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Behavioral correlations with aberrant patterns in humpback whale songs

Kevin Chu[1,2] **and Patricia Harcourt**[2]

[1] Department of Biology, Boston University, 2 Cummington St., Boston, Massachusetts 02215, USA
[2] Ocean Research and Education Society, 19 Harbor Loop, Gloucester, Massachusetts 01930, USA

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Summary. Humpback whales emit long, patterned vocalizations referred to as "songs". We analyzed songs from 22 recording sessions whick took place from January to April, 1980 on Silver Bank, Dominican Republic. The sequence of patterns (which we call "themes") in these songs is remarkably regular. In this sample, there were 427 transitions from one theme to another. Only 20 of these did not follow the expected sequence. We present evidence that some themes are sung out of their usual order far more often than others. We also show that when themes are sung out of sequence, the whale is at the surface, blowing. This finding provides a link between the song structure and humpback behavior. Because aspects of the song structure can be linked to breathing, we hypothesize that a function of the songs is to show how long a whale can hold its breath, and that the duration of a song may be an indication of stamina and physical condition.

Introduction

Humpback whales (*Megaptera novaeangliae*) emit sounds in long, repetitive patterns referred to as "songs" (Payne and McVay 1971). Recent work has begun to elucidate the behavior of singing whales (Winn and Winn 1978; Herman and Tavolga 1980; Tyack 1981; Whitehead and Moore 1982; Tyack 1983; Darling et al. 1983). Very little is known, however, about how specific parts of the song relate to humpback behavior. Until now, only one aspect of the song structure has been correlated with whale activity. Winn and Winn (1978) have described a sound in the Carribbean song called a "surface ratchet" which was heard just before blowing. Although the Hawaiian song does not have such a ratchet, there is apparently a "chirp" sound which often precedes blowing (Tyack in Herman and Tavolga 1980). Song volume decreases as a singer comes to the surface and increases again when the whale dives after a sequence of breaths (Tyack 1981). Our observations agree with those of Winn and Winn that there is a surface ratchet in the 1980 Caribbean song which usually, but not always, precedes blowing. This paper will discuss another attribute of the songs which is correlated with respiration.

In the analysis of humpback song patterns, we use the terminology proposed by Payne and McVay (1971). Discrete sounds called "units" comprise readily recognizable patterns called "phrases". An unbroken series of similar prases we call a "theme". A series of themes make up a "song". Songs themselves may be repeated again and again, and a continuous sequence of songs sung by one whale is called a "song session".

One of the least variable features of humpback songs is the order of the themes (Winn and Winn 1978; Payne et al. 1983; Frumhoff 1983). At any given time, virtually all whales within an area sing the same themes in the same sequence, (e.g. – 1, 2, 3, 4, 5, 6). Some songs do not follow the usual sequence perfectly, however. One or more themes may be omitted (e.g. – 1, 2, 4, 6). Some themes are omitted more often than others, and some themes are almost never deleted. Such rarely deleted themes have been called "fundamental themes" (Frumhoff 1983). Frumhoff defines a fundamental theme as one which is sung in all songs of at least 90% of the song sessions recorded in a given season and at least one contiguous season.

Correspondance to: Kevin Chu, Ocean Research and Education Society, 19 Harbor Loop, Gloucester, MA 01930, USA

Because we have recordings from only one season, we must modify Frumhoff's criterion. For this study, therefore, we define a fundamental theme as one which is present in 95% of all the song sessions in our sample. Like Frumhoff, we define an "aberrant theme transition" to occur when "two themes that are typically separated by one or more fundamental themes are sung in succession". A truncated song pattern such as (1, 2, 4, 6) would be considered aberrant if theme 3 were a fundamental theme, since in at least 95% of the song sessions themes 2 and 4 would not be juxtaposed. However, it would not be aberrant if only themes 2 and 4 were fundamental.

This paper will consider two questions about these aberrations. First, when an aberrant theme transition occurs, is the new theme chosen randomly or are some themes involved in aberrations more often than others? Second, do aberrations correlate with observable humpback behavior?

Methods

Humpback whales were recorded on Silver Bank (approximately 60 miles north of the Dominican Republic) from January to April 1980. The recordings were made from a 10 m sloop (*Elendil*). We used either a Gould UT-19 or an Aquadyne AQ-17 hydrophone with a Barcus-Berry 1330 preamplifier. The signal from the hydrophone was recorded with a Marantz "Superscope" tape deck onto Maxell UD-60 tapes.

Recording sessions lasted at least half an hour, and some whales were recorded for an hour or more. Singing whales were identified by listening for sudden decrease in the volume of the song and watching for the whale to surface during the brief period of attenuation (Tyack 1981). The whale was then identified by the shape of its dorsal fin and the markings on its flukes (Katona et al. 1979). When the whale surfaced during each subsequent attenuation of the song's volume, it could be repeatedly identified using these markings. During all daytime recording sessions, behavior notes on the singing whale were kept, including the time of each surfacing and any surface activities, including blows.

In all we collected 40 tapes. The 24 best half-hour recordings were chosen for further study. These tapes were selected only for their clarity. Good tapes had a high signal to noise ratio and were not confused by the simultaneous recording of more than one nearby whale. These 24 tapes contained 22 different song sessions. Although we were unable to photographically identify all singers, none of the 74 whales we photographed during the 1980 season were found on more than one day (Whitehead 1981), so we suspect that each recording session was of a different whale. From these recordings spectrograms were made using a Spectrodynamics 301 real-time analyzer making 20 scans per second and a Raytheon SAR-97 printer.

On each spectrogram, each phrase of each theme was marked and a chart was made of the order in which the themes were sung. Using the criterion described above, we identified the fundamental themes in our sample. Any aberrant juxtaposition of themes was noted.

To see if some themes are more likely to be sung out of order than others, we used a Cochran's Q test (Zar 1974). This method tests for differences in the distribution of a dichotomous variable in a random block experimental design. We considered each whale a "block" and scored the presence (=1) or absence (=0) of aberrant theme transitions to each theme.

Table 1. The number of times each theme is sung out of order in an aberrant theme transition

Theme	Number of times sung out of order
1	0
2	3
3	1
4	1
5	0
6	6
7	0
8	0
9	9
10	0

By comparing the timing marks on the tapes with times noted in our behavior notes, we were able to see which parts of the songs were correlated with surface behavior, particularly with respiration. Since the chronometer used on deck for the visual observations was not the same as the one used below deck while recording, however, we were only rarely able to locate the exact unit in the song during which the whale was blowing. Almost always, though, we were able to tell in which phrase or phrases a whale blew, and we were always able to correlate an observed behavior with a point in the song give or take 20 seconds.

We looked at each aberrant theme transition to see if it was associated with blowing. Any time a whale blew in the two phrases immediately preceeding an aberrant jump or in the two phrases immediately following one, we counted this as an association. We then compared the frequencies with which aberrant and non-aberrant theme transitions were associated with blowing. We also counted the number of times when the song became temporarily fainter within two phrases of an aberrant theme transition even though no blow was seen. We feel that it is likely that during these faint periods blows occurred which we did not see. To err on the side of caution in our statistics, however, we considered theme transitions to be associated with surfacing only if blows were actually seen. Theme transitions for which surfacing was suspected but not confirmed, were considered to be unassociated with surfacings for this analysis.

Results

Three themes in our sample fit our criterion for a fundamental theme. These were theme 1, theme 6 and theme 9. Theme 1 is the theme which contains the surface ratchet. Usually, blowing was observed after we heard this theme. In our sample there were at least three occurrences of theme 1 after which no blow was sighted or suspected, however.

The number of songs that were interrupted by an aberrant theme transition was surprisingly high in our sample. Frumhoff (1983) reports that only 11.4% of all the song sessions in his sample were aberrant. In contrast, we found that 40.9% of our

Table 2. A comparison of the number of aberrant and non-aberrant theme transitions which are associated with blowing

	Blowing	Not blowing	Blowing suspected but not seen	Total
Non-aberrant theme transition	68 (17%)	324 (80%)	14 (3%)	406 (100%)
Aberrant theme transition	13 (65%)	1 (5%)	6 (30%)	20 (100%)

song sessions (9 out of 22 whales) sang at least one aberrant theme transition. Despite the high percentage of songs which contain an aberrant theme transition, aberrations are still rare. In our sample, there are 426 theme transitions. Only 20 of these (4.7%) are aberrant.

Some themes were sung out of order more often than others ($P<0.25$). Thus, when aberrations do occur, the theme sung out of order is not chosen randomly. In the 1980 Caribbean song, two themes are sung out of order much more often than any of the others – themes 6 and 9 (Table 1). 15 out of the 20 aberrant theme transitions in our sample involved jumping to one or the other of these two themes. Note that both these themes are fundamental themes. Four out of the remaining five aberrations jumped to theme 2 or 3, which is the part of the song where blowing usually occurs.

Table 2 shows the frequency with which aberrant and non-aberrant theme transitions were associated with breathing. Blows were seen just before or just after 13 of the 20 aberrations which we analyzed (65%). In six other aberrant theme transitions (30%) the song got faint and blowing was suspected though not seen. Thus in 95% of all aberrant theme transitions in our sample, we either saw or suspected that the singer surfaced to breathe. In only one aberrant theme transition (5%) was there no evidence that the whale surfaced. This is markedly different than for non-aberrant theme transitions (χ^2 test, $P<0.001$), in which only 68 out of 406 (17%) were clearly associated with blowing. In 14 of the non-aberrant theme transitions (3%) blowing is suspected but not confirmed. Of the 68 non-aberrant theme theme transitions which were associated with blowing, 57 occurred between themes 1, 2 and 3, which were the part of the song in which blowing was expected to take place. We conclude that when whales sang aberrant theme transitions in the 1980 Caribbean song they were usually blowing. Blowing, then, was closely associated either with an aberrant theme transition or, more commonly, with the surface ratchet (theme 1) and its subsequent themes (2 and 3). There were only 11 theme transitions during which blowing was seen or suspected, but which were neither aberrant nor between those themes immediately following the surface ratchet.

Discussion

Each of the themes which we have found to be fundamental in the 1980 Caribbean song is associated with blowing. Theme 1 contains the surface ratchet. When this was heard, blowing almost invariably followed. Our results show that aberrant theme transitions are associated with blowing, and the other fundamental themes, themes 6 and 9, were the ones to which a whale would usually jump when making an aberrant theme transition. It is possible that these themes are common in humpback songs because they are somehow linked with breathing.

This analysis suggests that when aberrations in the song pattern occur whales are almost invariably in the process of blowing. A direct corollary of this finding is that when the whales are not at the surface there are virtually no aberrations. No matter where the whale starts singing when it surfaces, it will usually continue in the normal sequence of themes until the next surfacing. This raises the possibility that other whales could tell from the song pattern (or from aberrations in the pattern) when the singer is at the surface. The decrease in the loudness of the song when the whale is at the surface could serve the same function, although this volume decrease may be hard to detect at a distance or if many singers are present. Winn and Winn (1978) speculate that a possible function of the surface ratchet may be to let other humpbacks know that the singer is surfacing.

One piece of information which humpback songs contain, then, is when the singer is breathing. They also tell, therefore, when he is not breathing. One puzzle about humpback songs is why they are so long. The maximum reported song length of about 30 minutes (Payne and McVay 1971) is the same as the theoretical maximum breath-holding capability (Tomilin in Winn and Reichley 1985). Since the structure of humpback songs can

carry information about how long an individual can hold its breath, we hypothesize that singing whales are engaging in what amounts to a "breath-holding contest". The duration of the songs may be a demonstration and advertisement of a whale's stamina and physical condition. Stamina appears to be an important characteristic for success in other aspects of male humpback mating competition, notably in "rowdy groups" (Tyack and Whitehead 1983). A "higher quality" male would be able to hold his breath for a longer time and his song would be longer. Note that the ability to hold one's breath would be of great value to any mammal living in the sea.

Our hypothesis, that song duration is an important feature of the songs, generates several testable hypotheses. We predict that there are differences in behavior and perhaps in distribution based on the length of a whale's song. For example, because singing may be less advantageous to whales with short songs, they may be more likely to stop singing and use an alternative mating strategy. They may also sing in areas where singing competition is less intense. In addition, each humpback should sing as long a song as he is capable of, and singers of long songs should not be more stressed than the singers of short songs. Also, females should chose to associate with males on the basis of song length. This might be demonstrated by playback experiments using songs of different durations. Ultimately, longer songs should lead to increased reproductive sucess, though this may be impossible to show, since mating as seldom if ever been observed in humpbacks (Winn and Reichley 1985).

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