Unless otherwise indicated, these "period" means are means of means (since they are the means of the mean values for each song session rather than for each song). We chose to base our analysis on song sessions, rather than on songs, so as to give equal weight to the contributions of different whales. During the years this research has been carried out, we have had the benefit of knowing the identifications of many humpback whales thanks to the concurrent work with this same population by Darling, Gibson, and Silber (1983). They identified many singing humpbacks by photographing distinctive pigmentation patterns on their flukes (see Katona, Baxter, Brazier, Kraus, Perkins, and Whitehead 1979 for a description of this technique). Out of a large number of singers identified, Darling has resighted very few (see also Guinee et al. 1983). We believe, therefore, that most of the song sessions recorded come from different whales.

Results

Song Structure

The structure of humpback songs recorded from Bermuda in 1961-64 was described by Payne and McVay (1971) and is summarized diagrammatically in Figure 1. All songs we have studied from all times and places adhere to this format. Songs are composed of a series of discrete notes, or units. We define units as the shortest sounds in the song which seem continuous to the human ear.[1] Small repeated groups of units are called phrases. Phrases are usually uniform in duration. Many phrases consist of two

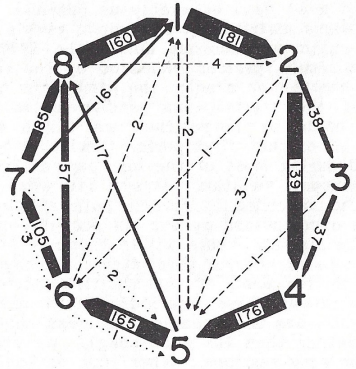

Figure 2. Transition probabilities from one theme to another in 1976-77. (All transitions from one theme to any other theme are included). The relative thickness of the arrows pointing from one theme to the next reflect the number of transitions from one theme to the next. The three types of reversal of theme order (7-6, 7-5, 6-5) are shown as dotted lines. These lines, as well as the dashed lines, are indicating transitions that were so rare that the arrows had to be drawn disproportionately thicker for the sake of visibility. The strictness with which whales maintain theme order, even when omitting themes, is obvious. Numbers indicate how many transitions of each type occurred in our 1976-77 sample.

subphrases, which may in themselves contain repeated sounds. All phrases of one kind make up a theme. Themes may contain any number of phrases and so their length is extremely variable.

We say a whale is singing when we hear groups of units repeated. A song is a series of different themes given in a predictable order. Successive songs are sung without pauses between them, and we refer to all songs in an unbroken sequence as a song session. The longest continuous excerpt from a song session which we recorded (in this case from an identified individual) lasted 10.5 hours; however, the complete session was longer, as the whale was already singing when we found it and still singing when we were forced to leave it.

Themes occur in an invariant order. This is a powerful constraint and makes the song highly ordered. Figure 2 shows the transition probabilities from one theme to another during the 1976-77 season. While it is obvious that deletions of one or more themes were common, there were only 5 reversals in the 1196 transitions. All but one of these reversals came from a single, highly aberrant song session which was highly aberrant in other aspects as well (Frumhoff 1983).

Evolution of the Song: Gradual Modification of Themes

General changes observed in two years. In this section we will give a preview of the kinds of gross changes we have observed and measured. In the following section we will present a more detailed analysis of our whole data set in terms of certain easily measured parameters.

Figure 3 shows a spectrogram of representative Hawaiian humpback songs from the middle of the 1976-77 and 1977-78 seasons, identifying the themes from each year and illustrating the differences between March songs of one year and the next. The tracing omits all extraneous sounds (e.g., ocean, ships, other whales, underwater echoes). Vertical lines running through the spectrograms from top to bottom of each one designate divisions between phrases.

Figure 4 presents a sample phrase from each theme of seven representative songs that were recorded at the beginning, middle, and end of the 1976-77 and 1977-78 singing seasons. It demonstrates the ways each theme changed during the two years.

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[1] Some units can be subdivided into subunits: sounds which, although they sound continuous to the human ear, can be seen on a spectrogram to be discrete. Grating or rasping sounds, composed of pulsive subunits, are examples.

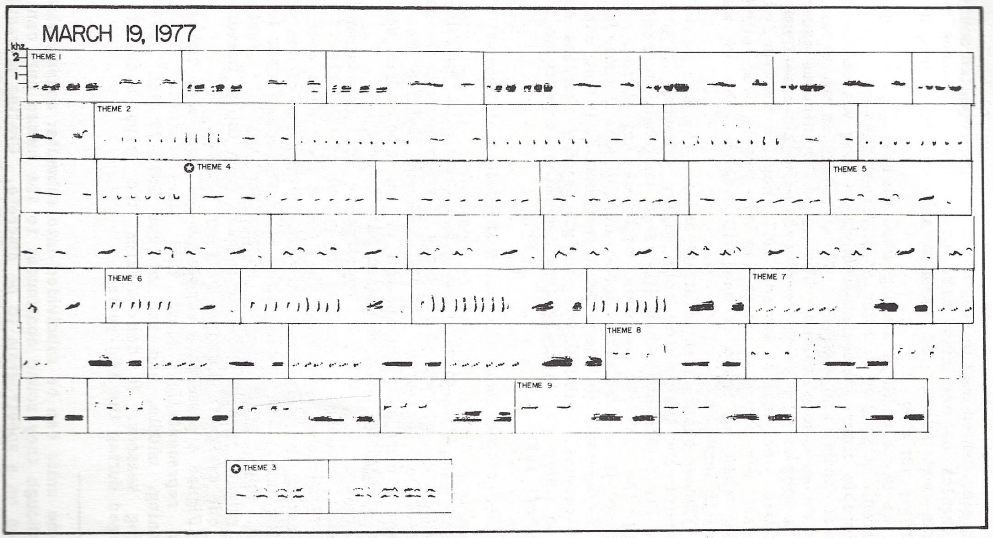

Figure 3A. (See caption on page 24.)

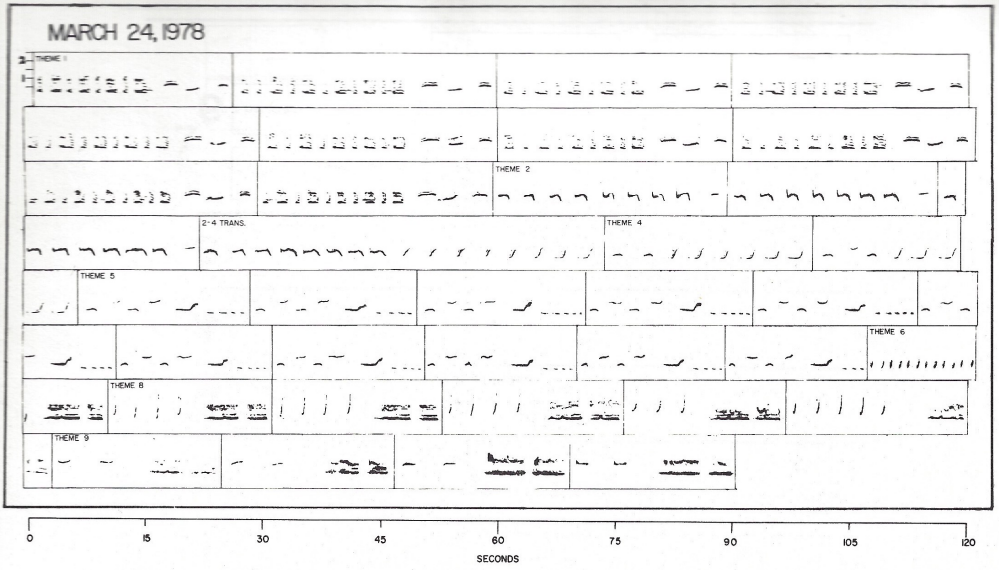

Figure 3B. (See caption on page 24.)

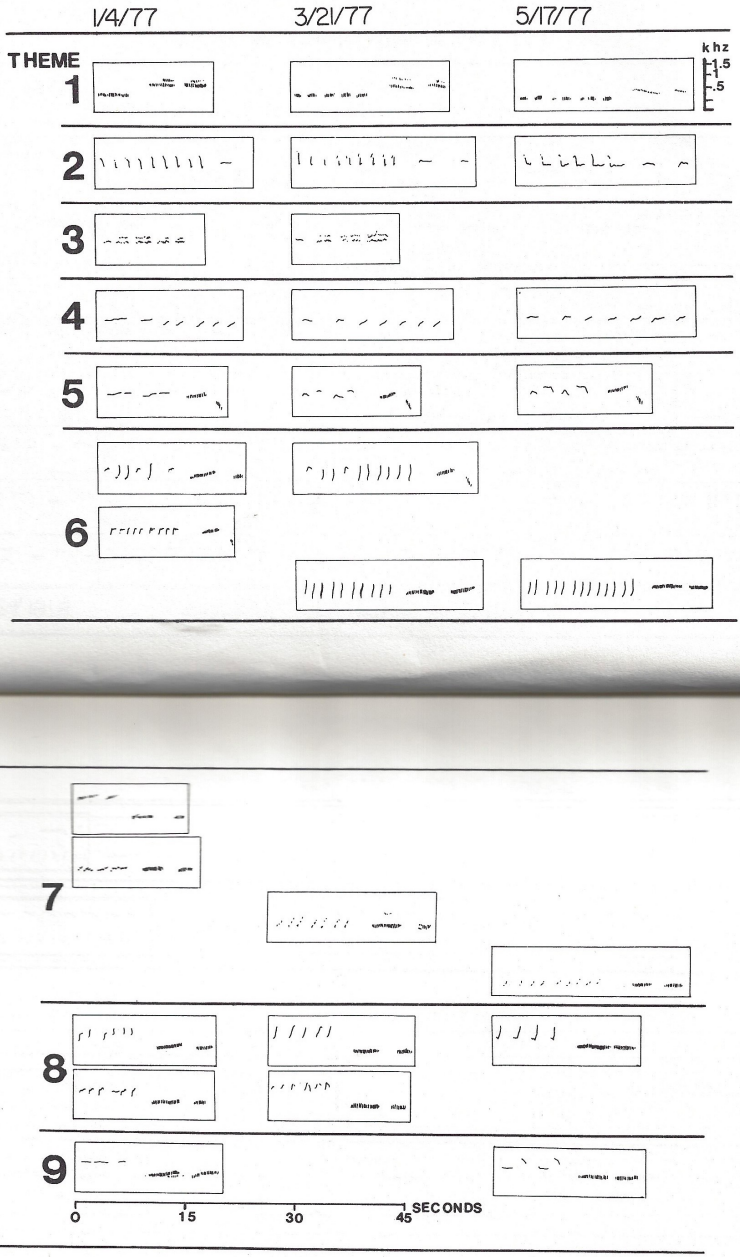

Figure 4A. (See caption on page 24.)

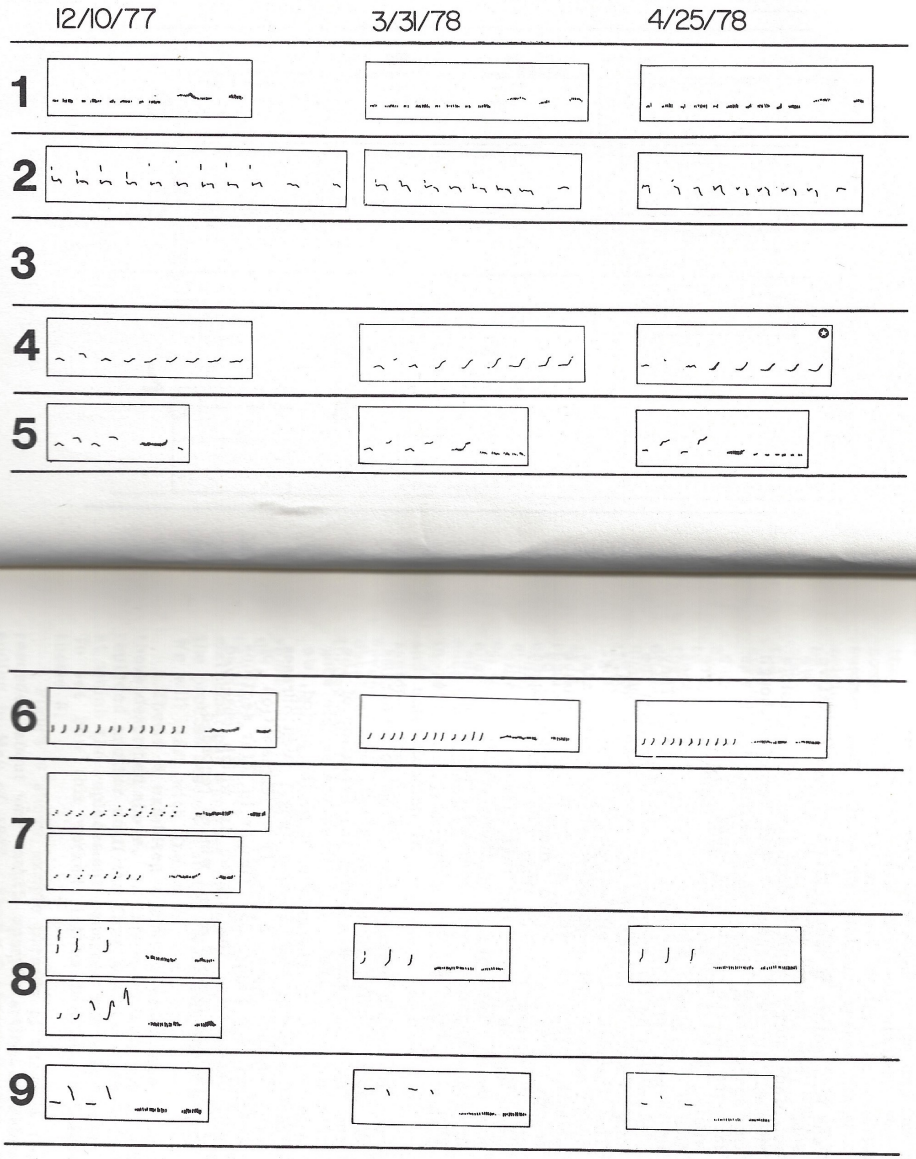

Figure 4B. (See caption on page 24.)

Figures 3A and B. Tracings of spectrograms of representative songs from March 1977 and March 1978. We selected songs which contained all possible themes. In 1977, theme 3 was rare. Although the sample song shown here omitted it, it was included in the next song sung by that same whale. The ✪ in the tracing indicated where theme 3 is placed when it is sung. Two phrases of theme 3 are then shown under the song. They are phrases by the same whale and came from the song it sang following the one fully traced here. The tracings omit all extraneous sounds (e.g. ocean noise - like ships, other whales, underwater echoes, etc.) as well as harmonics. Pulsive sounds are represented diagrammatically by closely spaced vertical lines which occupy the space on the spectrogram that showed the dense harmonics. The spacing of these traced lines is arbitrary and does not necessarily represent the repetition rate of the pulses.

Figures 4A and B. Sample phrases traced from spectrograms of representative songs throughout the 1976-77 and 1977-78 seasons showing the evolution of the themes, and of the songs. When the sample song omitted a theme characteristic of the period, we traced a phrase from another song. Such phrases are labeled with a ✪. (For explanation of tracings, see Figure 3). Graphs in later sections will demonstrate the degree to which observed changes are typical of all whales recorded.

It is apparent at once from Figure 4 that the last recordings in the 1976-77 singing season and the earliest in the 1977-78 winter were remarkably similar. The time when songs changed most was not during the relatively silent summer, but during the singing season itself. Thus our original hypothesis that the annual differences in song might be due to errors in memory was not confirmed. In fact, many of the changes progressed in such a predictable fashion that far from looking like accidents of forgetfulness, they appeared to follow set rules of progressive change.

Although we found that all themes changed, the characteristics which were changing varied from one theme to the next. The changes occurred at different rates and the peaks of change occurred in different time periods for different themes. It is remarkable that although the changes were so complex and asynchronous from theme to theme, all songs sung at any one time are very similar.

Figure 5 illustrates the evolution of theme 5 between 1976 and 1980. Even though the basic phrase structure remained recognizable through the 5 years, phrases changed conspicuously in the frequency, duration, spacing, configuration, and number of units, as well as in the duration of the average phrase. These processes did not occur all at once but in stages. The splitting of two units in the first subphrase to become four started in 1976 and was completed in 1977. But it wasn't until 1978 that the frequency range and unit duration in this same subphrase began expanding rapidly. The number of short units at the end of the second subphrase also increased between 1978 and 1980, while the duration of the whole phrase was increasing gradually throughout the five years from 1976 through 1980.

Analysis of specific changes in several themes over two years. Up to this point, we have selected examples from our data to illustrate changes in humpback songs. In the remainder of this paper, we will demonstrate changes by mathematical analyses of the complete data set, following the process described in the "Materials and Methods" section. We will start with Theme 6.

Theme 6 exhibited a change which was different from those described above. In this case, one type of unit slowly replaced another until the first was lost entirely. The rate at which the replacement occurred was surprisingly regular. To see how this worked, let us look at the structure of theme 6.

Figure 6 shows sample phrases of theme 6 from songs recorded about one month apart starting in February and ending in May of 1977. Theme 6 phrases consist of rapidly rising frequency sweeps followed by a long and then a

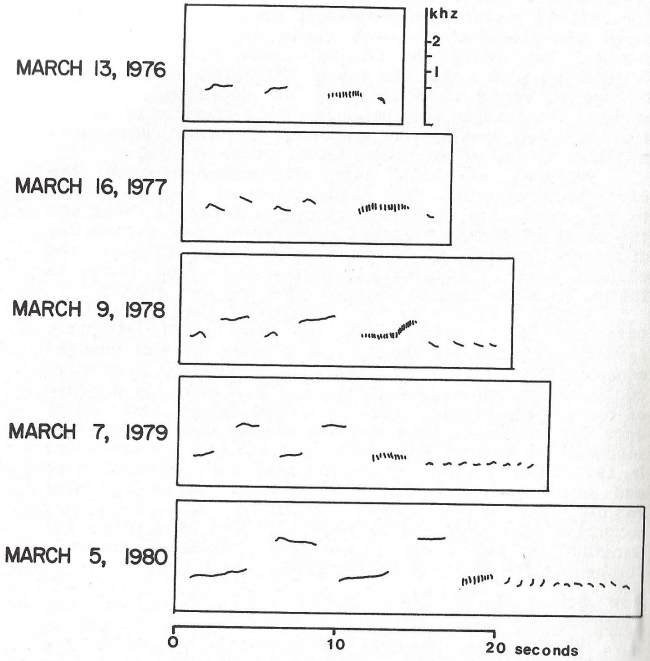

Figure 5. Sample phrases showing the evolution of theme 5 over five years. Note that phrases changed duration gradually. The units changed in frequency, duration, spacing, configuration and numbers. (For explanation of tracings see Figure 3). Figure 15 demonstrates the degree to which such changes are typical to our whole sample of songs.

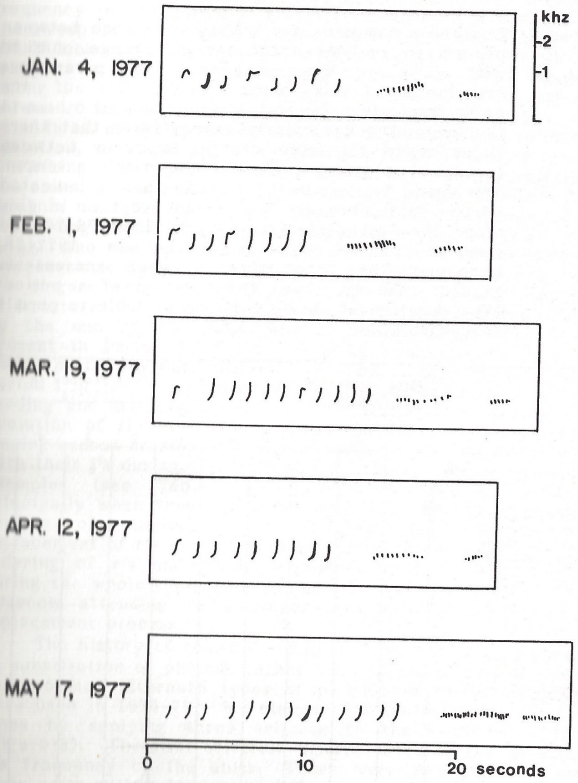

Figure 6. Tracings of single phrases of theme 6 showing that the first part consists of two different units, rs and js (see text) given in various mixtures. Note that the rs are replaced by js.

Table 2. This table compares the degree of change between periods to find when the largest change, marked with an X, occurred in each of the parameters described in this paper. While few of the parameters are completely independent of others in the table, the list clearly demonstrates that there is no trend for more change to occur between seasons than during any one period within a season. This result is even more dramatic than is indicated by the table, because the whales kept on singing after the last period we studied in 1976-77 and resumed before the first one in 1977-78. Moreover, the total time between seasons is greater than six times the duration of a period. (The duration of theme 3 is too variable to permit comparison.)

	Data Periods in 1976-77						Data Periods in 1977-78			
	2	3	4	5	6	June-Nov.	1	2	3	4	5
# Themes/Song		X									
Theme 5											
# Units/Subphr 1										X	
Phrase Duration	X										
# Phrases/Theme										X	
Theme Duration										X	
Song Duration				X							
Theme 6											
% r vs. % j					X						
Phrase Duration											
Theme 1						X					
Theme 2	X										
Theme 3	?										
Theme 4	X										
Theme 5	X										
Theme 6					X						
Theme 7								X			
Theme 8	X										
Theme 9										X	
% Songs with both Themes 8 & 9										X	
% Theme 1 in which subphrase 1 alternates long and short						X					

shorter pulse train. The frequency sweeps are of two types and differ principally by whether or not the highest frequency in the sweep is sustained. When it is sustained, the sweep has the form similar to the letter **r** and when it is not it looks more like a **j**. It is the ratio of **r**'s to **j**'s which interests us here. **r**'s are often scattered as if at random among **j**'s and sometimes a whale rendered each successive phrase of theme 6 as a different mixture of **r**'s and **j**'s.

In an effort to make some kind of sense out of so much variation, we found that a very simple form of analysis gave a striking result. We ignored all information on relative placement of **r**'s and **j**'s in a phrase and simply counted the total of each in the theme. Each was then averaged for every song session and then expressed as a percentage of the total. The result is shown in Figure 7. It is apparent that however else they may have been manipulating **r**'s and **j**'s, the singers were rapidly replacing **r**'s with **j**'s in theme 6. It is interesting to note that although **r**'s were almost gone by the end of the first singing season, they were still present in Period I of the following year. There is a 6 month period between Period VI of one singing season and Period I of the next, during which the whales are principally feeding and are singing very little. During this hiatus, the evolution of theme 6 slowed down, so that when the next singing season started, the whales were still mixing a few **r**'s with their **j**'s during the first period. This, along with other examples (see Table 2), suggests that songs evolve principally when they are being sung and very little during periods of silence. The regularity of the rate of replacement of **r**'s and **j**'s, in spite of there being no obvious ordering of **r**'s and **j**'s in successive phrases of theme 6 during the whole replacement, suggests that the whales were somehow attending to a simple law of ratios during the replacement process.

The history of theme 7 exhibits a type of change based on substitution of phrases rather than of units. There were four common alternate types of phrases in theme 7 which were used in 1976-77. We classified these alternate phrase types by applying three criteria to the first subphrase (Figure 8). The first criterion discriminated on the basis of the frequency of the units. There were two possibilities, those units with a fundamental frequency <900 Hz and those with a fundamental frequency >900Hz. The second criterion discriminated on the basis of the number of units in each "cluster" of units. Subphrase 1 of theme 7 consisted of groups of two or more units given in rapid sequence with pauses between the groups. We call these little bursts of short units "clusters". A complete phrase of theme 7 consists of between two and six clusters followed by a long

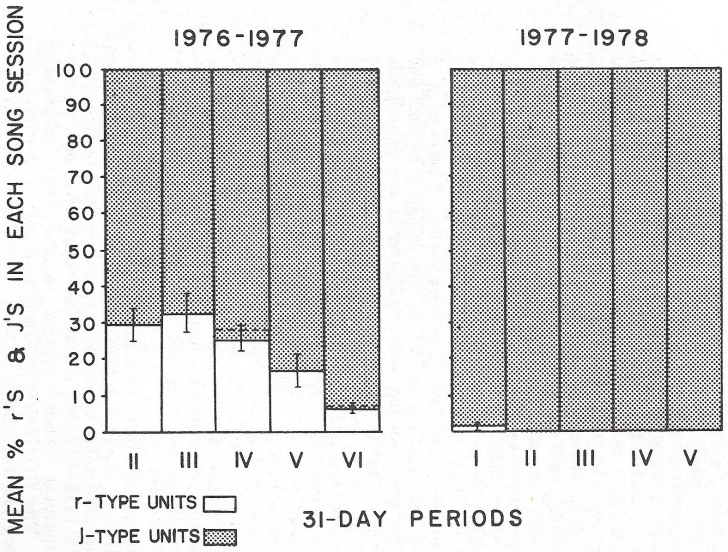

Figure 7. % of r and j units per song session versus time. The time periods (labeled 2-6 and 1-5 in the two different seasons, 1976-77 and 1977-78) are equal 31-day time periods. Periods having the same number start and stop on the same dates of their respective years. Notice that j units replace r units. Standard error is indicated by vertical lines. Dashed lines indicate means when aberrant songs are included in the calculations.

ALTERNATE FORMS OF THEME 7 SUBPHRASE I

	MINIMUM FREQUENCY	NUMBER OF UNITS IN EACH CLUSTER	RISE IN FREQUENCY WITHIN CLUSTER ?
7A	>900 Hz	N>4	NO
7B	<900 Hz	N>4	NO
7C	<900 Hz	2<N≤4	YES
7D	<900 Hz	N=2	YES
RARE INTERMEDIATE FORMS			
7BC	<900 Hz	2<N≤4	NO
7BC	<900 Hz	N>4	YES

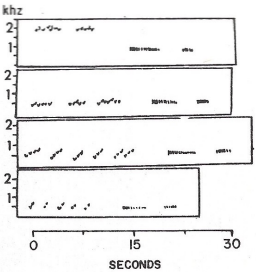

Figure 8. Alternate forms of the first subphrase of theme 7. Alternate forms are labeled 7A through 7D. They were all common at some point of the 1976-77 season. There were also two rare alternate forms of theme 7 which were intermediate between forms 7B and 7C. The tracings of spectrograms to the right of the alternate phrases 7A-7D depict examples of each type.

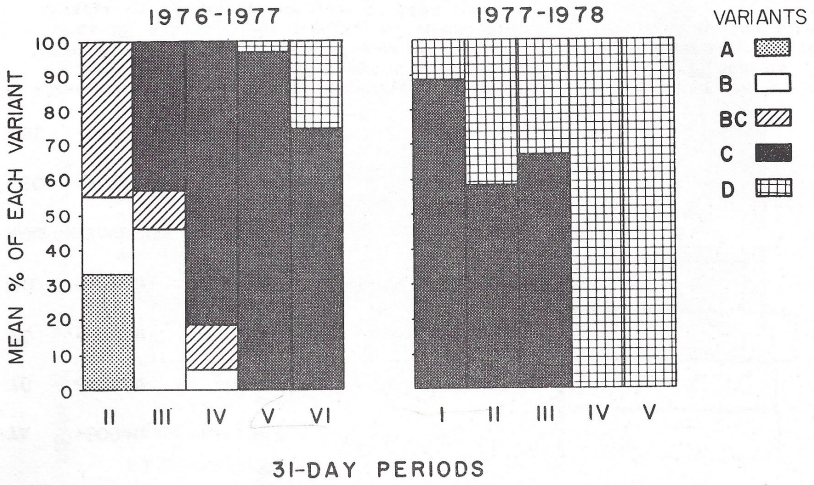

Figure 9. Several changes in the alternate phrases of theme 7. This figure shows the percentage of occurrence of each alternate form of theme 7 throughout each period of the 1976-77 and 1977-78 seasons. Only one song session in each of the last 2 1/2 periods of 1977-78 contain theme 7 because this theme was dying out. The percentages in each case thus reflect just this one song session.

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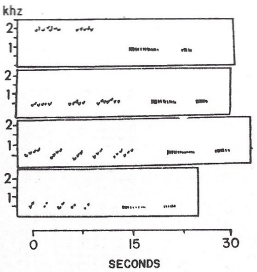
7D	<900 Hz	N=2	YES
RARE INTERMEDIATE FORMS			
7BC	<900 Hz	2<N≤4	NO
7BC	<900 Hz	N>4	YES



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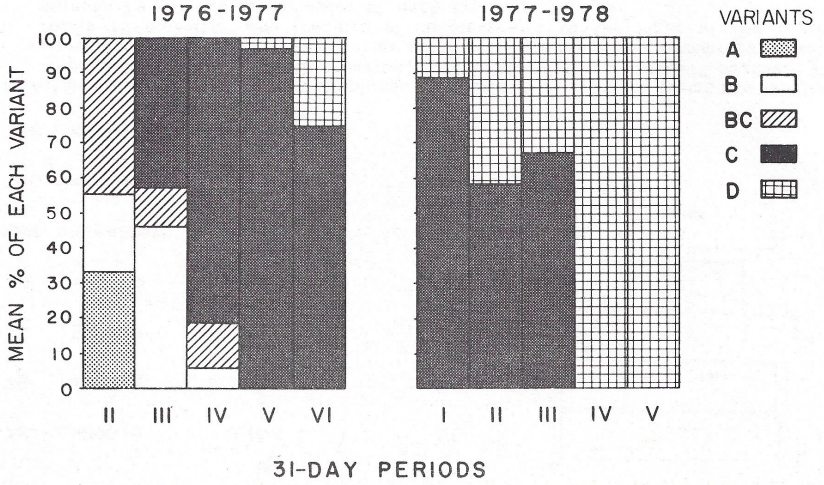

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ALTERNATE FORMS OF THEME 7 SUBPHRASE I

	MINIMUM FREQUENCY	NUMBER OF UNITS IN EACH CLUSTER	RISE IN FREQUENCY WITHIN CLUSTER ?
7A	>900 Hz	N>4	NO
7B	<900 Hz	N>4	NO
7C	<900 Hz	2<N≤4	YES
7D	<900 Hz	N=2	YES
RARE INTERMEDIATE FORMS			
7BC	<900 Hz	2<N≤4	NO
7BC	<900 Hz	N>4	YES

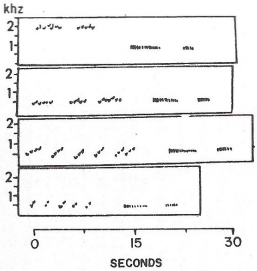


Figure 8. Alternate forms of the first subphrase of theme 7. Alternate forms are labeled 7A through 7D. They were all common at some point of the 1976-77 season. There were also two rare alternate forms of theme 7 which were intermediate between forms 7B and 7C. The tracings of spectrograms to the right of the alternate phrases 7A-7D depict examples of each type.

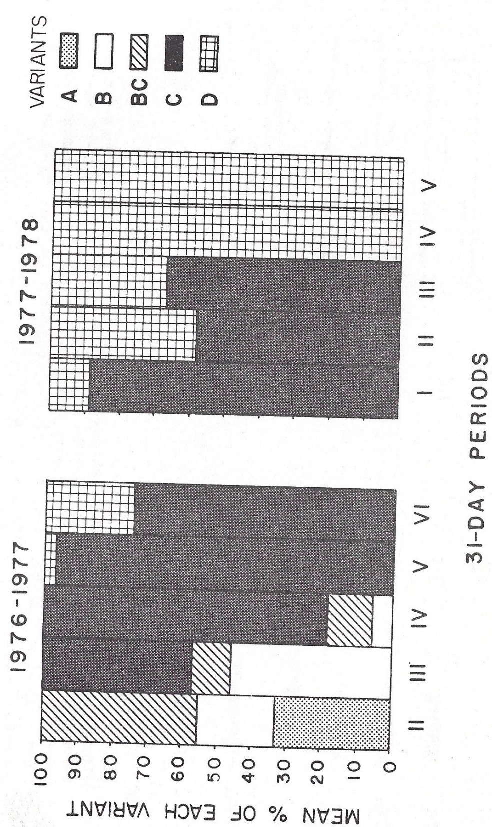


Figure 9. Several changes in the alternate phrases of theme 7. This figure shows the percentage of occurrence of each alternate form of theme 7 throughout each period of the 1976-77 and 1977-78 seasons. Only one song session in each of the last 2 1/2 periods of 1977-78 contain theme 7 because this theme was dying out. The percentages in each case thus reflect just this one song session.

and a short pulse train (Figure 8). Of the number of clusters possible, we chose three arbitrary categories: N=2, N=3 or 4, N>4. (Thus in the second criterion there were three possibilities.) Our third criterion discriminated on the basis of whether the units within a cluster were constant or rising in frequency. There were two possibilities in this case -- rising or constant. Taking our three criteria together, there were thus 2 x 3 x 2 = 12 possible phrase forms of theme 7. Yet, we saw only 6 out of these 12 phrase types. One half of the possible combinations simply did not occur, demonstrating that the alternate forms of phrases did not occur randomly but were selected by the whales.

The four common alternate phrases were not randomly dispersed through the season. Figure 9 shows the frequency of occurrence of the 4 alternate phrase forms of theme 7 which we labelled A, B, C, and D. Alternate phrase 7A, which was the most common form in the singing season, only occurred in the beginning of the 1977-78 season. Even in the first period, alternates 7B and 7C as well as the intermediate BC were also present but there was a steady progression of alternates, with different alternates predominating as the year progressed.

By closely examining the ways in which themes change, we found that new forms of a theme could be introduced at any point in the singing season. For example, the 7C alternate first appeared in February, 7D first appeared in April. We have found only two possible exceptions to the rule of gradual adoption of alternate phrases. In the very end of the 1976-77 singing season, two striking new phrase forms were adopted: in theme 2, phrases with elongated units began to appear, and in theme 1 phrases with alternating short and long units in the first subphrase took the song by storm. (Example phrases are shown in Figure 4).

In this last change, a theme which had been relatively chaotic became more organized. Phrases of theme 1 always contained in their first subphrase both long and short units (short units, < 0.5 length of the long ones). Until Period IV of 1977 the placement of long and short units appeared random, but in the last few recordings of the year, the two kinds of units alternated regularly (long-short-long-short, etc.). This new phrase form was precipitously adopted. By the start of the next period (Period I in 1977-78, following the migration to the summer feeding grounds and back), this form of theme 1 was almost universal, and the change was maintained (see Figure 10). This is one of the few changes we observed which occurred more between, than within, singing seasons: but even in this case, the onset of the change occurred within the singing seasons.

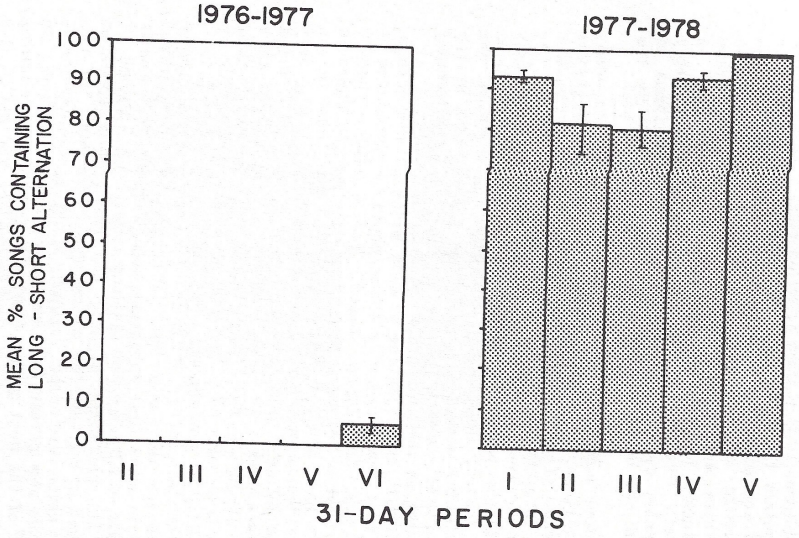


Figure 10. Adoption of a new phrase form which was introduced at the end of a season. Rhythmically organized phrases were observed only in the last few songs of 1976-77, but by the start of the next season, had become the prevailing form (see text). ▩ = songs in which long and short units alternated at least 50% of the time. Standard error is indicated by vertical lines.

Table 3. Types of phrases in themes 8 through 9 in 1976-77.

Phrase Type	Subphrase 1	Example
8	a series of high, short units, each lasting <1 sec. and in which most rise in frequency, the frequency change spanning at least 500 Hz.	
9	a series of high units in which at least one lasts ≥1 second. The units may rise or fall in frequency but the frequency change spans less than 500 Hz.	
8-9	a series of high units of which at least one lasts ≥1 second and at least one rises, changing in pitch by ≥500 Hz.	
misc.	a series of high units which falls into none of the above categories.	

Evolution of the Song: Birth and Death of Themes

Not only is there a turnover of units or alternate phrases within each theme, but entire themes gradually die out and new ones appear. Two themes -- themes 3 and 7 -- were sung less and less frequently; both were finally eliminated from the song (Figure 13). As of this writing (1981), we have never heard the sounds of either theme since in the Hawaiian song.

We have also witnessed the birth of new themes. This occurred in two different ways: 1) In 1979, a completely novel sound entered the song, became a pattern of phrases and established its own place in the orderly progression of themes (Payne and Guinee 1983). Whether this sound was spontaneously invented and then imitated, whether it developed from material in the songs that we did not happen to record, or whether it reflects interchange with whales that had learned phrases from another dialect, we do not know. To date, this is the only example of apparent *de novo* innovation that we have discovered. 2) More commonly, a theme which had been stable became variable and differentiated into two themes. The sequence of the variable phrase forms was at first unpredictable. Later, the phrases took on a definite sequence and eventually became two clearly defined themes sung in consistent order. An example of this was a section of the song following theme 7 which we called theme 8 in 1976-77, but which split to become themes 8 and 9 in 1977-78. In the first periods of 1976-77, this section of the song contained many kinds of loosely organized phrases that occurred in no particular sequence. All phrases could, however, be divided into four categories on the basis of units of the first subphrase (Table 3).

Figure 11A shows how these phrase types were distributed in the two seasons. In the start of the 1976-77 season, the two phrase forms which were to become themes 8 and 9, together constituted only 63% of the theme, while the remaining 37% was devoted to hybrid and miscellaneous phrases. As time went on, the miscellaneous and then the hybrid phrases dropped out, and eventually in the last period of 1978, only the 8 and 9 forms existed.

At the same time, the sequence in which the whales sang these phrases was also stabilizing, so that all phrases of type 8 were more likely to be completed before the whale began singing phrases of type 9 (Figure 11B). The number of songs containing both themes 8 and 9 was somewhat coordinated with this development. In Period I of 1976-77, 8 and 9 were sung in only 35% of all songs but by early 1978, they appeared in 100% of all songs, after which the percentage fell off somewhat (Figure 11C).

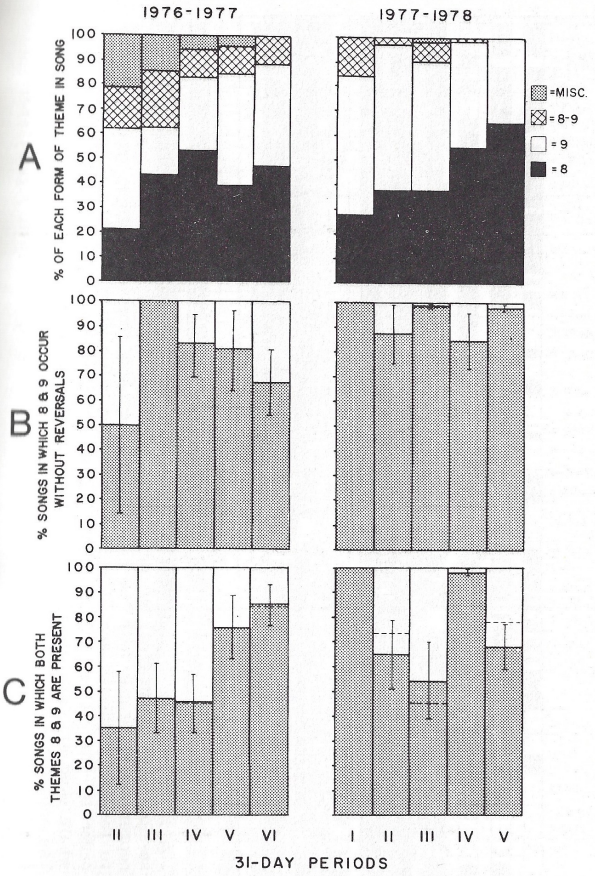


Figure 11. Development of two themes from one.
A % occurrence of four alternate phrase forms from themes 8 & 9 (two seasons).
B % songs containing no reversal of order of themes 8 & 9.
C % songs containing phrases of both themes 8 & 9.
In B and C, standard error is indicated by a vertical line. Dashed lines indicate means when aberrant songs are included in the calculations.

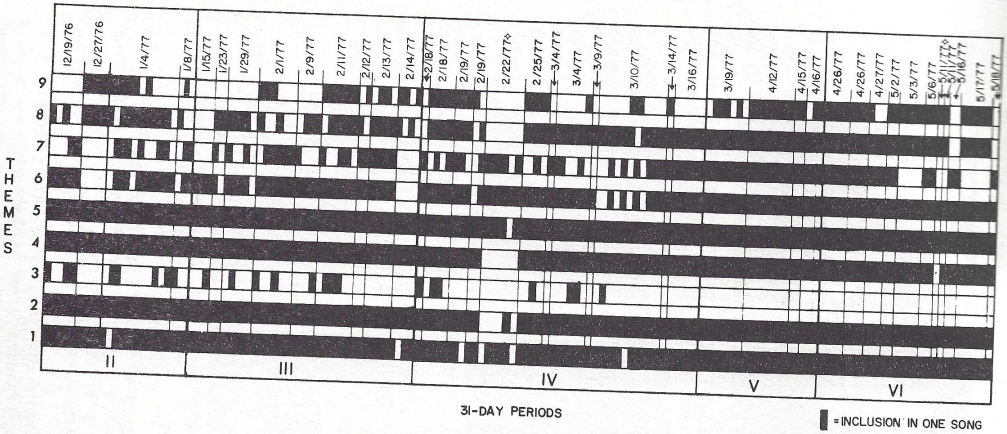


Figure 12A. The inclusion or exclusion of all themes in our total sample of 310 songs. Song sessions are identified by date. Each column within a given song session represents one song, with the nine themes occupying rows and reading from bottom to top. The themes are always given in the order sung. With any reversal of order by the whale, the record is advanced to the next song column. When a whale sang at least one phrase of a theme, the corresponding box was blackened. The sporadic nature of theme inclusion is obvious. Note also the loss over time of theme 3 and the blooming and fading of theme 7. A ⊹ is used to signify aberrant song sessions.

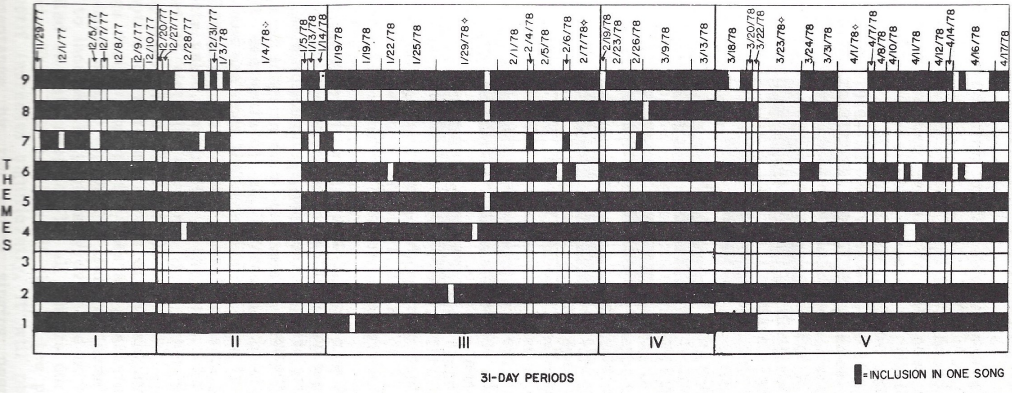


Figure 12A (continued).

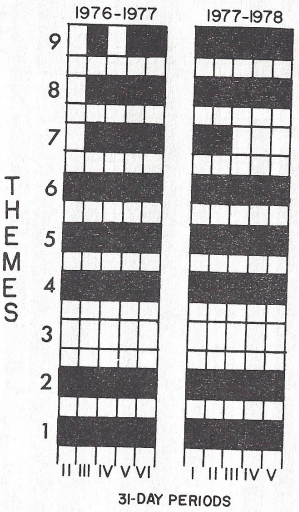


Figure 12B. A summary of 12A. Now the columns represent periods in which the majority of the songs in the majority of the song sessions contained a given theme.

The Changing Constitution of the Song as a Whole

We have presented the separate history of several themes through the two years. We will now consider the changing constitution of the song as a whole. We will examine this in terms of two features: 1) the amount of time devoted by the whales to each theme in the song; and 2) the changes in average duration of phrases, themes, and songs.

Figure 12A shows which themes were included in each song of every song session in our sample. For a theme to be counted as being present, at least one complete phrase had to be included in a song. It is immediately apparent that most songs are incomplete. For example, out of our total sample of 310 songs, only 3 included all 9 themes (these songs were recorded on 4 January, 11 February and 18 February 1977). This poor showing is of course largely an artifact related to the constant changing of the song. For example theme 3, which was never very strong in our sample, was dropping out in the 1976-77 singing season and was last heard 10 March 1977. Theme 7 also dropped out about a year later than theme 3: it was last heard 26 February 1978.

By examination of Figure 12A, one sees an apparent instability early in the 1976-77 season. The reason for this, as will be demonstrated below, is that themes 7, 8, and 9 were all undergoing development during these early months. It was a time when they were not sung by all whales and only sporadically by those that did sing them. Theme 7 dropped out the following year, but themes 8 and 9 became a part of almost every singer's repertoire. Three of the four singers that left these themes out entirely sang songs that were otherwise aberrant (Frumhoff, 1983).

Figure 12B, using broader criteria, gives a simplified overview of theme replacement.

The question of the relative popularity of the different themes -- i.e., the degree to which whales adopt and sing themes -- is worth pursuing. Figure 13 shows the percentage of songs in each song session which included each theme. It demonstrates an interesting point. The only stable themes are ones that are sung in close to 100% of the songs. Strangely, no theme seems to survive at some intermediate value, say in 50% of the songs. Rather, if it is not a part of virtually all songs it is either increasing or decreasing (e.g., themes 3,6,7,8,9).

Adoption of a theme by all of the singers for all of their songs during some period does not guarantee its tenure (e.g., themes 6 and 7), but so far, a theme which was observed to increase in popularity over two or more periods never failed to gain adoption by all singers during at least one period. Thus, one can predict that if the popularity of a new motif increases significantly, it will probably soon enjoy acceptance by the entire singing population. Its

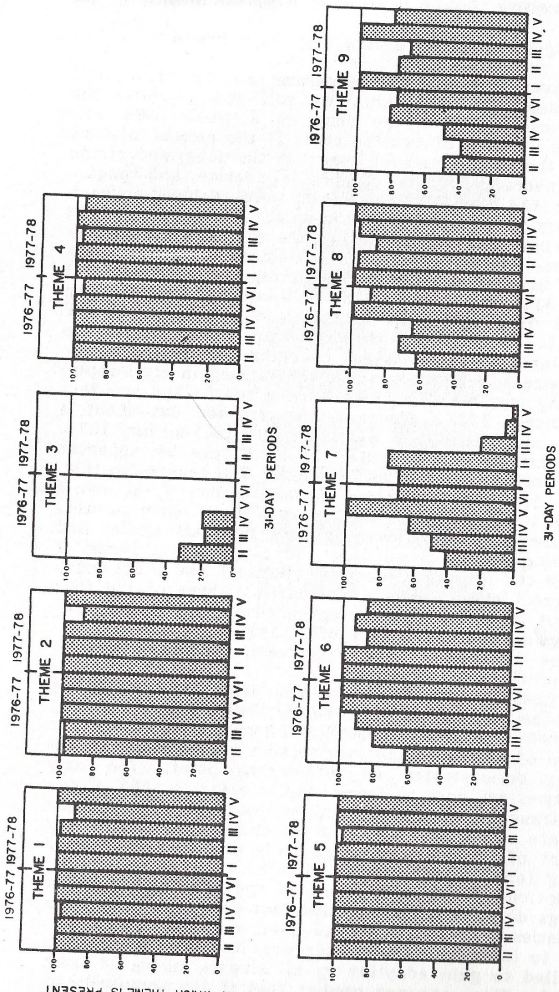


Figure 13. The percentage of song sessions which included each theme. It demonstrates several interesting points. The only stable themes are the ones that are sung in close to 100% of the song sessions. Strangely, no theme seems to survive at some intermediate value, say in 50% of the sessions. Rather, if it is not a part of virtually all sessions, it is either increasing or decreasing.

popularity will not remain at some fixed, intermediate value. Apparently its status in the song can only be stable for long periods when it has reached full acceptance by the entire population.

Progressive Changes in Duration

There was a great range in the length of humpback songs during the 1976-77 and 1977-78 Hawaiian seasons, from a minimum of 4.4 minutes to a maximum of 26.4 mins. (not including a few sequences of themes for which it was impossible to define what constituted a song). This variation followed clear trends throughout the song seasons. Figure 14A shows that in 1976-77, the songs more than doubled in average length between Periods II (7.5 mins.) and V (16 min.). The change is so marked that there is no overlap in song durations within the standard error for Periods II and V. A small decrease in duration occurred between Periods V and VI.

The dramatic increase in song length seen in 1976-77 was not repeated in the 1977-78 season. On the contrary, while song length increased in the first part of 1977 and decreased in the last part, exactly the opposite occurred in the 1977-78 season.

As we have seen in Figure 12, most songs do not include all possible themes. It seems likely that the variable number of themes per song might be largely responsible for the radical changes in song length. In Figure 14B, we have tabulated the average number of themes included in songs of each period, and indeed, the result is a curve remarkably parallel to that of song length: in early 1977 when many songs were incomplete, the average song was short. In Period V, when most songs included all possible themes, the song was more than twice as long. In Period VI, however, one theme (theme 7) was omitted, and the average song length again decreased. In 1977-78 as well, the number of themes included allows one to predict song duration (except in Period V, when some other factor must have come into play).

Song length is affected not only by the number of themes but also by the average duration of each theme. This in turn is the product of the number of phrases in the theme and the average duration of each phrase. In Figure 15, we see five different measures of theme 5. Theme 5 is an example of how changes at each level of the song affect the durations of other levels. At the most detailed level of the song, we can see that the increase in phrase length parallels the increase in number of units per phrase. In 1976-77, the average duration of phrases was increasing and the average number of phrases in the theme was also increasing. Theme length, being a product of these two

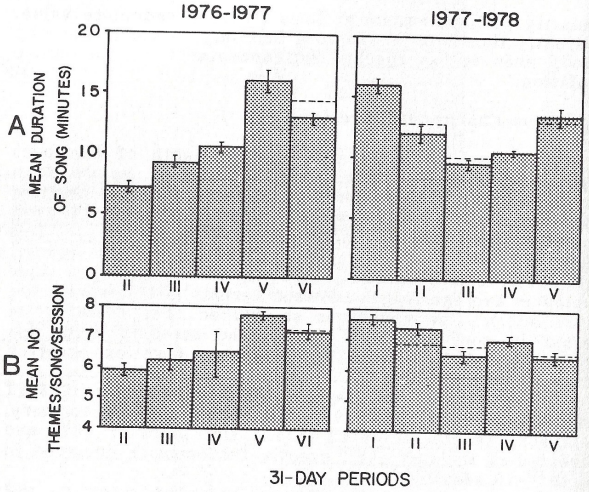
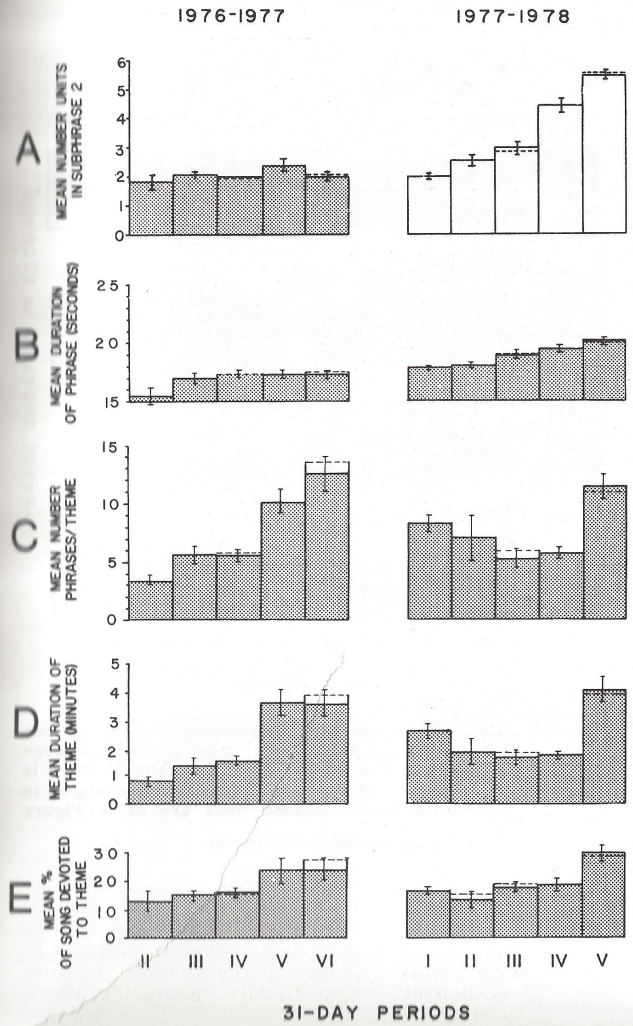


Figure 14. Parameters of song that changed together.
A: Average duration of songs through two singing seasons.
B: Average number of themes per song in each song session over two singing seasons.
Standard errors indicated. Dotted lines represent means when aberrant song sessions were included in the calculations.

Figure 15. Some changing parameters of theme 5 over two singing seasons.

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: % song occupied by theme 5.

Dashed lines indicate means when aberrant songs from these periods were included in the calculations. Vertical lines indicate standard errors.



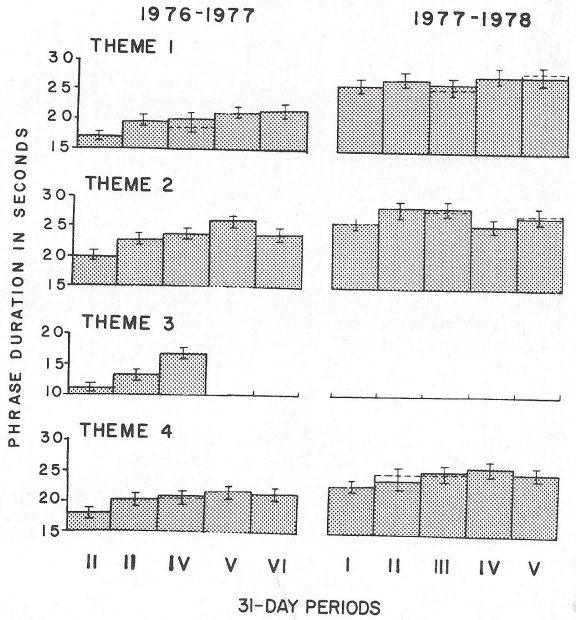


Figure 16. Mean phrase duration for every theme in two singing seasons showing: 1) most phrases increase in length as the theme gets older, and 2) there is no apparent annual cycle underlying changes in phrase duration. Dashed lines are as in Figure 15.

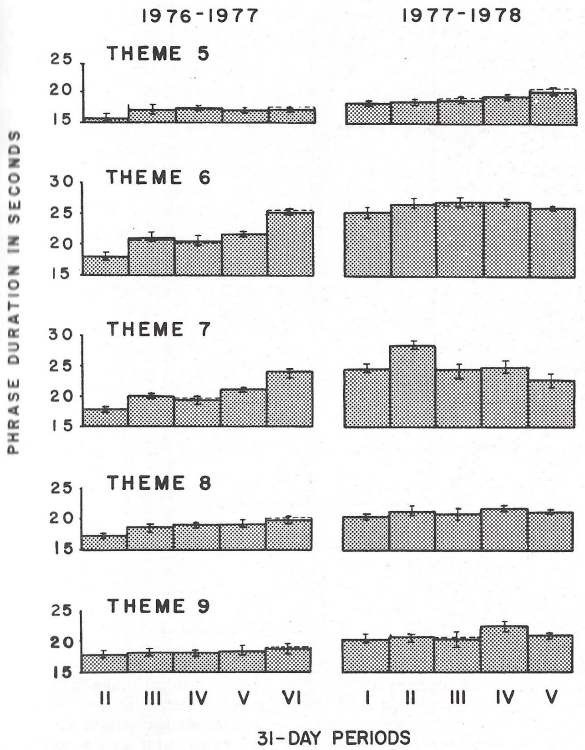


Figure 16 (continued).

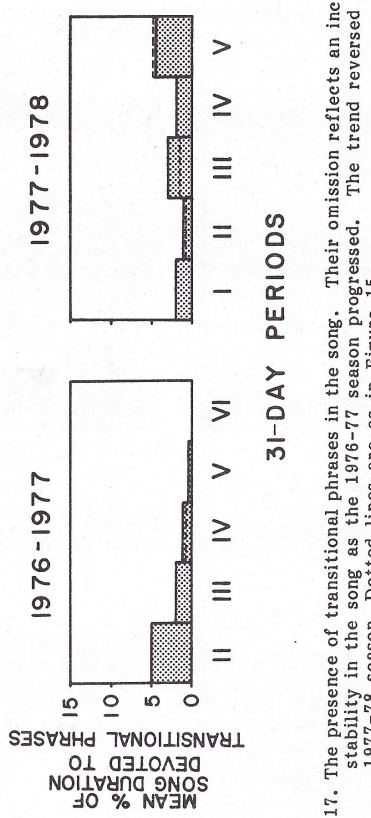


Figure 17. The presence of transitional phrases in the song. Their omission reflects an increased stability in the song as the 1976-77 season progressed. The trend reversed in the 1977-78 season. Dotted lines are as in Figure 15.

factors, shows, of course, an even more prominent increase. The only exception occurred in Period V, when (as we saw in Figure 11) the entire song was slightly declining in duration. However, even in that period, the growth rate of theme 5 was proportionately greater than the growth rate of other themes, with the result that theme 5 occupied an increasing percentage of the song in each time period in 1977. Although in 1976-77 the duration and number of phrases per theme worked together to lengthen the theme, the story was more complex in 1977-78, when the two factors affecting theme duration had opposite effects.

Figure 16 shows the average duration of all phrases in all themes for each period in the 1976-77 and 1977-78 seasons. A continuing tendency for phrases to lengthen with time is conspicuous in every theme (with a partial reversal in the last part of 1978). Similar increases in phrase duration were repeatedly noted in the Bermuda song from our 22 year sample (Payne and Payne, in press).

The tendency for phrases to expand not only within each season but continuously over almost two seasons provides clear evidence that these changes are not under control of environmental parameters such as water temperature or day length, which fluctuate on an annual or seasonal basis. Presumably, changes involving duration must have some sort of periodicity, but apparently a two-year sample is not long enough to discover a complete cycle.

Synchronization of Trends that Increase or Decrease: Variability in the Whole Song

It is interesting to observe that the progressive stabilizing of themes 8 and 9 in the 1976-77 singing season coincided with a general increase in stability of several other aspects of the song as well. As noted above, the whales were the most consistent in terms of which themes they included between late 1977 and early 1978 (Figures 12A and 12B): a time when the number of themes in each song was highest (Figure 14B). It was also the time when the fewest transitional phrases were present (Figure 17).

A transitional phrase is a phrase occurring between two themes which combines features of both (Payne and McVay, 1971). The 24 March 1978 song presented in Figure 3 shows a very simple one made by joining of incomplete phrases from themes 2 and 4. Some transitional phrases mix units from two adjoining themes in a more complex way. Transitional phrases may occur between any two themes, or occasionally replace one or more themes that are omitted from the song.

During the times when the song was least stable in terms of which component themes were present, it contained transitional phrases between all themes: but at the end of the 1976-77 season, when all themes were firmly established,

there were no transitional phrases left. In Period IV of 1977, the song structure was rigid and unambiguous, nearly every possible theme was included in each song by each whale, and every phrase could be clearly assigned to one theme, with no miscellaneous, hybrid, or transitional forms. In other words, the song was maximally compartmentalized, organized, and predictable. Thus stabilization in many factors of the song occurred synchronously.

To return to the thesis with which we opened this study, we had expected that in the end of the season, when whales in Hawaii had been listening to each other for several months, the song would be maximally stereotyped. As a corollary, we had expected the least stereotypy in the beginning of a season (at the end of the relatively silent feeding period when the whales might be expected to have difficulty recalling the song). The 1977 data fulfilled these expectations completely, but in the 1978 data, all the trends reversed! Thus although tendencies for stabilizing the song do seem to rise, peak, and decline together, the influence which drives them does not operate on a seasonal cycle and remains to be discovered.

Further evidence that the stabilizing tendencies are not on a seasonal cycle is obtained by looking for periods of greatest change in the song and paying particular attention to whether these changes occur more between singing seasons or within them. In Table 2, we have noted between which two periods the largest changes occurred in every parameter presented in this paper. In only 2 out of the 27 parameters measured did the greatest change occur during the six months of non-singing. Frumhoff (1983) notes that the only period in which aberrant songs were not recorded was in Period I -- the time when one would expect the most aberrancy in songs, were memory failure a major factor.

These facts suggest that song change is not merely a consequence of forgetfulness, or of other accidents during the summer or during the migrations to and from the singing grounds. On the contrary, the overwhelming majority of major changes occurred while singing was in full swing. Thus, the song is probably not mixed up or changed significantly during the relatively silent summer months. Rather, it is retained intact in the singer's memory. It appears that for a humpback whale, to remain silent is to keep the song in a fixed state, whereas to sing is to change.

Discussion

We have seen that the songs of humpback whales are at once highly organized and also labile. During the time of year when they are heard, they are constantly changing in a wide variety of ways. The most pronounced changes are adopted by all singing whales, while old forms of phrases and

themes become obsolete and disappear in a coordinated fashion shared by all singers.

One might postulate that humpback songs convey information about the environment, but because they are so repetitious, it seems unlikely that much new information is conveyed with each repeat. However, it is possible that changes in the song might in some way reflect changes in the environment. Most environmental changes of a kind likely to be of importance to the lives of whales (e.g., changes in the food supply, the time to migrate, etc.) are cyclical in nature and likely to repeat on some regular basis. If the changes in the whales' songs are related to these phenomena, they would probably repeat in synchrony with them. But they do not repeat at all.

Three basic cycles affect living systems the most. They are based on the day, the lunar month, and the year. Since several days must pass before even rapid song changes can be detected, a change based on daily cycles is ruled out. But lunar and annual cycles are also ruled out because the changes made by humpback whales do not correlate with either of these cycles (indeed, they do not seem to repeat at all). Therefore, it seems unlikely that songs are detailed comments on changing features in the natural environment, and more likely that they are displays and thus internally controlled.

Ever since Darwin, it has been recognized that one of the processes which can drive evolution of displays is sexual selection. Large repertoires in songbirds seem to have evolved by sexual selection. In test situations, female canaries tend to select males which are singing a more varied repertoire. Kroodsma (1976) has shown that not only are female songbirds reproductively primed by the song of conspecific males, but exposure to more varied song repertoires stimulates female canaries (*Serinus canarius*) to engage in more nest building and egg laying behavior (he was, however, unable to rule out the possible special effect of particular songs). Studies in the field by Yasukawa, Blank, and Patterson (1981) indicate that male Red-winged Blackbirds (*Agelaius phoeniceus*) with large repertoires tend to have higher reproductive success than males with small repertoires, although this finding is complicated by the fact that males with large repertoires tended to have other attributes like greater age that might make them more likely to succeed in reproduction regardless of song repertoire. McGregor, Krebs, and Perrins (1981) have shown the same in Great Tits (*Parus major*) in a study which was controlled for age.

We have noted that the changes in the songs of humpback whales which we have described cannot be caused only by accumulation of copying errors between seasons, since most of the greatest changes in the parameters of song

Table 4. Five hypothetical stages in the evolution of singing, using as a criterion the mechanisms by which variability is introduced into the songs. Humpback songs can be seen as an advanced stage in the increase of variability in a hypothetical continuum between songs of crickets and those of humans.

SINGING TYPE	REPRESENTATIVE SPECIES	MECHANISM OF INTRODUCING VARIABILITY	RESULT
1	Cricket, Doves	No vocal learning variability introduced genetically, by mutation or by hybridization	Rigidly fixed songs with little variability
2	Chaffinch, White-crowned sparrow	Learning from conspecifics during sensitive period in early life.	Modest song repertoires.
3	Mockingbird, Canary, Red-winged blackbird	Learning throughout lifetime from conspecifics or from other species	Larger song repertoires present at a given time.
4	Humpback whale possibly Yellow-rumped Cacique	Continuous learning from conspecifics of new versions of song, as it changes constantly within set laws of form.	Rapid, continuous song evolution: small song repertoire at any given time but enormous repertoire over many years.
5	Human being	Learning *de novo* compositions governed only by laws of form.	Rapid, discontinuous, largest and most varied song repertoires.

that we measured occurred during the singing seasons. Recent studies by Tyack (1981) indicate that the songs of humpback whales play a role in their reproductive behavior similar to that in songbirds. Female choice may drive the changes we have observed in humpback song the way female choice drives some songbird species to large vocal repertoires.

The peculiar characteristics of humpback whale songs and their unique attributes when compared with the songs of other animals suggest that they may demonstrate an important step in the evolution of singing and provide an interesting point along a continuum of song development from invertebrates to humans. In order to explain this point further, we will broaden the definition of singing to mean a display employing repeated sounds. We will then look for common aspects in the many kinds of singing found throughout the animal kingdom.

If we focus on the mechanisms by which variability is introduced into the singing performances of different species, we find that singing falls rather naturally into five distinct categories or singing types (Table 4). We suspect that the higher the number of the singing type, the fewer the number of species in it.

Type 1 Singing. Songs that are characteristic of this type are genetically determined and often relatively simple. Learning seems to play no role but variations can be introduced genetically through mutation or hybridization. Doves (Lade and Thorpe 1964) and crickets (*Teleogryllus* sp.) are examples of this type. Bentley and Hoy (1972) showed that in F_1 cricket hybrids, intervals between calls are intermediate between corresponding parental intervals.

Type 2 Singing. In singers of this type, song variation is introduced through learning, but only during a critical period, and in some cases the song which is learned must be a song for which the animal has a predisposition. The White-crowned Sparrow (*Zonotrichia leucophrys*) is an example (Marler 1970). In some species, for example the Chaffinch (*Fringella coelebs*), several songs may be learned by the same male (Marler 1956; Hinde 1958) during a critical period (Thorpe 1958), but after the critical period is over, the song repertoire remains fixed.

Type 3 Singing. In this type, song variability is introduced by learning throughout much or all of the animal's life. The mimicry of Mockingbirds (*Mimus polyglottos*) is an example (Wildenthal 1965), as are Red-winged Blackbirds (Yasukawa et al. 1981). Other probable examples are canaries (Nottebohm and Nottebohm 1977). Singers of this

type have various different songs in their repertoire at any time. Old songs are not necessarily lost when new songs are added, but may be retained.

Type 4 Singing. Song variability in this type also reflects continuous learning; however, a population abandons songs it learned first and only sings one song at a time. This song undergoes constant changes which rapidly spread through the population. Trends in the changes are subject to certain set rules of form and nearly always involve modifications of pre-existing material. Past versions of the song do not recur - thus if, as seems likely in humpback whales, an individual male sings for many years (see Guinee et al. 1983), his repertoire over his whole life is very large, but at any given time consists only of the single current version of the song.

Humpback whales are, to date, the best documented and certainly the most extreme example of type 4 singing, but there is a bird, the Yellow-rumped Cacique (*Cacicus cela*) which may constitute a second example (Feekes 1977).

Type 5 Singing. Singers of this type combine some of the features of types 3 and 4 and add new complexities. The only limits on song variability in type 5 are learned conventions (e.g. scales, rhythmic patterns, rules of harmony, forms, etc.). Like type 3 singers, individuals have a large repertoire of songs at any time. Like type 4 singers, they have the capacity to create new songs adhering to certain fixed rules of form. However, in type 5 singing, new songs do not have to be derived from existing ones but can be created *de novo*. Humans seem to be the sole practitioners of this kind of singing.

In summary, the study of whale songs has unexpectedly demonstrated a kind of missing link in the continuum of sound display leading from simple stereotyped singing to the full complexity of human song. Instead of viewing human song as an isolated phenomenon, as has often been done in the past, we see now that it may well have developed through a simple step-by-step evolution, the stages of which can still be studied by listening to several disjunct species, each singing to us from their respective branches of the phylogenetic tree.

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