Z. Tierpsychol., 68, 89—114 (1985)

ISSN 0044-3573 / InterCode: ZETIAG

Large Scale Changes over 19 Years in Songs of Humpback Whales in Bermuda

By KATHARINE PAYNE and ROGER PAYNE

With 8 figures

Received: August 8, 1983
Accepted: September 29, 1983

Abstract and Summary

163 songs of humpback whales (*Megaptera novaeangliae*) recorded near Bermuda during April and May of 13 years between 1957 and 1975 have been analysed as continuous sound spectrograms and compared. In each year's sample, all whales were singing basically the same song. However, the song was changing conspicuously and progressively with time so that songs separated by a number of years were very different in content. All the songs showed basic structural similarities so that it is possible to define a song form which characterizes songs from many years. We present some basic characteristics of the song form and consider the nature and extent of changes in content as a function of time. An analysis of the songs sung by groups of whales shows that normal singing continues even when whales are close enough, presumably, to hear each other. Such analysis demonstrates inter- and intra-individual variability, none of which is as great as the variation between songs of consecutive years. We do not understand the significance of changing songs. We know of no other non-human animal for which such dramatic non-reversing changes appear in the display pattern of an entire population as part of their normal behavior.

Introduction

Humpback whales (*Megaptera novaeangliae*) migrate annually between shallow tropical or semi-tropical waters where they spend the winter and spring, and colder waters nearer the poles where they spend the summer and fall. Their principal behavior in the cold areas is feeding. In the warm waters, calves are born and courtship occurs. Gestation takes 11 to 12 months (CHITTLEBOROUGH 1958).

It appears that there are a number of discrete feeding grounds and a number of discrete breeding grounds in both the North Atlantic and the North Pacific. Current evidence suggests that individual humpback whales are loyal to the same feeding areas over the years (KATONA et al. 1980; DARLING 1983).

It is surprising, however, to find members of the discrete feeding groups mixing during the breeding phase of their lives. Several cases in the North Pacific even show known individuals changing breeding grounds from year to year (DARLING and JURASZ 1983). These findings indicate for both oceans that apparently small groups of whales which remain discrete on the feeding grounds are part of a much larger, perhaps ocean-wide, population which can mix during the rest of the year. The exact sizes of these populations are unknown, though MITCHELL and REEVES (1983) estimate the western North Atlantic population at 1500 to 2000 animals and DARLING (1983) estimates at least 2100 animals in the North Pacific.

In the western North Atlantic, the spring gathering places of humpbacks include several islands and banks in the West Indies (WHITEHEAD et al. 1978) as well as migratory way stations such as Bermuda and its offshore banks. These islands and banks have steep slopes rising abruptly from deep ocean, a topography which may enhance sound transmission over relatively long distances. The whales are very vocal while lingering in these areas, and most of their sounds occur in long, elaborate, cyclical patterns or "songs", as first described by PAYNE and MCVAY (1971). The behaviour that accompanies singing indicates that it probably plays a part in courtship analogous to the role of singing in birds (TYACK 1981). In the summer, when humpbacks are feeding, singing is very rare. D. MCSWEENEY and W. DOLPHIN (pers. comm.) have heard a few full songs in Alaska. H. WINN (pers. comm.) reports song fragments from the Atlantic feeding grounds. However, these findings follow many years of trying to record songs in feeding grounds with no results (SCHEVILL and WATKINS 1962; WINN et al. 1971; PERKINS and WHITEHEAD 1977; WINN and WINN 1978).

On both the feeding and the breeding grounds, humpback whales also make a variety of discrete non-song sounds, or social sounds, that are heard most often when the whales are interacting in groups (THOMPSON et al. 1977; G. SILBER, pers. comm.). These sounds appear to be subject to quite different rules from those influencing songs. In this paper we will discuss only songs. We will present the songs as evidence that the whales singing near Bermuda are a single population, with a behavioral trait that is little known in non-human animals, a display (in this case vocal) which changes with time, the current version being adopted by all displaying members in the area.

Methods

We have studied a sample of humpback whale songs from 13 out of the 19 years between 1957 and 1975. Songs from 1969 to 1975 were recorded during one- to five-week expeditions to Bermuda, principally sponsored by the New York Zoological Society. Tapes from the 6 years prior to 1969 were generously provided by the late F. WATLINGTON of the Lamont Geophysical Field Station in St. Davids, Bermuda. W. SCHEVILL and W. WATKINS gave us a tape recorded by V. COLEMAN in 1963. A. PERRONE of the Naval Underwater Sound Laboratory at Gibbs Hill, Bermuda gave us the recordings from 1968. All recordings were made within a few miles of Bermuda and all except the 1968 sample were made in mid or late spring. These recordings provide a sample of songs from Bermuda at roughly one-year intervals near the end of each singing season.

Recording

The recordings which we analysed were made under a variety of different circumstances. In 1957, 1958, and 1959, F. WATLINGTON was recording on Challenger Bank in the presence of humpbacks with hydrophones trailed behind a ship; in 1961, 1963, and 1964, his hydrophones were fixed at a depth of approximately 700 m about 3 km off Bermuda and connected by a cable to his office. PERRONE's 1968 tape was also recorded from hydrophones on the sea floor, but they were located much farther from shore. When the deep hydrophone recordings were made, no observers were present, and our evidence that humpback whales were responsible for the sounds is simply that they are similar, in all of the ways that will be described in this paper, to sounds known to be from humpbacks. The types of sounds, their pacing, the ways in which they are organized into phrases, themes, songs, and song sessions, the duration of songs and the level and types of variability are all typical of humpback songs; and no other animal is known to produce songs in which these same characteristics are combined.

Our own recordings, comprising all the material from 1969 through 1975 and constituting 172 of the 180 h of analysed tapes, were usually made in stereo from a pair of broad band hydrophones. The hydrophones were at a depth that varied from 10 to 25 m. They were deployed from a small sailboat moving very slowly or lying stationary in the water. The hydrophones were suspended from bamboo poles which allowed a separation of about 5 m. The stereo recordings proved somewhat useful in making a rough determination of the direction from which underwater sounds were coming, so that in analyzing the tapes we could sometimes separate out voices of whales which were singing simultaneously. The rest of the apparatus typically included a pair of preamplifiers and a Sony TC770 tape recorder capable of broad band recordings at frequencies of about 40—16,000 Hz. (The WATLINGTON and PERRONE recordings were similarly broad band.) Announcements of the behavior of visible whales and instrument settings were superimposed onto one of the two channels recording whale sounds.

There is no doubt that the sounds analysed here were made by humpback whales. Usually we were able to find humpback whales near the boat when we heard singing. On many occasions when we were recording an especially loud (thus probably close) signal, we could correlate bouts of breathing of a nearby humpback with attenuation in intensity as the whale reached the surface, or with pauses in the song. Breathing tended to occur at a predictable point in the song (first noted by WINN et al. 1971). On days when we saw no humpbacks, we either heard no sounds or heard only distant singing.

Analysis

We made spectrograms of several 100 h of tape using a Spectral Dynamics SD-301C real time analyzer. We used a logarithmic frequency scale to improve the visualization of low frequency components in the songs.

As the ocean is a very noisy environment. the spectrograms contain much that is not whale sounds. In order to simplify our analysis, we traced the spectrograms, leaving out ocean and ship noise, echoes, distant whales, and harmonics (except in the case of pulsive sounds, which depend on their harmonic structure for their effect on the human ear). We show pulse trains diagrammatically as groups of closely-packed parallel vertical lines. Whales' songs include a wide range of pulse rates. Our choice as to whether to classify each sound as pulsive or tonal was based on listening: sounds discontinuous to our ears, having fewer than about 65 pulses per s, are represented in our tracings as pulse trains (e.g., Fig. 7, Theme 2).

Since the dynamic range of the analyzer was less than that of the signal, we made several spectrographic versions of every song. Our tracings have been made from our best spectrographic version of each sound.

Our tracings of spectrograms are interpretive in three ways: 1) we have designated a beginning and end for each song, when, in fact, the songs presented here are excerpted from

Table 1: Summary of the data used in this paper

Year	# of h of useful recording	# of analyzable songs	Evidence for song being characteristic of more than 1 whale	# of songs analyzed	# partial songs of which fragments were used as supporting evidence	Recordings accompanied by behavior notes
1957	1	1 1/2	none	1 1/2	6	no
1958	2 1/4	3	good	3	6	no
1959	1 1/2	1 1/2	good	1 1/2	6	no
1961	1	4	none	2	1	no
1963	3 1/2	20	partial	7	8	no
1964	2 3/4	20	partial	12	3	no
1968	3/4	4	none	3 1/2	0	no
1969	48	181	good	41	40	yes
1970	57	154	good	21	75	yes
1971	29 1/2	99	good	18	46	yes
1972	5	10	good	17	10	yes
1974	5	12	good	4	6	yes
1975	15	64	good	25	18	yes

a continuous flow of sounds in song sessions containing many songs. (Any complete cycle of themes, no matter where one started it, could be considered a song.) 2) Vertical lines between phrases are added to the tracings. 3) We have labeled the tracings with border patterns to demonstrate parallels between song elements in different years.

The amount of data in the years sampled varies greatly and is summarized in Table 1.

Our discussion and conclusions are based on the years for which we have good samples along with evidence that they are representative. The other years, even when poorly sampled, confirm our observations. However, we should not include them without describing their limitations. The sample from 1957—1961 is very small but does include at least one complete song and several song fragments from each year. In years for which we have many data, we find that the most atypical songs usually occur in sessions which are inconsistent from song to song. This idea has been tested and found true in large samples of humpback songs from Hawaii (FRUMHOFF 1983). Since the song sessions from which our 1957—1961 samples were drawn are consistent, we feel they are probably representative of other songs from the same periods.

The 1968 sample was also very small: only four songs by one individual. It was recorded in January rather than in late spring.

In order to present complete songs with good signal-to-noise ratios for 1957 and 1959, we had to piece together spectrograms from two consecutive songs. The splices are marked by an X in Fig. 1. They are justified by the rest of our sample from those years.

With the exception of 1968, these early samples, however incomplete, suggest a sequence of events which continued naturally and logically in the years for which we have thorough documentation.

Fig. 1: Tracings of spectrograms of "type specimens" of humpback whale songs from Bermuda in 13 years. Tracings omit noise and include only sounds made by the singing whale. Themes are numbered at their start. Border patterns at the top of a row of spectrograms point out similarities in thematic material from year to year, similar material labeled the same every time it recurs. Phrases without border patterns contain material in one year only

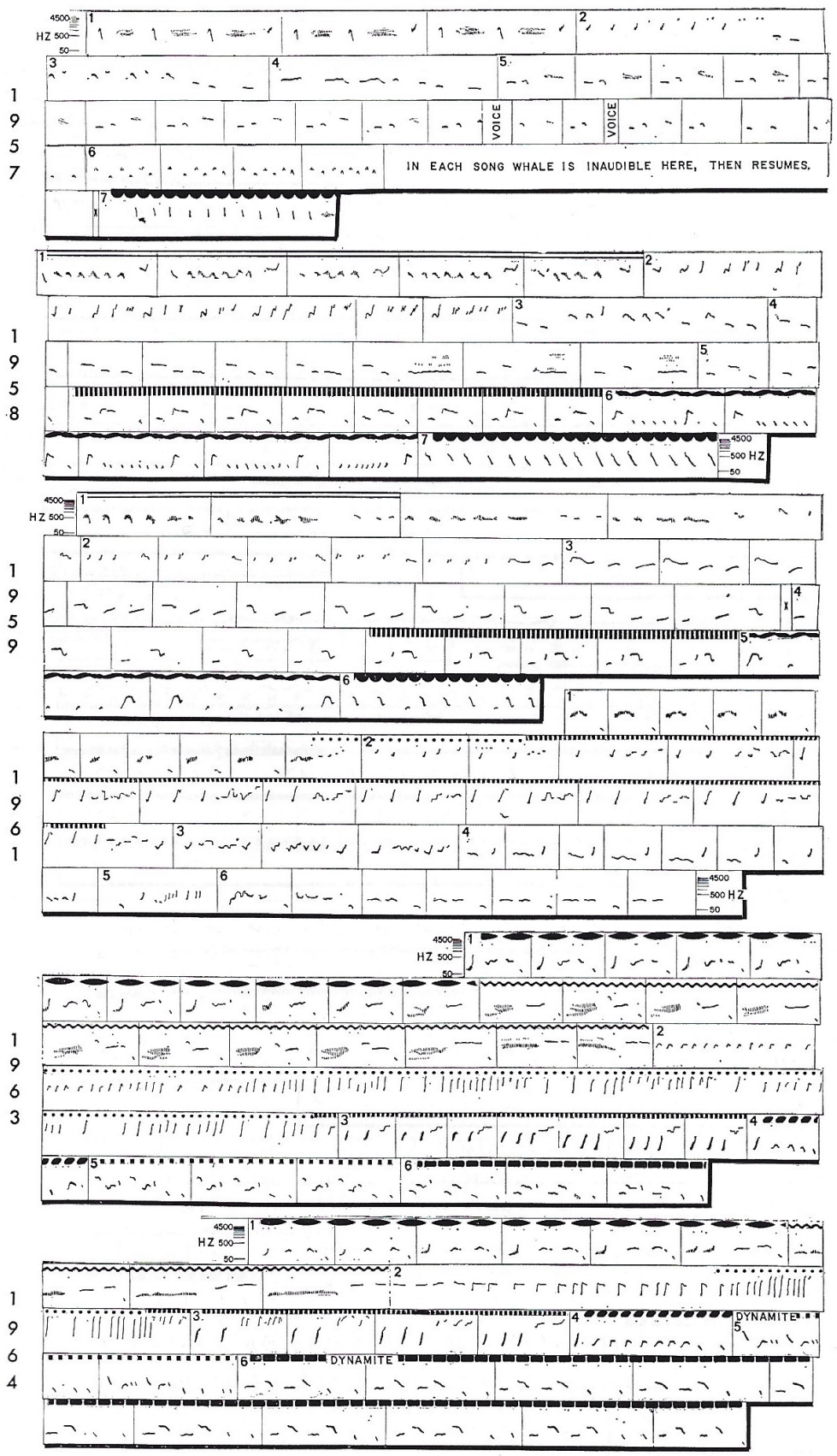


Fig. 1a: Songs from 6 years between 1957 and 1964 in April. All were recorded by F. WATLINGTON. Notice that the degree to which old thematic material is replaced each year varies, some pairs of years being nearly identical (e.g., 1963 and 1964) while others have hardly any elements in common (e.g., 1957 and 1958)

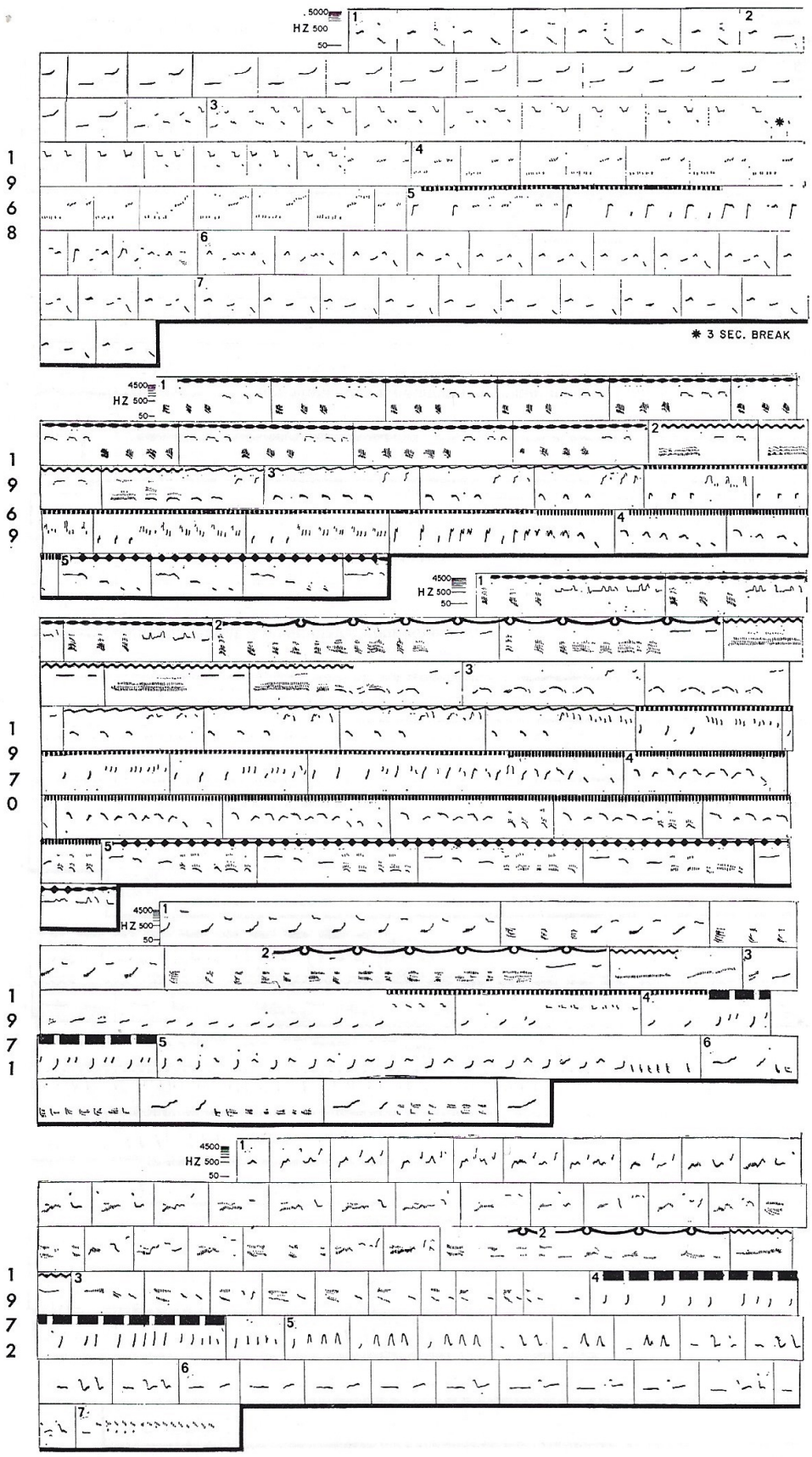


Fig. 1b: Songs from 1968 to 1972. The 1968 song was recorded in January. All others were recorded in April and May. Songs from 1969 and 1970 closely resemble one another, with 1970 songs being slower. Songs of 1971 are roughly intermediate in form between 1970 and 1972. Whales usually breathe in the (~~~~) sections

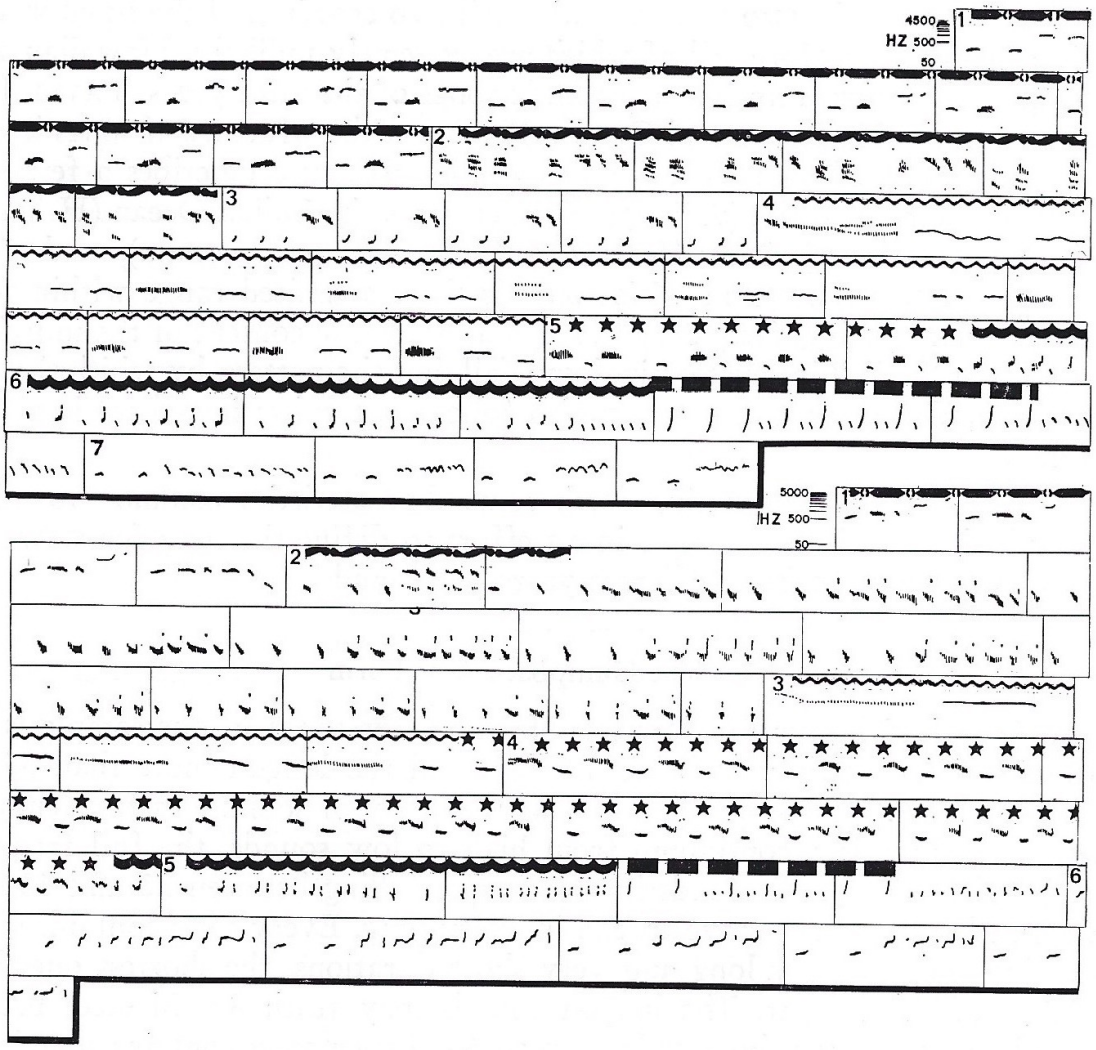


Fig. 1c: Songs from 1974 and 1975. Songs from this pair of years, like songs from 1963—1964 and 1969—1970, are very similar in most themes. The theme where the whale breathes (~~~~) contains the longest, slowest pulse trains we have heard

Results and Discussion

Single songs from each of the 13 years sampled are presented as "type specimens" (Fig. 1) because each one contains phrases characteristic of the whole sample for its year. The border patterns on the tracings indicate obviously similar patterns of sounds (as determined by eye and by ear) which are present in more than one year. They make it immediately apparent that in most years a song contains some unique material (no border) and some that is carried over from the year before (the same border in two years). Similar material runs through only a few years before it is replaced by something else.

Thus it takes only a few years for the songs to change substantially. If this is true, can one recognize a humpback song as such, even if it has only a few elements previously heard? The answer is yes. We have analyzed songs of humpbacks in Hawaii (PAYNE et al. 1983), a population almost certainly not in acoustic contact with Bermuda humpbacks now or in the recent past, since

contact between the two areas would entail two crossings of the equator and a trip around Cape Horn, all of which are extremely unlikely. Hawaiian songs are quite different from North Atlantic songs of the same years (PAYNE 1979; WINN et al. 1981; PAYNE and GUINEE 1983), yet the structure of songs in these seemingly isolated areas is similar. A similar structure describes a few songs sampled from Australia (S. EARLE, pers. comm.), the Indian Ocean (H. WHITEHEAD, pers. comm.), New Zealand (W. DAWBIN, pers. comm.), and Tonga (G. KAUFMAN, pers. comm.). Not only is there a limited range within which the duration, pacing, frequency range, and harmonic content of the individual sounds (or "units" in our terminology) fall, but the pattern by which the units are assembled to produce a song also follows set rules: i.e., there is a "song form".

We will start by setting forth some characteristics common to all the humpback songs in our sample in an effort to define the song form. We will then compare songs from different years in Bermuda.

The Humpback Song Form

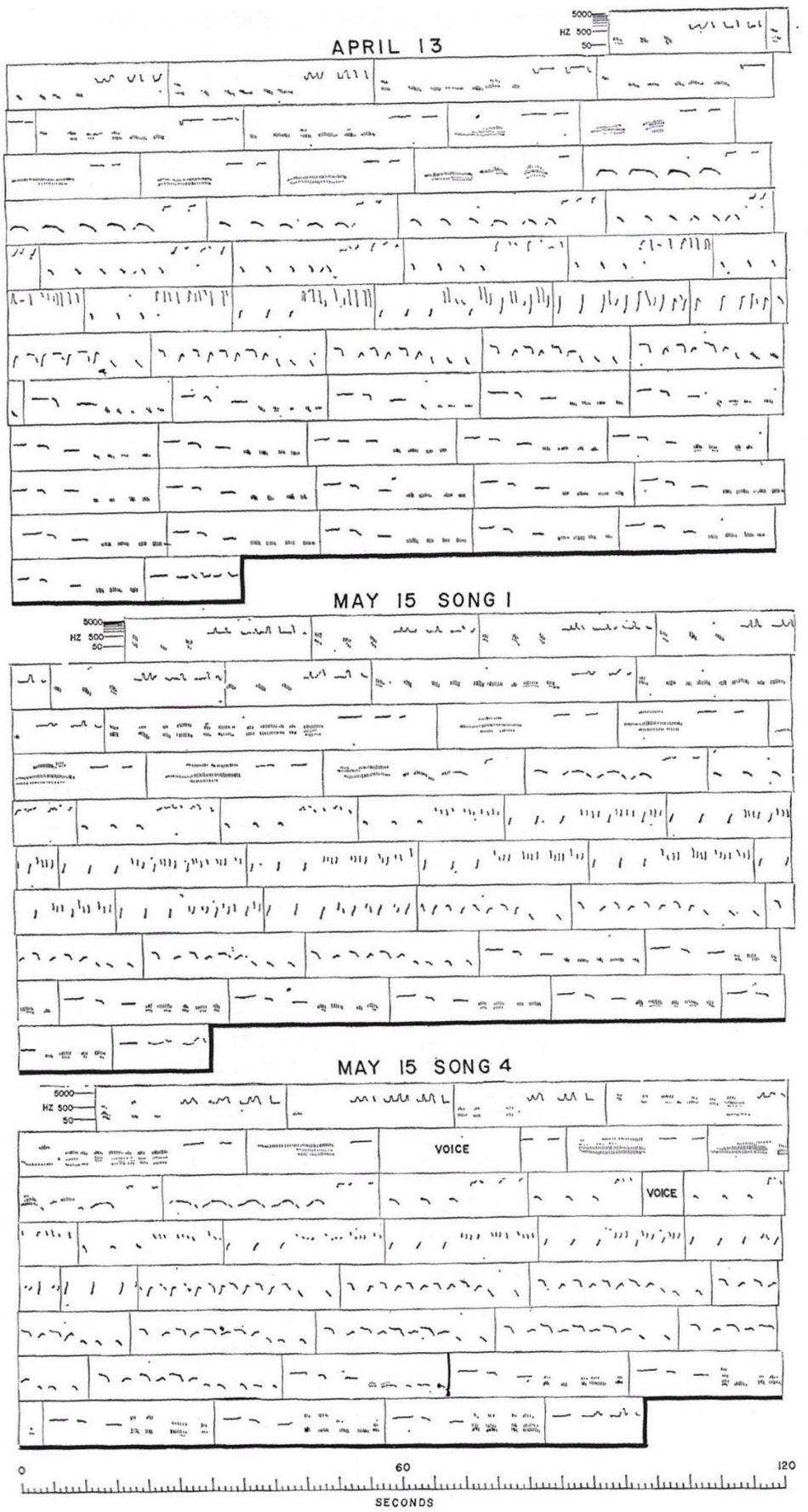
Length. The typical duration of humpback songs in our sample is 8 to 16 min, with the shortest being 4.5 min, and the longest more than 35 min.

Contents. The songs contain a wide variety of sounds. In frequency, for example, there is a continuum from high to low sounds, the full frequency range of fundamental sounds in our sample falling between 30 and 4000 Hz with at least a three octave spread in every song. Every song contains sounds ranging between very long and very short durations, the shortest ones being $< 2\%$ of the longest. The longest sounds may reach 8 s. Silences between sounds may be very short or last up to 6 s. Every song contains sounds that are simple and complex in harmonic structure (ranging from tonal to noise bursts); loud and soft; abrupt and gradual in onset; and changing and constant in frequency with frequency sweeps both up and down.

Hierarchical structure. All humpback songs we have studied have a structure roughly similar to that described by PAYNE and MCVAY (1971) and confirmed for Hawaiian songs by PAYNE et al. (1983). We will adhere to their terminology here, calling the shortest sound that is continuous to our ears in real time a "unit", a series of units which make up a repeating group a "phrase", a consecutive group of similar phrases a "theme", the sequential combination of all the themes a "song", and a series of songs within which there is no pause longer than 1 min a "song session".

In any given year, each song in our sample consists of several themes (typically 5 to 9) arranged in an inflexible order. Each theme leads without a pause into the next. There is apparently no fixed beginning or end to a song, although, as mentioned above, the whale usually breathes at the same place

Fig. 2: Traced spectrograms of three humpback whale songs from Bermuda on April 13 and May 15 in 1970, showing inter- and intra-individual variation in one season. The two songs from May 15 are from a single song session, thus they are two examples of songs by one individual. The April 13 song is likely to be the product of a different whale (see text).



The uniformity of the three renditions of the song is remarkable. For an example of the degree of change between samples 1 year apart, compare these to the songs from 1971 in Figs. 7 and 8

in the song; and many songs may be linked together in a song session without interruptions. A song session may last many h.

These rules are so universally adhered to that it has been possible to label the few exceptions as "aberrant" and to analyze them as phenomena unto themselves. FRUMHOFF (1983) found 14 aberrant song sessions out of a total of 123 examined from the years 1976—1977, 1977—1978, and 1978—1979 in Hawaii.

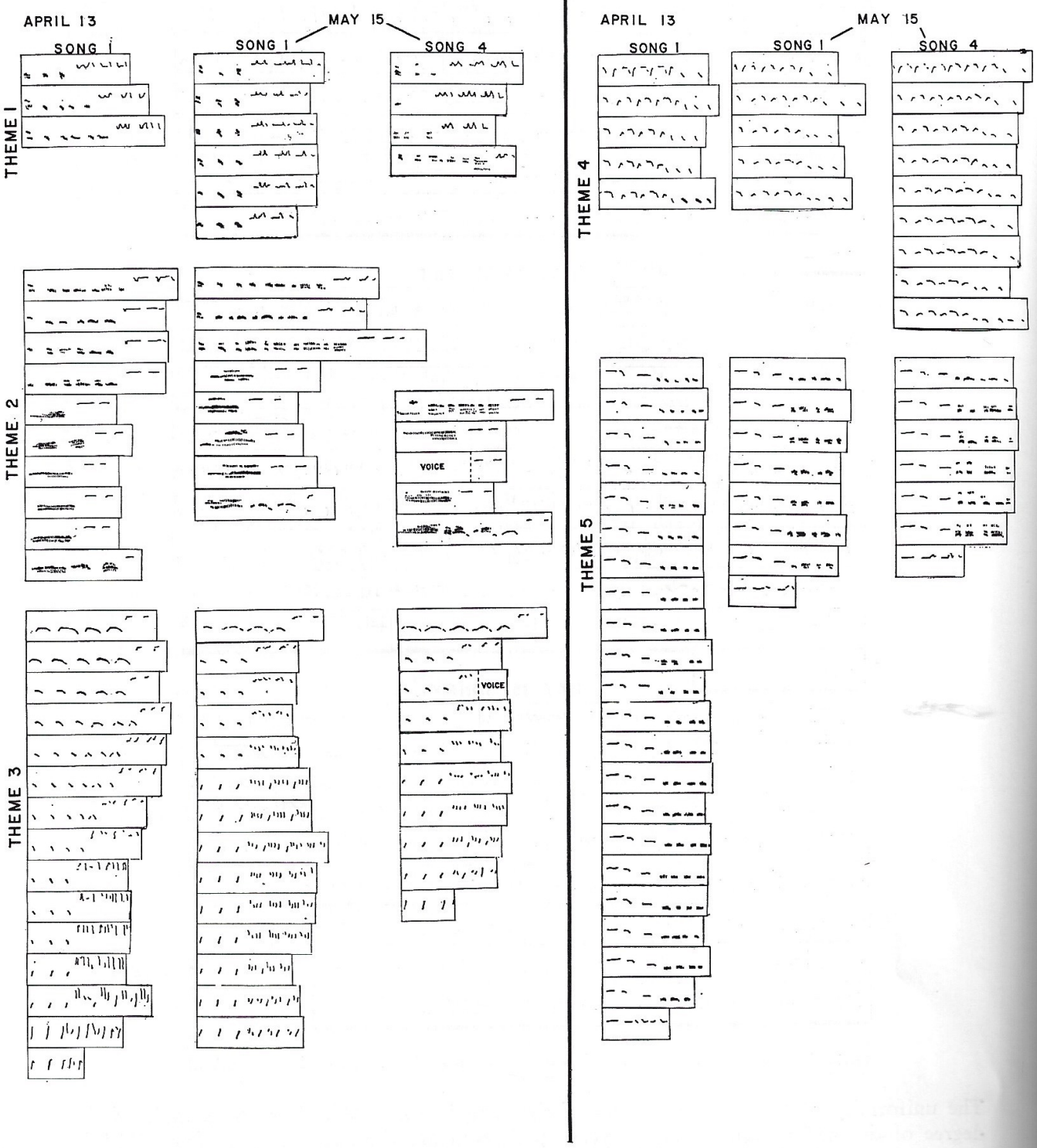


Fig. 3: A theme-by-theme comparison of the songs in Fig. 2

It is a curious fact that, although the structure and sequence of themes within a song are quite predictable, their duration is variable. There are two principal causes of this. 1. The number of phrases per theme varies. This is true even between songs in the same session by the same individual. As far as we can ascertain, there is neither a preference for consistency, nor any clear pattern of alternating long and short themes in consecutive songs. 2. One or more whole themes may be omitted from a song. In these cases, the normal sequence of the remaining themes is still maintained.

Most of these rules of song form are apparent in the three songs from 1970 shown in Fig. 2. The irreversible progression from theme to theme, the variability in the number of phrases per theme, and the clear similarity of phrases within a theme are immediately obvious. In Fig. 3, we have traced all the phrases from Fig. 2 and aligned them sequentially so as to compare them. This makes it easy to appreciate certain other generalizations. The variability in the number of phrases per theme is particularly apparent in Themes 4 and 5.

Types of themes. Different themes are organized in different ways. Over the years, a theme may change from one type of organization, or theme pattern, to another. The most common patterns are:

1. "static" themes, whose phrases are nearly identical with every repeat (Example: Fig. 3, April 13, Theme 5);
2. "shifting" themes in which successive phrases evolve progressively from one form to another. As phrase follows phrase, units within them gradually shift in frequency and/or form, duration, or numbers, or are delivered at a slower or faster rate. The sequence in which such a change occurs is predictable for a given theme, but the number of phrases in which it is accomplished varies from song to song (Example: Fig. 3, April 13, Theme 3);
3. "unpatterned" themes, consisting of a variable number of units which have no clear organization and thus cannot be subdivided into repeating phrases (Example: Fig. 1a, 1963, Theme 2).

At the junction between two themes, there may be a transitional phrase. This is a phrase combining material from the theme that precedes it with material from the following theme (Example: Fig. 3, May 15, song 4, Theme 2, last phrase).

Table 2 lists further examples. All the songs we sampled included a variety of ways of organizing themes.

Figs. 2 and 3 also give a sampling of intra- (and probably inter-)individual variability over the longest period we sampled in Bermuda: April 13 to May 15, in 1970. The two songs from May 15 were part of an uninterrupted sequence by one whale. The song from April 13 is probably the product of a different whale. Although the singers were not individually identified, there is a basis for this assumption in the work from Hawaii, where during three years only 4 out of 56, or 7.14 %, identified singers were whales that had been

Table 2: Examples of theme types and transitional phrases from 1957—1975 Bermuda songs

	Theme types			Transitional phrases
	static	shifting	unpatterned	
1957	5			7-1
1958	1, 6	4	2	
1959	5	4		2-3
1961	1	2, 4	3	2-3
1963	5, 6	1, 3	2	
1964	5, 6	1, 3	2	2-3
1968	1, 2, 7	4	3	2-3, 3-4, 5-6
1969	4, 5	1, 3		2-3, 5-1
1970	5	2, 3		2-3, 3-4, 5-1
1971	6	1		3-4
1972		5	3, 4	
1974	1, 3	4, 7		5-6
1975		2, 3	5	4-5

previously sighted (DARLING, pers. comm.). This makes the probability extremely low that two songs from different sessions on different days would belong to the same whale.

The differences between the two sessions in Figs. 2 and 3 are well within the range of individual variation. A comparable sample of inter- and intra-individual variation in songs of the next year (1971) will be presented below (Fig. 7). It is obvious from inspection that all songs in either year are much more similar to other songs from the same year than to anything from the adjacent year's sample. A statistical verification of the same claim for three years of humpback song in Hawaii has been obtained using discriminant analysis by GUINEE et al. (1983). In the present sample, there is abundant justification for assuming that the type songs we will now compare are representative of the years concerned[1]).

Comparison of Songs from Different Years

The border patterns in Fig. 1 label themes from different years which are obviously similar. The decisions were made both by listening and by visually comparing the spectrograms. When there was ambiguity, we emphasized similarities in efforts to find relationships between the songs of different years.

---

1) The songs in 1963 and 1964 were very similar (see Fig. 1a). Our sample, containing only two song sessions from 1963 and one from 1964, isn't adequate to say whether the consistent differences throughout the songs are idiosyncracies of individuals, or characterize the singing population as a whole. However, in the 13 years sampled in Bermuda, and also in a 7-year sample of songs from Hawaii (K. PAYNE et al. 1983), there is a conspicuous tendency for phrases in later years to be longer than their counterparts in earlier years. Since we observe this difference between songs from 1963 and 1964, it seems likely that in a larger sample, the lengths of phrases would be adequate to distinguish songs of the two years.

The classification is an oversimplification in that we are forcing themes of great variety into just two categories: "similar" and "different". Some pairs of years contain themes which are obviously similar in both the structure of the units and their organization (e.g., Theme 4 in 1963 and 1964). But, when only one of these parallels is apparent, the similarities are less obvious (e.g., the first themes in 1969 and 1970, more similar in organization than in detailed structure of units). Our methods of classifying themes for similarity is thus arbitrary, but they suffice to trace the largescale changes in song during the two decades. Even if all the ambiguous cases were interpreted differently, the overall rate and extent of change in the songs would appear roughly the same as the border patterns suggest. About half the themes have border patterns, meaning they were present in more than one year.

One of the parameters that is subject to gradual change over time is rate of singing. When a pattern was present in two years but sung at different rates, we called it similar. For example, the 1970 song is little more than a slower version of the 1969 song, both the units and the silences between them being expanded so that every phrase takes longer in 1970 than its counterpart in 1969. In Themes 3, 4, and 5 this takes an intriguing form: units that were continuous in the first year are split in half in 1970 with pauses inserted between the halves. Interestingly enough, humpbacks often sing similar themes at different rates in adjacent years, and in almost every case the later song is the slower version (some examples are the first two of the last three themes in 1958 and 1959; Themes 3, 5, and 6 in 1963 and 1964; a rare exception is Theme 2 in 1961 and its counterpart, Theme 3 in 1963). In all years for which we have large samples, we can exclude the possibility that the expanded timing is due to individual variation. Thus it appears that whales tend to sing old themes more slowly than new ones. This same tendency has been documented in Hawaiian humpback songs (PAYNE et al. 1983).

We have also indicated as similar some themes which are quite variable. Themes in Fig. 1 with the border (. . . . .), while they are the least specifically comparable, have certain characteristics in common: most units are rapidly rising sounds of medium to high pitch; and their rhythm is less predictable than the rhythm in other themes.

The material in Fig. 1 which we have labeled (~~~~~~~~) is also variable, but in every case the basic phrase includes a long pulse train. It is delivered at various rates in different years. In 1974 and 1975, it is so slow that the individual pulses are seen on the spectrograms. There is also a behavioral parallel from year to year here, for this is the theme in which the whale usually breathes. The remaining parallels indicated by the borders in Fig. 1 are more self-evident.

We will now look through the songs chronologically. The final themes in 1957—1959 all contain rapidly descending tonal units. We have no data for 1960 or 1962, but 1961, 1963, and 1964 do not contain any theme with rapidly descending units. In fact, 1957—1958 was the only period out of the 13 years we have sampled in which such a theme type was heard. In 1959 it was slightly modified and then it disappeared.

There were also two phrase types, (▮▮▮▮▮▮▮▮▮▮▮▮) and (〰〰〰〰), which were only heard in 1958 and 1959. Not only these specific themes but also their sequence in the song was parallel.

We have no data for 1960. Some degree of similarity between 1959 and 1961 songs is apparent in the first themes (long pulsive units) and the second (three short rising units followed by one or more longer high unit). However, the differences were more conspicuous, so we categorized these as "different" themes.

We have no data for 1962, but two of the themes from 1961, though modified, were present in 1963 in the same sequence. Every theme in 1964 was closely similar to one in 1963 and the sequence was the same. But by 1968 and 1969, all the old themes except one had changed markedly.

Our sample for the 6 years between 1969 and 1975 is missing only one year of data. No matter which year we choose, it is apparent that the song is a composite of original material and material carried over from songs of the previous year.

The following general conclusions emerge from a survey of Fig. 1:

1. Songs from nearly every year include material unique to that year which distinguishes it from all others (op. cit.). The material which is unique to each year includes not only the phrases without border patterns but numerous details within the bordered phrases as well. The unique features include both pitch and rhythm. In fact, we have found that it is possible to identify the year from which a sample was drawn simply by observing the rhythmic sequence of its component themes.

There are indications of the importance of rhythm to other species. Extensive playback experiments indicate that species recognition in several bird species is based at least as much on rhythm as on pitch (FALLS 1969; EMLEN 1972). The case is even better documented in frogs. STRAUGHAN (1973) reports the temporal pattern, specifically the pulse repetition rate, is used to code species-specific information in mating calls of *Hyla ewingi*. Although we do not understand why humpback whales change their songs, it is interesting that rhythm plays a prominent part in the changes.

2. Most songs include some thematic material that is not unique to that year, and consecutive years usually have more in common than widely separated years. Note, for instance, that the 1958 song shares four themes with the 1957 and 1959 songs but none with songs from 1961 and later. As the number of years between samples increases, the similarities are less exact, so that even when our border patterns run through several years we find the closest detailed similarities in adjacent years.

However, even in adjacent years the ratio of different to similar material is erratic. Songs of some adjacent years are extremely similar throughout, while others have only one theme in common. For example, the songs for 1957 and 1968 each contain only one theme closely resembling, by our definition, material in any of the other 12 years of our sample while the songs from 3 pairs of years (1963 and 1964, 1969 and 1970, and 1974 and 1975) are similar in most

themes. Other pairs of adjacent years (e.g., 1970—1971 or 1971—1972) contain about half new and half overlapping material.

We have compared the number of similar themes or partial themes in songs that are 1, 2, 3 . . . 18 years apart. The songs span the period between 1957 and 1975. On the average, 63 % of all themes were shared in songs of adjacent years, 20 % in songs separated by 2 to 11 years, 5 % in songs separated by 12 to 14 years, and 0 % in songs from 15 or more years apart. Only in adjacent years' songs were as many as four whole or partial themes shared and, in general, the wider the separation in time, the fewer and less exact similarities we find between songs.

3. Similar themes have the same relative position in the song. For instance, not only do the same border patterns occur in 1969 and 1970, but they also occur in the same sequence.

These parallels in the songs make it clear that singers of each year are familiar with the songs of the year before. The most parsimonious conclusion is that the changing songs are the product of a group of whales, at least some of whose members are overlapping from year to year. This conclusion has been confirmed in Hawaii. Not only have individuals been resighted over the years (DARLING et al. 1983) but songs have been recorded from the same individual over periods spanning as much as a year. The individual's song changes just as does the song of the group (GUINEE et al. 1983).

No song type, once lost, has returned in its entirety although most of the units and some of the phrases are reminiscent of other years. But the changes appear to be progressive, not cyclical.

Do all themes have the same rate of extinction? A glance at Fig. 1 shows that they do not. Some themes last only one year while others last up to 7 or 8 years. There is one theme (with the border pattern ~~~~~~~~) that retains its identity through 15 years. In the years when we took behavioral notes while recording, we found that whales typically breathe during this theme (first noted by WINN et al. 1971). The common ingredient is a long, drawn-out pulse.

Since Fig. 1 omits the years for which we have no data, it is likely that the rate of change appears more erratic than it was. In Fig. 4, we plot the replacement of themes and suggest by extrapolation what may have occurred in the missing years. The picture obtained by this means shows a fairly gradual and orderly procession of themes, with old material overlapping with new in every year. Every 5 or 6 years, a period of relative stability was reached, during which songs remained quite similar throughout a pair of years.

A detailed study of humpback whale songs recorded through two consecutive years in Hawaii illuminates, on a finer scale, some mechanisms by which songs change in that population (PAYNE et al. 1983). There is little doubt that the differences we observe in our annual sampling of songs from Bermuda are the result of a similar process continuing over many years.

PAYNE et al. (1983) demonstrate that humpbacks change their songs in many ways continuously throughout the six months of each singing season, with all singers roughly concurring on the nature, rate, and extent of each

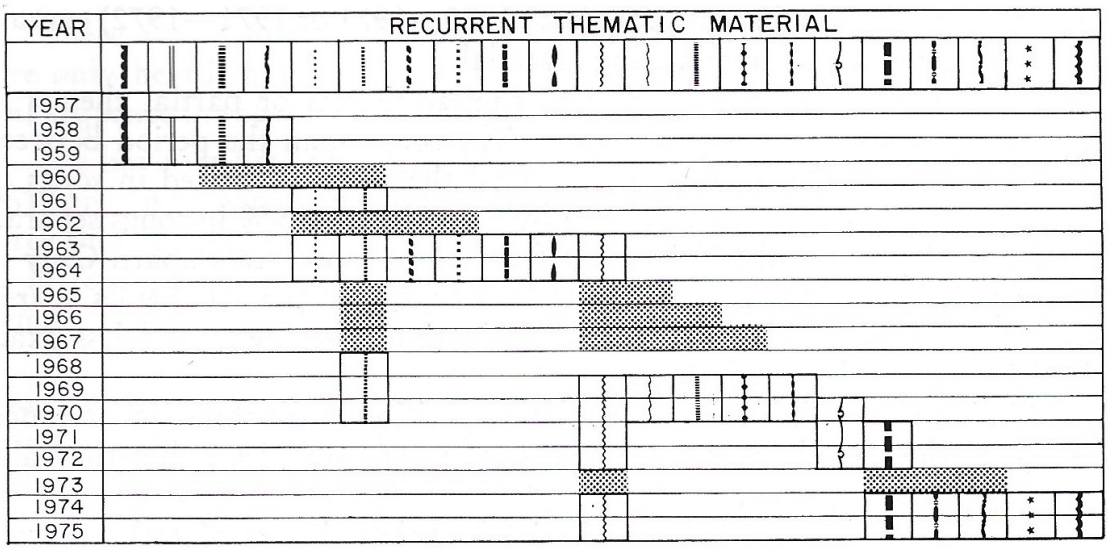


Fig. 4: The evolution of songs between 1957 and 1975, as revealed by the presence of themes that persisted two or more years in the song. Themes heard only in one year are not included. The designs are the border patterns from Fig. 1 and refer to the same material

change. The song is then stored with only a small amount of change until the following year, and when it is first heard it is sung much as it was last heard in the previous season. As the year advances, the songs diverge progressively from the songs heard at the start of the season.

The average amount of change from the Hawaiian song type in January to the song type in May of the same year is within the range of the average amount of change observed in Bermuda samples one year apart. The Bermuda songs analyzed in this present paper thus probably represent a series of glimpses, at one-year intervals, into a continuous process of change during the singing months of many years.

1968: An Exception or a Non-representative Sample?

The song from 1968 has far less in common with the song from 1969 than do any other adjacent years' songs in our sample. Let us experiment by omitting the 1968 song from our sample. Because we have no data for 1965—1967, this leaves the 1964 song to be compared with 1969. They show some interesting similarities. Both have first themes which alternate pulsive with tonal units, second themes which include the longest pulses in the song, third themes which alternate high squeaks with pairs or trios of rising units, and fourth and fifth themes which are static and contain only low frequencies.

The correspondence not only of theme types but also of their sequence argues for a continuity between songs from 1964 and those of 1969. In fact, these two songs from 5 years apart have quite a lot more in common with each other than either of them has with the sample from 1968. All this combines to make the January 1968 song an exception to an otherwise logical progression.

Group Singing

Circumstances in which only one singing whale is audible on the offshore banks are relatively rare. At least a duet or trio is usually audible, and if we separate out the voices in a recording of several voices, we find that all individuals are singing songs and that all songs are typical for that time period. The songs overlap randomly and with typical internal variability, as if each singer were oblivious of the specific progress of the others around it and was locked into its own routine. At times, particularly at night, "choruses" of many voices are heard, though they are never heard in unison; one can laboriously separate out the loudest voices and find the predictable progressions of continuous, overlapping songs typical to the period in which they occur.

We will demonstrate this by unravelling here a quartet of whales recorded on April 28, 1971. This is not an unusual example. The method of analysis is as follows. Listening with earphones to a stereophonic recording of a group of simultaneous voices, one can distinguish differences in loudness, in voice qualities (sometimes due to the effect of ocean conditions between the hydrophone and the whales), and in gross directions to the various participating voices.

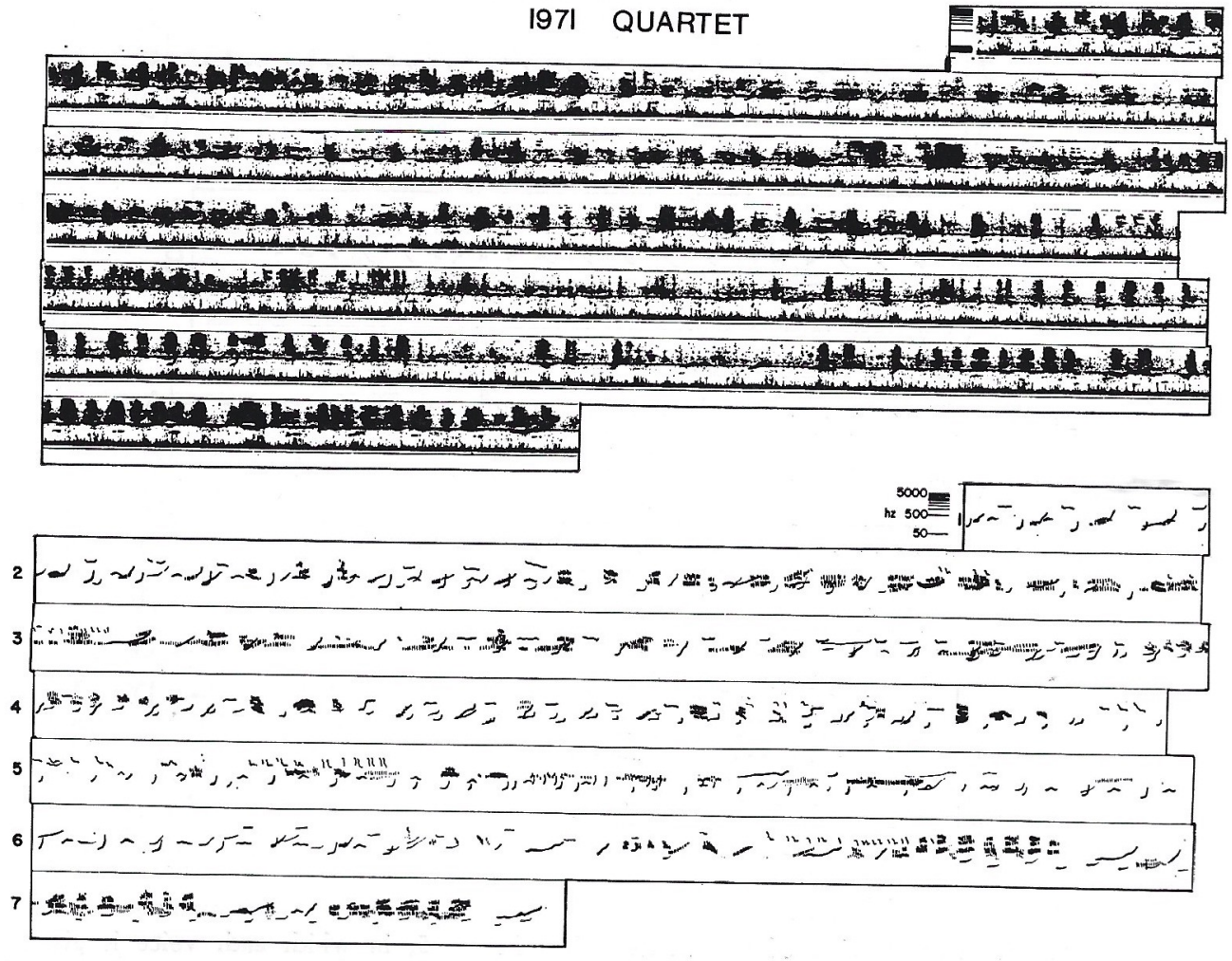


Fig. 5: Spectrogram made from a recording of four humpback whales singing simultaneously. Below, we have traced out the separate voices (see text for method of telling the voices apart). The selection includes one complete song by one of the voices

One then chooses the clearest (probably closest) voice, and traces out the sounds believed to be that voice only, from the spectrographic representation of all the sounds, while listening to the tape from which the spectrogram was made. One then goes back through the tape and traces a second voice, and so on. Looking at the results later, the validity of the tracing is weighted in favor of the best heard voices as the others contain gaps where the softest sounds were not picked up by the spectrograph. There is no way of being sure whether the next sound following a gap was made by the same animal. In general the likelihood of confusion increases the fainter the voices become.

Fig. 5 shows a spectrogram and tracing of a quartet recorded in 1971. Fig. 6 is a direct retracing of the tracing in Fig. 5, with each voice portrayed

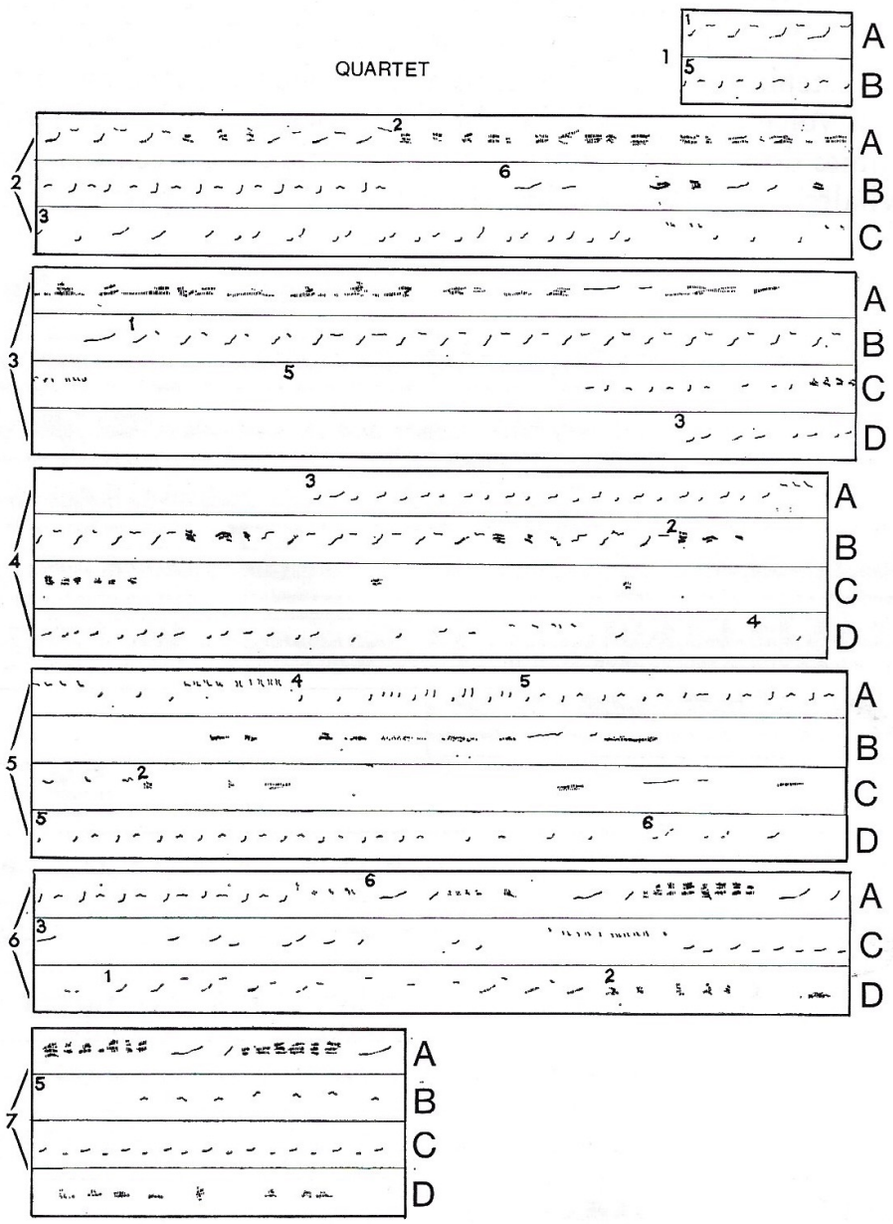


Fig. 6: A direct tracing of the whale voices in Fig. 5, in which each voice is given a separate line (as in an orchestral score). Numbers on the left refer to the line of the original spetrogram from which the voices were traced. Letters on the right identify the whale responsible for each line

on a separate line, as in an orchestral score. The standard 1971 themes are identified in each voice by numbers corresponding to the labels on Fig. 1b. From this we see that although the whales are singing asynchronously, each whale is following the same sequence of themes as the others and as the type song for 1971.

In Fig. 7, we compare the songs of the quartet with each other and with two consecutive songs from a solo session recorded on the same day. Because our recordings that day were continuous we know that the solo whale was Whale A in the quartet. We notice no differences between Whale A's performance when singing alone and when other voices were audible.

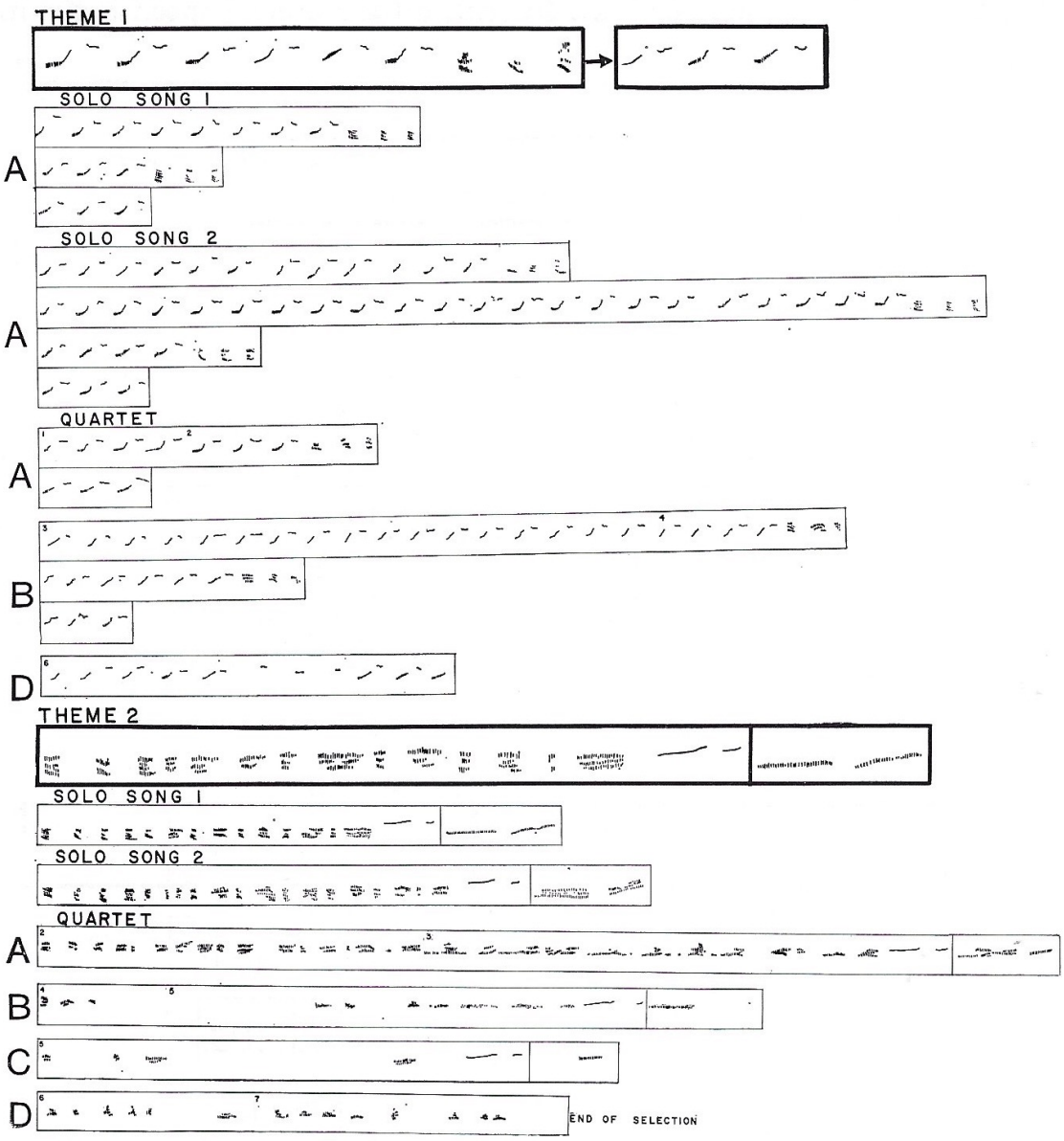
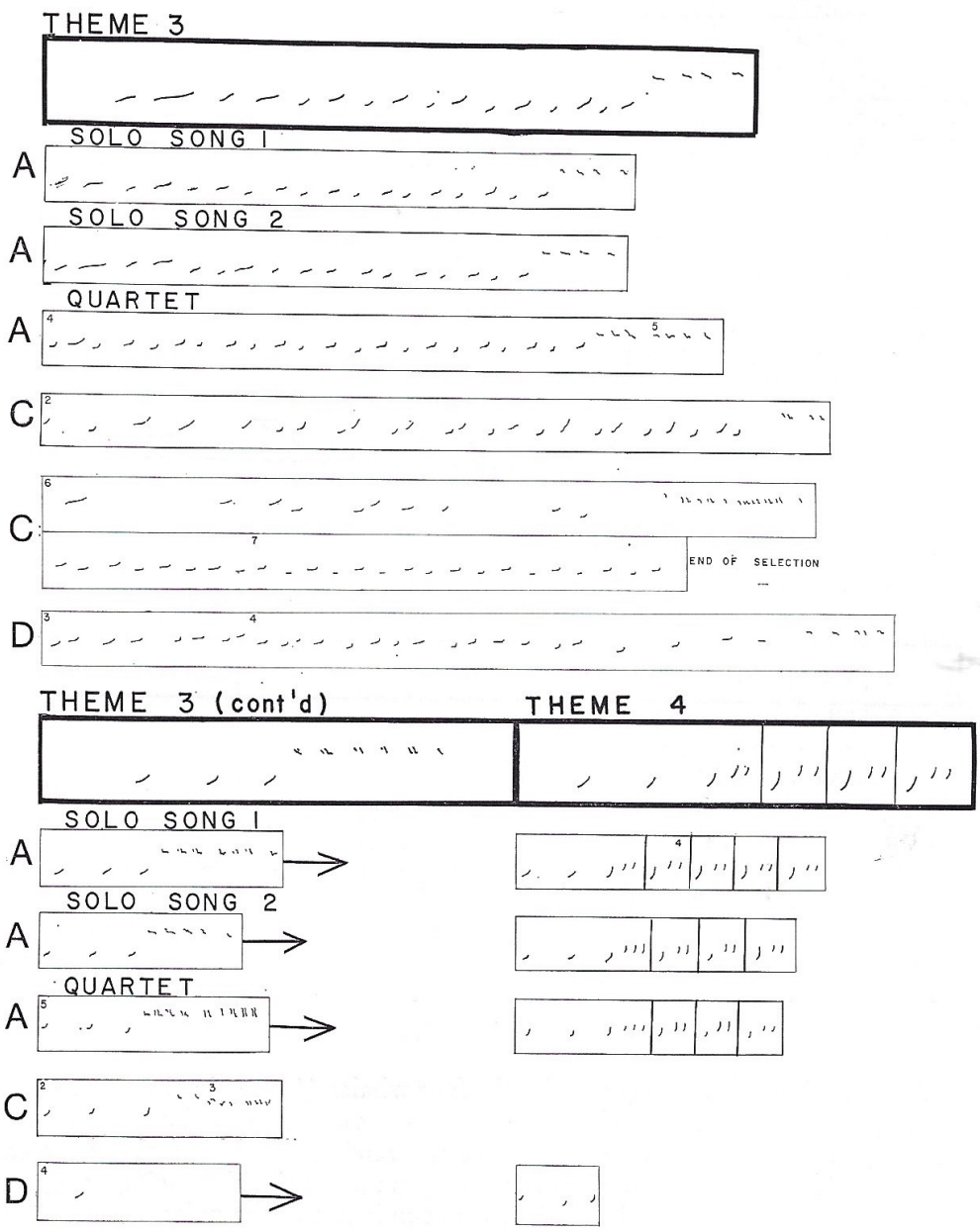


Fig. 7: A comparison of the songs sung by the four whales (A—D) in the quartet (from Figs. 5 and 6) with two songs from a whale singing alone on the same day. A typical phrase is shown under each theme title, and under this the renderings of that theme by each whale. Small numbers identify the line in the spectrogram from which tracings originated. Long spaces probably indicate sounds lost in the noise

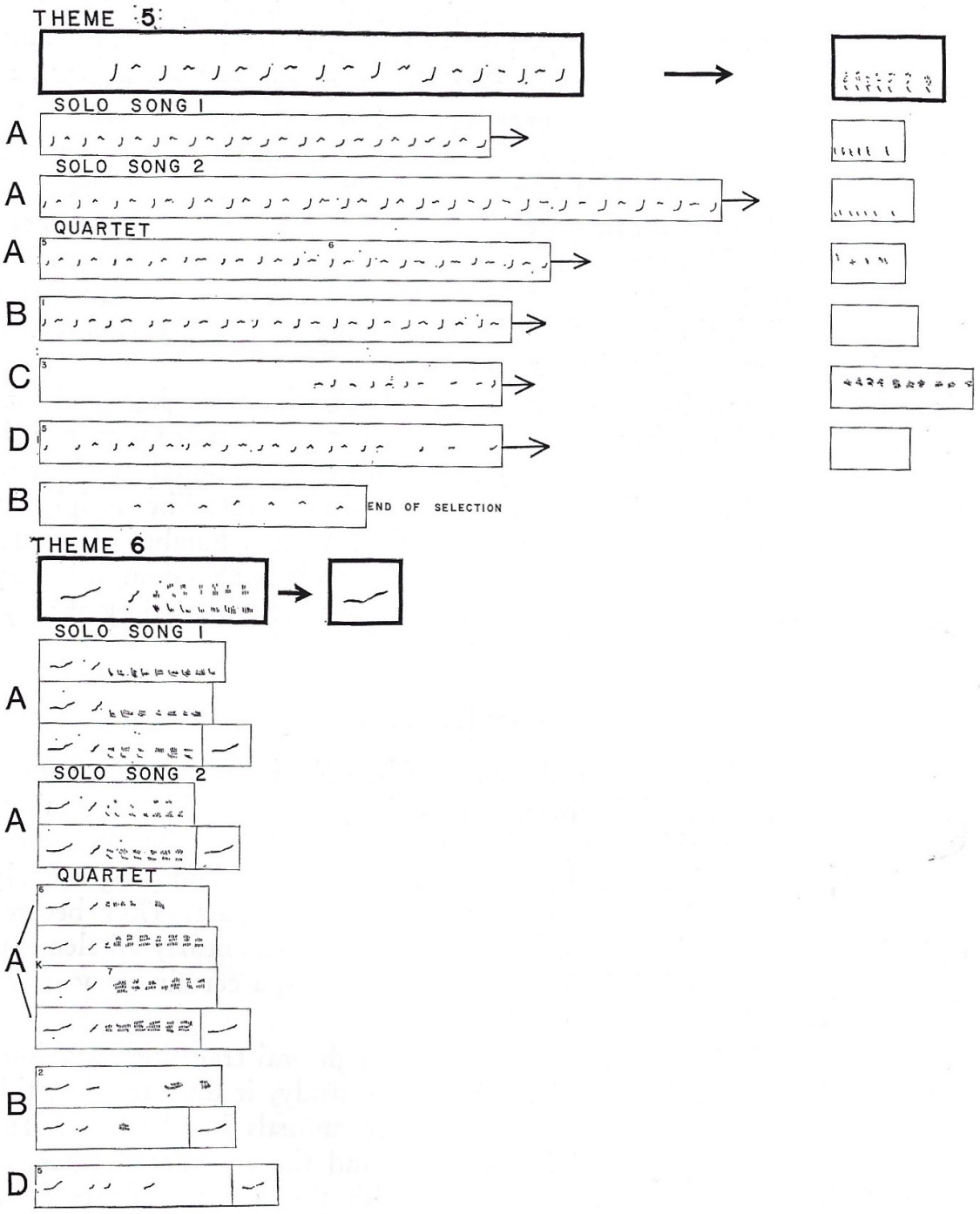
From this analysis we get an indication of intra-individual variation (by comparing the two solo songs and voice 1 of the quartet) and of inter-individual variation (by comparing the four quartet voices). While a good deal of variation of both types existed, it was all within a much narrower range than the variation between different years. For example, the most variable theme (Theme 3) contained much latitude even in the three renditions by the same whale, but its overall construction was such that we would not confuse even the most atypical rendition of it with a theme in another year's song.

We have analyzed in the same way tapes containing several simultaneous, overlapping songs from 1969 and 1970. These two years were chosen because they contain much similar material, and we wondered whether individual variation might be great enough so that songs from the two years could be confused. But this was not the case. In fact, all the annual-specific qualities



of each year were retained throughout both selections, with even more consistency than in the 1971 quartet. The data we present in Figs. 5—7 shows the greatest inconsistency of the multiple-voiced selections that we have analyzed.

Less detailed analyses, both by ear and by superficial examination of spectrograms, extend the general conclusion to all years for which we have trios, quartets, etc. In every case we hear only material characteristic of that time period, and all singing voices adhere, with occasional interruptions and minor exceptions, to the same sequence of material as that heard in solo sessions.



Do Whales Sing in Unison?

When whales sing within audible range of each other, do they modify their songs? In the sample for 1971, no alteration of the solo whale's song is obvious when it participates in the quartet as the "voice 1". However, it is conceivable that the apparent asynchrony of songs in most situations where several voices overlap could be due to differential delays in sound arrival over different distances from the receiving hydrophones. Several objections to this argument can be cited, of which we will mention three: 1. For a sound to arrive at the hydrophone with a 1 min delay, the whale making it must be roughly 60 miles away, which is probably much farther than the sounds in humpback song carry (PAYNE and GUINEE 1983), yet many of the asynchronous themes heard in group singing are more than 1 min out of phase with each other. 2. If a whale very close to the hydrophone were attempting to sing in synchrony with others, the hydrophone should report that the songs are at least roughly in phase with each other; this hardly ever happens in our sample. 3. If whales were attempting to sing in synchrony, all simultaneously recorded songs would be roughly the same length, and would have roughly the same number of phrases per theme. Such is not the case. Fig. 8 gives an example: A three-voiced selection from 1970 which we analyzed the same way as the 1971 quartet. The loudest whale took 24 min to complete one song (it repeated the third theme 15 times and the fifth theme 23 times), while during this same period one of its companion singers completed three songs!

While we have not found any long example of whales singing synchronously, it is possible that other more sophisticated ways of coordinating their sounds are of greater interest than singing in unison. Occasional portions of whale choruses can be described in terms of musical effects like antiphony, fugue, or pedalpoint. We can only comment that when a number of whales sing together, if the timing and overlapping of themes is not random, it is very sophisticated indeed, for in the selections we have studied, the variety of ways of combining voices seems almost limitless.

Concludings Remarks

In summary, we have studied the songs of humpback whales from one- to five-week samples collected in Bermuda in 13 years spanning a total of 19 years. All whales within one year's sample sing virtually the same song, which is long and complex. But the songs change strikingly and progressively over time. Songs of adjacent years always overlap in part. They become increasingly different as time elapses, and after 3 or 4 years nearly all elements in the song have been modified. A song type — that is, a certain sequence of themes — once lost, has not been heard again.

Studies of gradual changes in "culture" through oral tradition have long been the province of anthropologists. With this study, it appears that this concept may be relevant to the lives of other animals besides man. The existence of different songs in different areas, and the constant progressive changing of the song in each area, together with the recent evidence from

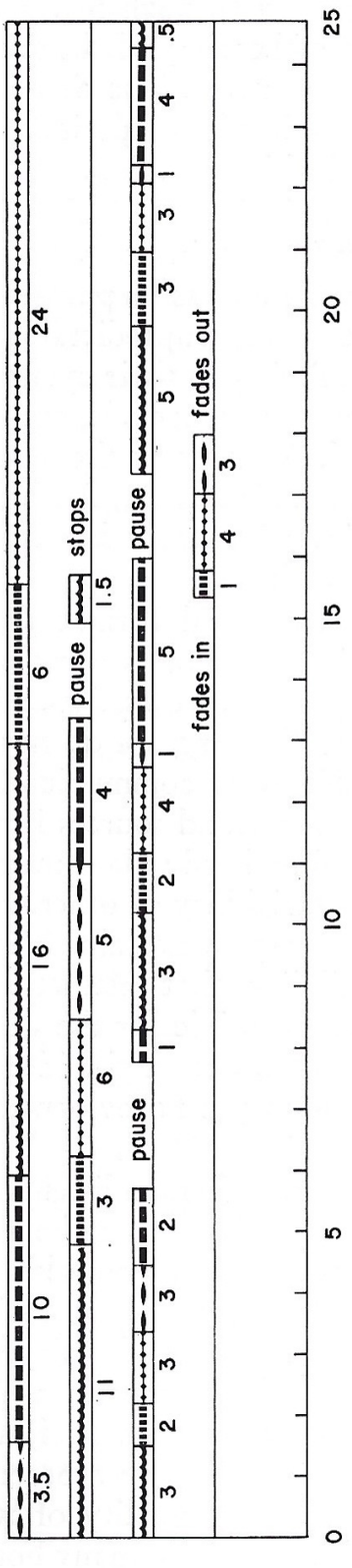


Fig. 8: Lengths of songs of three different whales heard singing together on April 13, 1970. Each line represents one whale, each pattern one theme. The number of phrases in each theme (given under the appropriate pattern) is the factor chiefly responsible for the different lengths of songs

Hawaii that individuals change their songs as does the group, leave no doubt that humpback whale songs are transmitted through learning. Through this, we believe that the whales are capable of hearing all the frequencies in their songs and of memorizing long complex patterns. The changing of humpback song thus constitutes evidence that the brain of one species of mysticete whale is capable of processing complex acoustical information.

The common ingredients of all humpback songs include a propensity for change, but they also include stability in certain formal characteristics. All songs we have studied are similar in the structures of phrases and themes, and in the predictability of sequence, but they are unpredictable as regards numbers of phrases in any theme. Songs are similar in their cyclic nature, the association of breathing with the completion of a song cycle, and the nature of the units of which all songs are constructed. Apparently the species inherits a set of constraints (roughly equivalent to syntax in language) which guide the form that all songs take. The changes which occur, whether by error, drift, or improvisation, are limited by these constraints.

There are other qualities besides structural format that all humpback songs share. Perhaps the most interesting of these is complexity: every song contains a remarkable range of contrasting frequencies, dynamics, and rhythms. What part these play in the function of the song we do not know, although they probably reflect some of the problems of communication in the ocean, of pulling signals out of noise and locating sound sources in water. In particular, sections of the songs which are loud and redundant may be interpretable over fairly long distances. The extreme variability of other sections, especially those containing high soft sounds, is less easy to explain. HARTSHORNE (1956, 1973) has raised the intriguing possibility that aesthetic enjoyment and avoidance of monotony may be partly responsible for the variety and spacing in bird songs. Although we are prepared to accept the idea that such things play a part in humpback songs, there is as yet no evidence one way or the other.

It is interesting in this context that many human listeners consider humpback songs to be beautiful and intriguing. This seems to be a consequence not only of the tonal qualities of many of their sounds, but also of their complex and subtle organization. Elements contributing greatly to their fascination are the many "developments" of thematic material in the different theme types of every song, the rhythmic surprises in the themes in which phrases progressively expand or shrink and give rise to new material, and the fact that a once stable and predictable portion of a song may become unstable and transitional. The environment also changes the quality of whale voices and one may wonder whether a whale which remains for many hours in deep water just over the edge of a bank where the echoes are particularly rich is pleased by what it hears. In the words of D. R. GRIFFIN, "Perhaps animals perform some of the behavior patterns we observe because they enjoy the resulting experience . . . One can even postulate that pleasant feelings that result when a physiological capacity is exercised are in themselves adaptive" (GRIFFIN 1976: 18).

In any case, it does give one pause to realize that the ocean has been resounding with whale song for millions of years, and that the ocean's inhabitants have long been swimming in the midst of these echoing choruses. It is not altogether surprising to find that humans nearly extinguished the whole source and only in the last few years have we begun to hear the music.

Zusammenfassung

In 13 Jahren (1957—1975) wurden bei Bermuda, jeweils von April bis Mai, 163 Gesänge von Buckelwalen aufgenommen und analysiert. In jedem Jahr sangen alle Wale im Grunde denselben Gesang. Über die Jahre änderten sich diese Gesänge deutlich; Gesänge, zwischen denen mehrere Jahre lagen, waren deutlich verschieden.

Alle Gesänge haben den gleichen Grundaufbau, an dem sich Änderungen über die Zeit aufzeigen lassen. In Walgruppen treten Gesänge auch dann auf, wenn die Tiere in Hörweite voneinander sind. Intra- und interindividuelle Unterschiede waren kleiner als die Unterschiede zwischen aufeinanderfolgenden Jahren.

Die Bedeutung der Gesangsänderung ist unbekannt. Von keinem anderen Tier ist solche Weiterentwicklung eines Signalverhaltens einer ganzen Population berichtet worden.

Acknowledgements

We are grateful to the New York Zoological Society for its support of all aspects of the work reported here. This research was also sponsored in part by the National Science Foundation. We are grateful to the late Frank WATLINGTON, who first introduced us to the sounds of humpback whales and whose tapes are the source of all our data in the years 1957—1964, except for the 1963 tape from SCHEVILL, WATKINS and COLEMAN. We thank Anthony PERRONE for the 1968 tapes. We are particularly grateful to Dr. and Mrs. H. Clay FRICK, David WINGATE, and David LINES for the generous contribution of their boats and facilities during a number of expeditions. Peter MARLER and Donald GRIFFIN of The Rockefeller University gave us equipment and help. We have received much help both on expeditions and in data analysis from friends: Oliver BRAZIER, Eleanora D'ARMS, Jane FRICK, Paul HYSLOP, Jim and Steve JOHNSON, Ron JOHNSON, Anthony KAESBEY, Victoria ROWNTREE, and Henry WASHBURN, to name a few. We are grateful to John and Walter MCILHENNY for their support during the final revisions and manuscript preparation. Nancy CISON and Linda GUINEE typed the whole iceberg of which this manuscript is just the tip. The graphic work in Figs. 4 and 8 is kindness of Victoria ROWNTREE. For critical reading of the manuscript in various stages we thank James BIRD, Eleanor DORSEY, James GOULD, Stephen GREEN, Linda GUINEE, Jan HEYMAN, Donald KROODSMA, Peter MARLER, William SCHEVILL, and William WATKINS. There are many others who have helped. Thanks to all.

Literature Cited

CHITTLEBOROUGH, R. G. (1958): The breeding cycle of the female humpback whale (*Megaptera nodosa*) (Bonnaterre). Aust. J. Mar. Freshw. Res. 9, 1—18.

DARLING, J. D. (1983): Migrations, abundance, and behaviour of "Hawaiian" humpback whales (*Megaptera novaeangliae*). Ph. D. Diss. Univ. Calif., Santa Cruz • DARLING, J. D.,

K. M. GIBSON and G. K. SILBER (1983): Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off West Maui, Hawaii 1977—79. In: Communication and Behavior of Whales. (PAYNE, R., ed.) Westview Press, Boulder, pp. 201—222 • DARLING, J. D., and C. M. JURASZ (1983): Migratory destinations of North Pacific humpback whales (*Megaptera novaeangliae*). In: Communication and Behavior of Whales. (PAYNE, R., ed.) Westview Press, Boulder, pp. 359—368.

EMLEN, S. T. (1972): An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour **41**, 130—171.

FALLS, J. B. (1969): Function of territorial song in the white-throated sparrow. In: Bird Vocalizations. (HINDE, R. A., ed.) Cambridge Univ. Press, Cambridge, pp. 207—232 • FRUMHOFF, P. (1983): Aberrant songs of humpback whales (*Megaptera novaeangliae*): Clues to the structure of humpback song. In: Communication and Behavior of Whales. (PAYNE, R., ed.) Westview Press, Boulder, pp. 81—127.

GRIFFIN, D. R. (1976): The Question of Animal Awareness. Rockefeller Univ. Press, New York • GUINEE, L. N., K. CHU and E. M. DORSEY (1983): Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). In: Communication and Behavior of Whales. (PAYNE, R., ed.) Westview Press, Boulder, pp. 59—80.

HARTSHORNE, C. (1956): The monotony-threshold in singing birds. Auk **73**, 176—192 • HARTSHORNE, C. (1973): Born to Sing — an Interpretation and World Survey of Bird Song. Indiana Univ. Press, Bloomington.

KATONA, S. K., P. HARCOURT, J. S. PERKINS and S. D. KRAUS (eds.) (1980): Humpback Whales: A Catalogue of Individuals Identified in the Western North Atlantic Ocean by Means of Fluke Photographs. College of the Atlantic, Bar Harbor, Maine.

MITCHELL, E., and R. R. REEVES (1983): Catch history, abundance, and present status of Northwest Atlantic humpback whales. In: Historical Whaling records. (TILLMAN, M. F., and G. P. DONOVAN, eds.) Rep. Int. Whaling Commn. Special Issue 5, Cambridge, pp. 153—209.

PAYNE, K., P. TYACK and R. PAYNE (1983): Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii. In: Communication and Behavior of Whales. (PAYNE, R., ed.) Westview Press, Boulder, pp. 9—57 • PAYNE, R. (1979): Humpback whale songs as an indicator of "stocks". Abstr. Pres. Third Biennial Conf. Biol. Marine Mammals, Seattle, Wash. • PAYNE, R., and L. N. GUINEE (1983): Humpback whale (*Megaptera novaeangliae*) songs as an indicator of "stocks". In: Communication and Behavior of Whales. (PAYNE, R., ed.) Westview Press, Boulder, pp. 333—358 • PAYNE, R. S., and S. MCVAY (1971): Songs of humpback whales. Science **173**, 585—597 • PERKINS, J., and H. WHITEHEAD (1977): Observations of three species of baleen whales off northern Newfoundland and adjacent waters. J. Fish. Res. Bd. Can. **34**, 1436—1440.

SCHEVILL, W. E., and W. A. WATKINS (1962): Whale and Porpoise Voices. A phonograph record. Woods Hole Oceanogr. Inst., Woods Hole, Mass. • STRAUGHAN, I. R. (1973): Evolution of anuran mating calls: Bioacoustical aspects. In: Evolutionary Biology of the Anurans. (VIAL, J. L., ed.) Univ. of Missouri Press, Columbia, pp. 321—327.

THOMPSON, P. O., W. C. CUMMINGS and S. J. KENNISON (1977): Sound production of humpback whales, *Megaptera novaeangliae*, in Alaskan waters. J. Acoust. Soc. Am. **62**, 89 • TYACK, P. (1981): Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behav. Ecol. Sociobiol. **8**, 105—116.

WHITEHEAD, H., B. BAXTER and G. NICHOLS, Jr. (1978): Preliminary report on the populations of humpback whales on Silver, Navidad, and Mouchoir Banks during the winter 1977—1978. Ocean Res. Educ. Soc., Boston • WINN, H. E., P. J. PERKINS and T. C. POULTER (1971): Sounds of the humpback whale. 7th Ann. Conf. Biol. Sonar Diving Mammals, Menlo Park, Calif. • WINN, H. E., T. J. THOMPSON, W. C. CUMMINGS, J. HAIN, J. HUDNALL, H. HAYS and W. W. STEINER (1981): Song of the humpback whale — population comparisons. Behav. Ecol. Sociobiol. **8**, 41—46 • WINN, H. E., and L. K. WINN (1978): The song of the humpback whale, *Megaptera novaeangliae*, in the West Indies. Mar. Biol. **47**, 97—114.

Authors' addresses: Katharine PAYNE, Laboratory of Ornithology, Cornell University, Ithaca, N.Y. 14850, U.S.A.; Roger PAYNE, World Wildlife Fund — US, 1601 Connecticut Ave. NW, Washington, DC 20009, U.S.A.