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## Song copying by humpback whales: themes and variations

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**Abstract** Male humpback whales (*Megaptera novaeangliae*) produce long, structured sequences of sound underwater, commonly called “songs.” Humpbacks progressively modify their songs over time in ways that suggest that individuals are copying song elements that they hear being used by other singers. Little is known about the factors that determine how whales learn from their auditory experiences. Song learning in birds is better understood and appears to be constrained by stable core attributes such as species-specific sound repertoires and song syntax. To clarify whether similar constraints exist for song learning by humpbacks, we analyzed changes over 14 years in the sounds used by humpback whales singing in Hawaiian waters. We found that although the properties of individual sounds within songs are quite variable over time, the overall distribution of certain acoustic features within the repertoire appears to be stable. In particular, our findings suggest that species-specific constraints on temporal features of song sounds determine song form, whereas spectral variability allows whales to flexibly adapt song elements.

**Keywords** Baleen whale · Sounds · Acoustic · Mysticete · Song learning

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### Introduction

Insects, humans, frogs, birds, and whales produce a wide variety of structured sound sequences, commonly described as songs. Some animals (e.g., birds) learn to sing specific songs based on their sensorimotor experiences during development, whereas others (most notably humans) can learn to sing new songs throughout adulthood. Experimental studies of song learning in birds have revealed that experience-dependent song variation during development is often constrained by stable core attributes such as species-specific sound repertoires and song syntax (Marler 1997). Song development in birds typically involves progression toward a final adult song (or set of songs) that “crystallizes,” becoming fixed in structure and content. Song learning in adult humans is clearly more flexible than in adult birds and may therefore depend on substantially different learning mechanisms. It is not yet clear whether any species learns to sing in ways that are comparable to humans.

Song learning is a special case of vocal learning, and vocal learning can be viewed as a special kind of imitation. Relatively few mammals have the ability to imitate either sounds or actions (reviewed by Whiten 1992; Janik and Slater 1997; Caldwell and Whiten 2002; Herman 2002), limiting the species that could potentially be used in studies of song learning. Based on currently available data, there appears to be only one group of mammals other than humans that can vocally imitate: marine mammals. In particular, bottlenose dolphins spontaneously imitate sounds in their environment (Reiss and McCowan 1993) and can be trained to imitate sounds on command (Richards et al. 1984). Most cetaceans do not naturally learn to sing, and it is questionable whether it would be possible to teach cetaceans to produce rhythmic sound sequences. There are a small number of cetacean species that do naturally sing, however, all of which are baleen whales (for review, see Clark 1990; Edds-Walton 1997).

The extent to which baleen whales (mysticetes) learn the songs they sing is largely unknown. The best evidence of mysticete song learning has been obtained from

humpback whales (*Megaptera novaeangliae*). All studies of song learning in humpback whales to date have been observational, consisting of subjective comparisons of sound sequences produced underwater by singing whales and recorded at a distance using hydrophones (e.g., see Winn et al. 1970, 1981; Payne and McVay 1971; Winn and Winn 1978; Payne et al. 1983; Payne and Guinee 1983; Payne and Payne 1985). These studies have revealed that humpback whale songs consist of a cyclical pattern of several “themes” made of repeated “phrases,” which in turn consist of individual sound “units”; songs are repeated continuously within a “song session.” Consecutive songs sung by a whale within a song session are not identical, typically differing in total duration and in the number of times phrases of specific themes are repeated. Songs may also differ in theme composition (Payne et al. 1983; Helweg et al. 1990). Singing humpback whales progressively modify theme and phrase characteristics throughout a single season and from one year to the next (Payne et al. 1983; Payne and Payne 1985). Even so, at any given time, songs produced within a population are highly similar, suggesting that singers copy one another (Guinee et al. 1983; Payne et al. 1983; Payne and Payne 1985). In contrast, the specific themes and phrases within songs produced by geographically separated populations may differ greatly (Winn et al. 1981; Payne and Guinee 1983; Helweg et al. 1990, 1998).

Unlike most songbirds, developing humpback whales do not converge on a species-typical song. Rather, humpbacks progressively change their songs throughout their lives. Humpback whale songs also differ from bird songs in that they usually last for 10 min or more, whereas bird songs typically last a few seconds; and humpback whale songs are repeated continuously without intervening pauses, whereas bird songs are usually separated by silent periods (Payne and McVay 1971). Although similarities between singing whales and singing humans have been reported (Gray et al. 2001), whale songs are clearly more constrained in structure and content than songs produced by humans. The rules that constrain the form of humpback whale songs are only beginning to be identified.

One “universal” rule of humpback whale song formation is that themes within a song will progress in a fixed sequence. Sequential ordering of themes is so typical that songs that do not follow this pattern are called aberrant songs (Frumhoff 1983). Other features of humpback whale songs are sufficiently prototypical that experienced investigators can recognize recordings as being from a singing humpback without hearing a complete song or theme. These recognizable features have yet to be quantitatively defined but appear to depend on subjective impressions of the timbre of units, as well as the spectrotemporal structure of phrases.

Phrase structure in humpback whale songs is much more flexible than in bird songs and can even be progressively modified within individual songs (described by Payne and Payne, 1985, as shifting themes). In shifting themes, units within phrases can change in number, frequency, frequency modulation, duration, and rate of

production. Some themes are composed of more stable phrases, which are repeated almost identically within individual songs (Payne and Payne 1985; Mercado et al. 2003). In contrast, other themes consist of sound sequences with no apparent structure (Payne and Payne 1985). The sound repertoire used by singing humpback whales appears to be continuously changing over time (Tyack 1981; Payne et al. 1983; Payne and Payne 1985). Cato (1991) noted that changes in the sound types produced by Australian humpback whales across just 2 years (1983–1985) were so pronounced that “they had to be considered to be new sound types, even though they may have evolved from the old ones” (p. 286). There are no reports of adult birds using such dynamic sound repertoires to construct their songs.

Although phrases within humpback whale songs are highly dynamic, recent analyses have revealed that both shifting and stable phrases can recur across populations and decades (Mercado et al. 2003). The first such phrase to be reported is known as a surface ratchet. This phrase is continuously modified throughout production within a theme, is frequently correlated with surfacing by a singing whale, and has been recorded near Hawaii (Helweg et al. 1990), the West Indies (Payne and Payne 1985), Australia (Cato 1991), and Mexico (Cerchio et al. 2001). Other recurrent phrases include a stable two-unit pattern recorded in the West Indies (Payne and McVay 1971) and Hawaii (McSweeney et al. 1989; Mercado et al. 2003), and a more complex multi-unit pattern recorded in the West Indies (Winn and Winn 1978), Australia (Mednis 1991), and Hawaii (Mercado et al. 2003). The discovery of these universal patterns suggests that elements of humpback whale songs are more tightly constrained than suggested by prior subjective analyses of song structure. A better understanding of which features of humpback whale songs are learned, versus which features are species typical, is needed to assess whether song copying by whales involves mechanisms comparable to those used by birds or humans.

To clarify this issue, we analyzed the variability of song units produced by humpback whales in Hawaii over 14 years. The acoustic characteristics of humpback whale song units were measured in detail from waveform and spectrographic representations and compared within and across years. Unlike prior multi-year analyses of humpback whale song that focused on changes in song structure observed in songs recorded from long distances (Payne and Payne 1985; Cato 1991), we focused exclusively on analyzing the basic acoustic properties of individual units within songs recorded from nearby singers. Variations in the acoustic characteristics of units over time were evaluated to derive a quantitative as well as a subjective evaluation of song unit variability. Consistent with past reports, we observed that the sound repertoire used within humpback whale songs varied substantially across years. Additionally, our findings suggest that the sound repertoire used by singing humpback whales is more tightly constrained in the temporal domain than in the spectral domain. We speculate that singing humpback whales are

selecting spectral modulations within a species-specific temporal template based on their experiences.

## Methods

### Materials

Humpback whale songs were recorded at a number of locations in Hawaii from 1981 to 1995 by researchers from the Kewalo Basin Marine Mammal Laboratory in Honolulu. Most recordings were made near the Kawaihae Harbor on the northwestern coast of the island of Hawaii, in waters less than 180 m deep. Recordings collected from 1992 to 1995 were made using an uncalibrated Labcore customized hydrophone (sensitive to 12 kHz) attached to an Archer customized mini-amplifier (catalog no. 227-1008B) that was connected to a Marantz cassette recorder (Model PMD430, frequency flat to 17 kHz). The hydrophones and recording equipment used to make recordings in other years varied but reportedly all had frequency responses flat from 50 Hz to 10,000 Hz. Recordings were made by deploying a hydrophone from a small boat positioned less than 50 m from the singing whale. Recording singers from short distances minimized propagation-related distortion (e.g., absorption, multipath-ing) of recorded units. The quality of these recordings was initially assessed through aural and spectrographic inspection. One hundred tapes, containing approximately 50 h of recorded humpback whale song, were evaluated using a

rating system based on signal amplitude level, amount of intermittent noise, amount of constant noise, and presence of multiple singers. A sample of 35 recordings was then selected from these tapes based on their quality (e.g., signal-to-noise ratio), the year and month in which they were recorded, and their duration. Thirty-seven songs were isolated from these recordings for analysis; 4 songs were isolated for each year from 1985 to 1989 and from 1992 to 1995, and 1 song was isolated from 1981. Although only a small sample of high-quality recordings was available for analysis, songs from each year were highly similar and thus are likely representative of other songs produced in Hawaii during the same year. Recordings were not available from 1982 to 1984 and 1990 to 1992. For some years (1985, 1987, 1994) during which only a few high-quality recordings were made, 2 songs were taken from a single recording (i.e., sounds were sampled from 2 songs produced by an individual whale). It is unlikely that other sampled songs included whales that were re-recorded on different occasions, because singers are seldom recorded in the same area twice (Guinee et al. 1983; Payne and Payne 1985; Cerchio et al. 2001). The possibility remains that one or more whales were re-recorded on separate occasions, which could potentially bias comparisons between years. Note that this bias would apply equally to all acoustic measures and therefore should not affect variability between measures.

Tapes were played back using a Marantz cassette recorder Model PMD430 with a frequency response flat to 17 kHz ( $\pm 3$  dB). The signal from the cassette recorder was

**Table 1** Abbreviations of descriptors. *PRR* Pulse-repetition rate; *kpps* kilo-pulses per second

Abbreviations of descriptors	Descriptors	Units
Temporal descriptors		
DUR	Unit duration	s
INT	Interval of silence after a unit	s
TIMPK	Percentage of unit occurring before the peak amplitude	s/s
PRRMN	Mean PRR estimate	kpps
DPRR1	Change in PRR estimate from beginning to middle of the unit	kpps
DPRR2	Change in PRR estimate from middle to end of the unit	kpps
Spectral descriptors		
MINHZ	Minimum frequency with visible energy in spectrogram	kHz
MAXHZ	Maximum frequency with visible energy in spectrogram	kHz
PKHZ	Frequency with peak spectral energy	kHz
DPKHZ	Change in PKHZ from beginning to end of the unit	kHz
DNRG1	Relative change in energy from lower to middle frequency band	$\mu\text{J}/\mu\text{J}$
DNRG2	Relative change in energy from middle to upper frequency band	$\mu\text{J}/\mu\text{J}$

TIMPK was calculated by dividing the time until the peak amplitude by the total duration (DUR) of the unit. Calculation of PRRMN differed for short-duration and long-duration units. For long-duration units, six IPI samples were reduced to three intermediate values corresponding to the mean of the first and second, third and fourth, and fifth and sixth samples so that comparisons with shorter units could be made. PRR estimates were obtained for each of the three IPI values by calculating the number of IPIs that would occur over 1 s (e.g., an IPI of 10 ms would give a PRR estimate of 100 pulses per second, or 0.1 kpps). PRRMN was then calculated by averaging the three PRR estimates. DPRR1 was calculated by subtracting the first PRR estimate from the second, and DPRR2 was calculated by subtracting the second PRR estimate from the third. Calculation of DPKHZ differed for short-duration and long-duration units. Three PKHZ samples collected for long-duration units were reduced to two intermediate values corresponding to the mean of the first and second sample and the mean of the second and third sample, again to allow for comparisons with shorter units. DPKHZ was then calculated by subtracting the second PKHZ measurement, corresponding to the second half of the unit, from the first PKHZ measurement. DNRG1 and DNRG2 were calculated by dividing energy measurements from the lower, middle, and upper frequency bands by the total energy of the unit, and then differences between these ratios were determined.

fed directly into the sound input of an Apple Power-Macintosh 7100/80 computer. Waveforms and spectrograms were produced on the Macintosh using Canary software (version 1.2B) from the Cornell Laboratory of Ornithology (Bioacoustics Research Program). A sampling rate of 22.05 kHz was used for all analyses and spectrograms were made using a filter bandwidth of 43.7 Hz. The SAS statistical analysis program (version 6.08), running on an IBM 9121 mainframe computer, was used for all statistical analyses.

## Procedure

Songs were initially assessed for thematic structure through repeated aural analyses. This involved identifying sets of repeated sound patterns and noting where on the recording the singing whale transitioned from one pattern to the next. Exemplary phrases were then selected from each theme based on clarity (i.e., signal-to-noise ratio) and aural distinctiveness from previous phrases. Individual units were extracted from these phrases. Transitional units (sounds typically found at the junction of two themes) and units that occurred only once within a song were also included in the sample. The goal of this purposive sampling technique was to characterize the range of individual sound variability present within each song.

Several quantitative measures were collected from each unit. Measurements of temporal characteristics such as unit duration and the duration of silence after a unit were collected from waveforms. Estimates of the pulse-repetition rate within a unit were obtained by measuring the duration of inter-pulse intervals sampled from the beginning, middle, and end of the waveform (i.e., the approximate first, second, and last third of the waveform). More extensive measurements were collected from spectrograms including time of peak signal amplitude, maximum and minimum frequency, frequency with peak energy overall, frequency with peak energy during the first and second

half of the unit, total energy, and distribution of energy across the upper, middle, and lower bandwidth of the unit. The precision of frequency measurements was constrained by the sensitivities of the tape playback system (described above).

## Data Analysis

Twelve variables were used to describe individual units sampled from humpback whale songs, including 6 temporal descriptors based on waveform measurements and 6 spectral descriptors based on spectrographic measurements (see Table 1). All unit descriptors were either direct measurements or calculated values derived from direct measurements.

The range of measured values for each descriptor was divided into 21 intervals. The number of units having acoustic features falling within the boundaries of each interval was then tabulated to form frequency distributions for each descriptor (i.e., each frequency distribution was represented by a 21-element vector, Table 2). Frequency distributions of measured sound characteristics were used to evaluate quantitatively the overall variability of sound repertoires both within and across years. The variability of a particular descriptor over time was first evaluated by comparing frequency distributions from each individual year with the distribution representing all measurements of that descriptor from all years. Frequency distributions were normalized by dividing each vector element by the standard deviation of the vector elements. The difference between two distributions ( $D$ ) was then calculated by taking the square root of the sum of the squared differences between the corresponding elements of the two distribution vectors to be compared, a Euclidean distance measure (see Table 2). Two identical distribution vectors would result in  $D$  equaling zero, and the magnitude of  $D$  for non-identical distributions reflects the geometric distance between the vectors representing

**Table 2** Process of converting frequency distributions into vector representations (example). *DUR* Unit duration

Vector representations of frequency distributions

*DUR* (1981–1995)

[23 183 219 135 70 49 24 16 14 11 15 11 5 6 5 8 5 7 2 2 3]

*DUR* (1995)

[7 23 26 9 3 1 1 1 1 1 1 2 0 0 2 2 1 4 0 0 1]

Normalized vector representations

*DUR* (1981–1995)

[0.4 2.9 3.5 2.2 1.1 0.8 0.4 0.3 0.2 0.2 0.2 0.2 0.1 0.1 0.1 0.1 0.1 0.1 0 0 0]

*DUR* (1995)

[1 3.2 3.6 1.3 0.4 0.1 0.1 0.1 0.1 0.1 0.3 0 0 0.3 0.3 0.1 0.6 0 0.1 0.1]

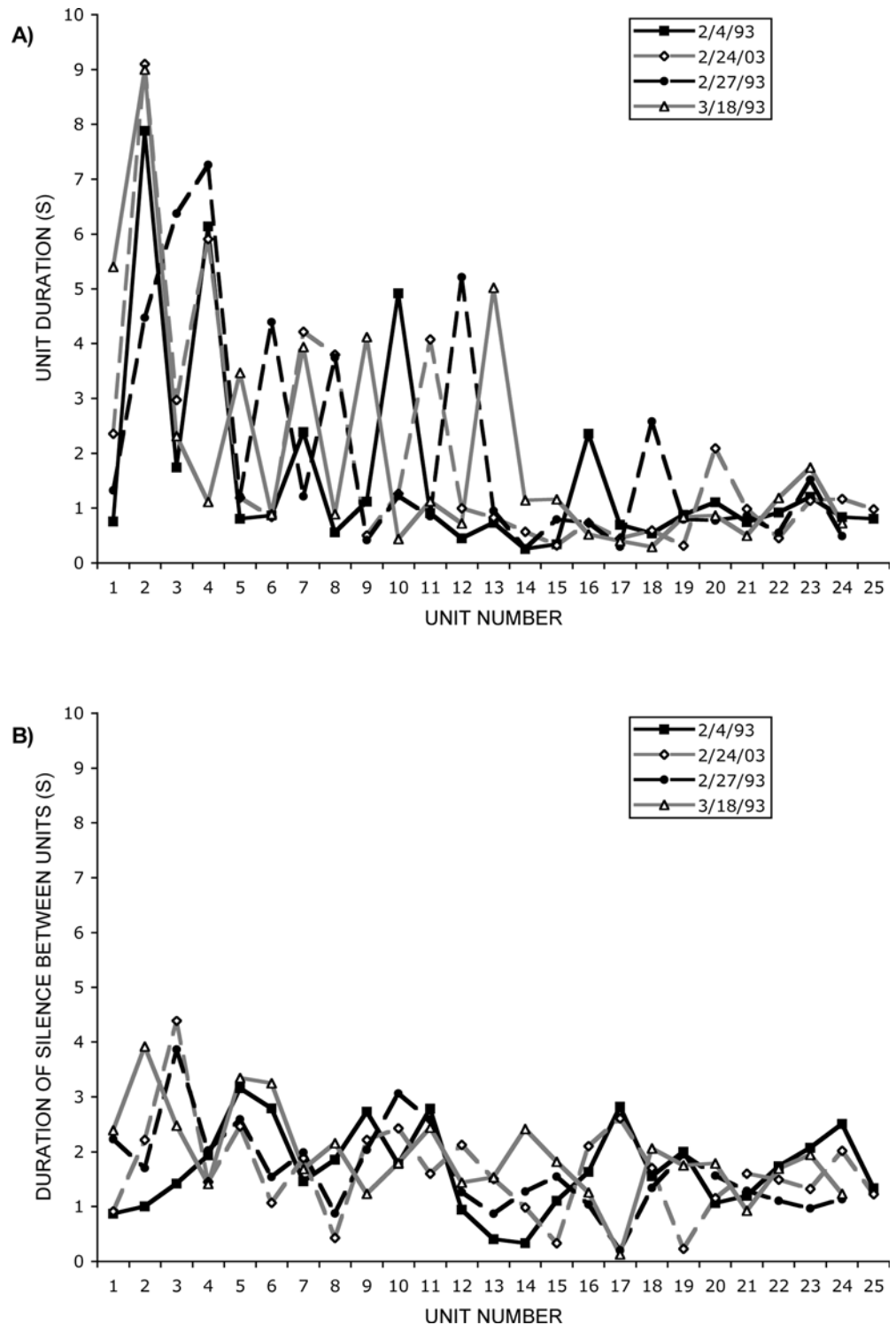
Distance calculation

$$D = \sqrt{(0.4 - 1)^2 + (2.9 - 3.2)^2 + \dots + (0 - 0.1)^2} = 1.6$$

Each element within the *DUR* vector corresponds to an interval of 0.5 s. The first element corresponds to the number of sampled units lasting less than 0.5 s. The second element corresponds to the number of sampled units lasting between 0.5 s and 1 s, and so on. Vectors were normalized to account for sample size by dividing each element by the standard deviation of the elements. The distance between two vectors was then calculated using a Euclidean distance measure.

the two frequency distributions. Pair-wise comparisons between frequency distributions from individual years were also calculated to assess the cumulative variability over time. Mean correlations were calculated by first converting correlation coefficients to  $z$  scores (Corey et al. 1998). The statistical significance of mean differences between distributions of distance measures was assessed with  $t$  tests.

**Fig. 1** Temporal characteristics of all units sampled from humpback whale songs recorded in 1993, shown in the order that units were sampled. Note that the number of units sampled from each recording differed by no more than one unit. Both **a** unit duration and **b** the duration of silence separating units decreased with song progression.



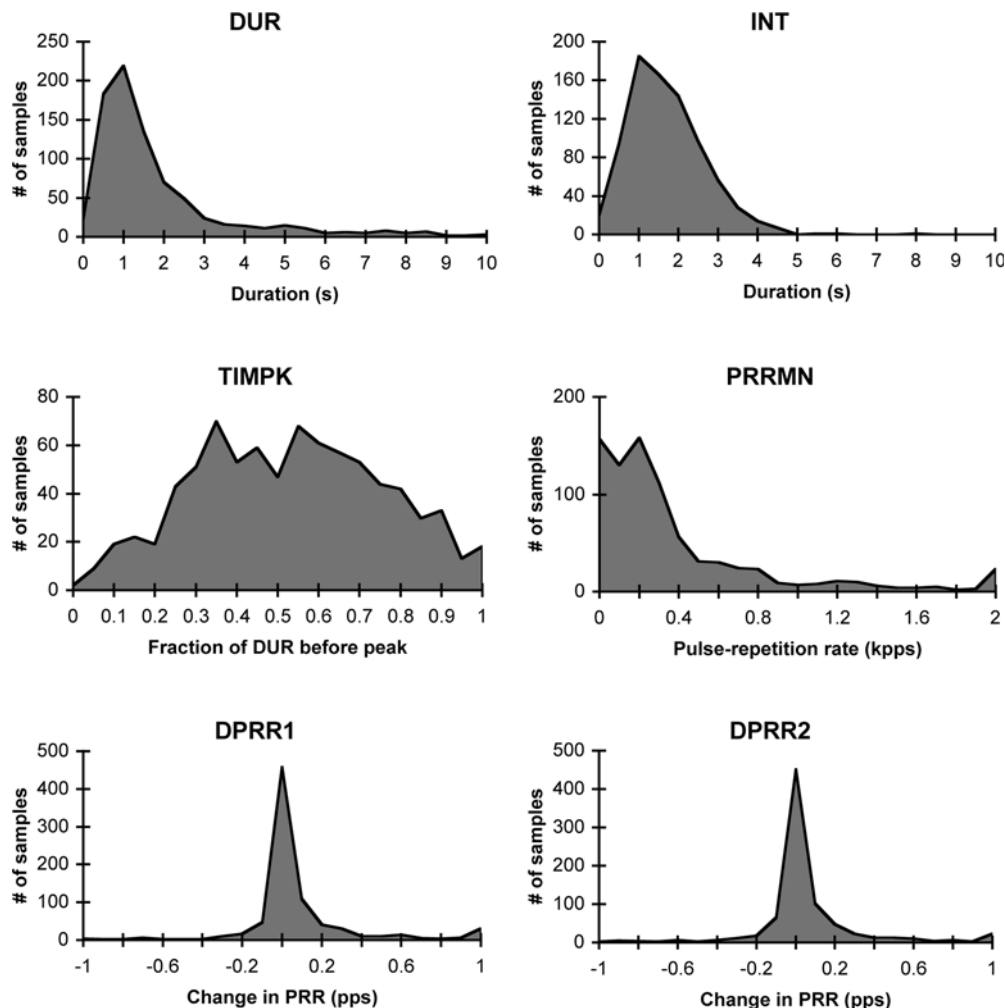
30; the number of units sampled generally reflected the number of themes present within a particular song. When comparable numbers of themes were present in all songs from a particular year, the number of units sampled from each song was highly similar (see Fig. 1). The mean number of phrases isolated from each song was  $6.6 \pm 1.5$ , and the mean number of units collected from each phrase was  $3.2 \pm 1.6$ . Songs recorded on different days within a particular year typically contained different subsets of the themes produced within that year, precluding detailed within-year analyses of repertoire variability. The one exception was songs recorded in 1993, all of which contained the same nine phrases. In all songs from 1993, a systematic decrease in unit duration with song progression was apparent ( $r_{98} = -0.5$ ,  $P < 0.001$ ; Fig. 1a); intervals of silence following units decreased as well ( $r_{98} = -0.3$ ,  $P = 0.0005$ ; Fig. 1b). No progressive changes in either maximum frequency ( $r_{98} = -0.1$ ,  $P = 0.3$ ; see S1a in the supplementary material) or peak frequency ( $r_{98} = 0.04$ ,  $P = 0.7$ ; see S1b) were evident.

Within-year comparisons of samples collected from songs recorded in 1993 provide a measure of the consistency in unit features recorded during a single year as well as a measure of the reliability of the purposive sampling technique used in this study. For example,

distributions of the durations of units and associated silent intervals were highly similar across recordings. The mean correlation between distributions of duration measurements in 1993 (mean  $\pm$  SD,  $n=6$ :  $0.96 \pm 0.02$ ) accounted for 92% of the common variance, and the mean correlation between distributions of interval measurements (mean  $\pm$  SD,  $n=6$ :  $0.97 \pm 0.03$ ), accounted for 94%. These high levels of consistency indicate that the sampling techniques used in this study were reliable, and that the temporal features of singers' sound repertoires in 1993 were stable. Interestingly, two spectral descriptors that might be expected to correlate (maximum frequency and peak frequency) showed less consistency across recordings. The mean correlation between distributions of peak frequency measurements (mean  $\pm$  SD,  $n=6$ :  $0.83 \pm 0.2$ ) accounted for 70% of the common variance, and the mean correlation between distributions of maximum frequency measurements (mean  $\pm$  SD,  $n=6$ :  $0.50 \pm 0.4$ ) accounted for only 25% of the common variance. These differences (see S2 for details) illustrate how basic acoustic measures can provide evidence of differential stability in the unit properties used by singing humpback whales.

Consistent with prior reports (e.g., Winn and Winn 1978), unit comparisons based on subjective aural analyses and visual inspections of spectrograms across

**Fig. 2** Overall frequency distributions of temporal characteristics, including sounds sampled from 1981 to 1995. See Table 1 for abbreviations.



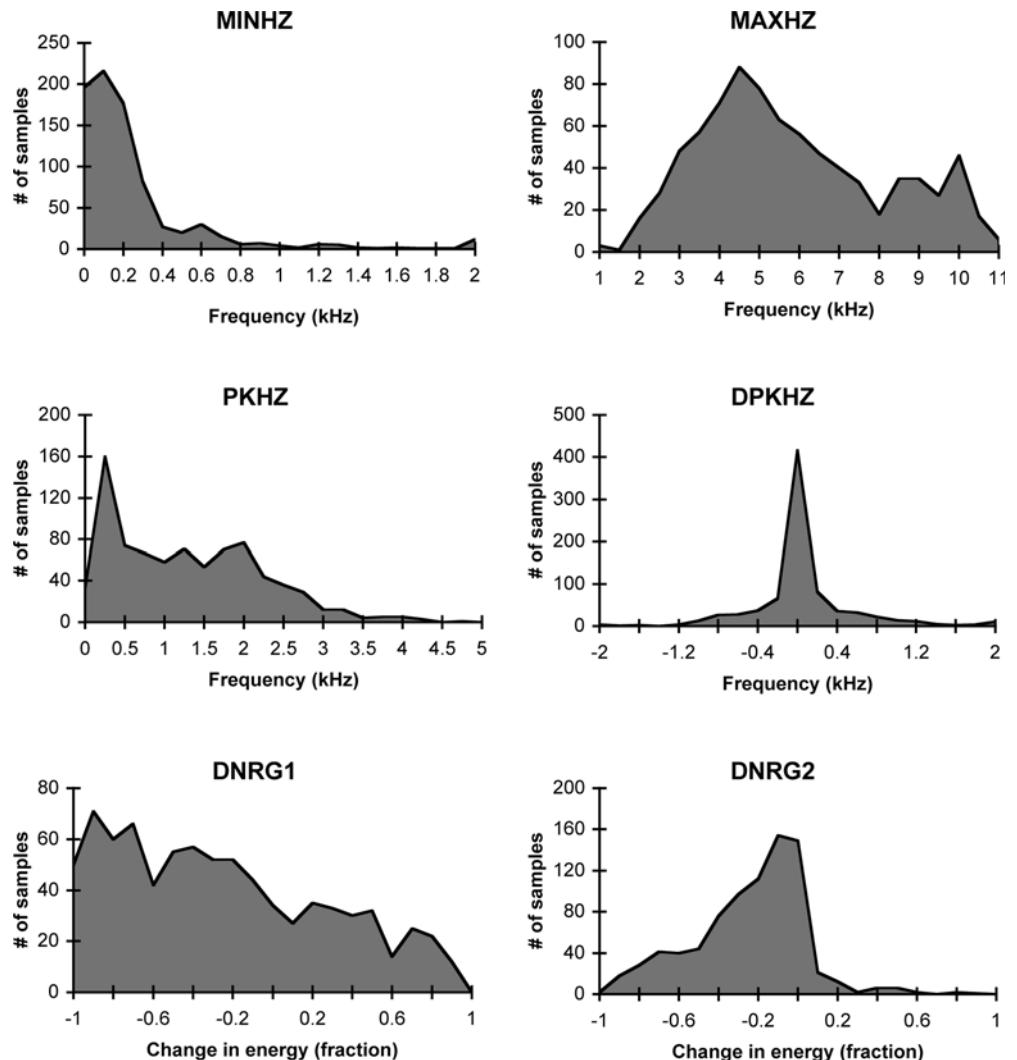
consecutive years revealed considerable overlap in the sound repertoires being used, whereas comparisons across non-consecutive years revealed fewer similarities. When representative spectrograms from songs separated by several years were compared, it was difficult to match units across years with confidence. Additionally, spectrographic analyses were sometimes misleading in that units that looked similar in spectrograms seemed dissimilar when analyzed aurally. Aural analyses of the variability of units sampled from different years generally corresponded well with spectrographic analyses but revealed more subjective variability than was apparent from spectrograms.

Frequency distributions of the quantitative measures of temporal descriptors for each year (see S3), and across all years (Fig. 2), were primarily unimodal. The duration of units within songs varied widely, ranging between 40 ms and 13.1 s. Most units were shorter than 2.0 s in duration (mean  $\pm$  SD:  $1.8 \pm 1.8$  s; median: 1.2). Interestingly, the interval of silence following units within humpback whale songs was distributed similarly to unit duration. In particular, the range (0.1–8.0 s) and mean duration ( $1.7 \pm 0.9$ ) of silent intervals following units within songs were

similar to those of unit duration; most silent intervals were less than 3.0 s in duration (median: 1.6). The point in time at which an individual unit reached its peak energy level was quite variable. Typically, units reached their peak energy about halfway through production of the unit. The mean pulse-repetition rate ranged between 0.01 kpps and 4.67 kpps (kilo-pulses/second), with a mean of  $0.4 \pm 0.5$  kpps. Changes in the pulse-repetition rate from the beginning to the middle of the unit, and from the middle to the end of the unit, showed similar distributions. The pulse-repetition rate of most units remained relatively constant, with a slight tendency to increase rather than decrease.

Frequency distributions of the quantitative measures of spectral descriptors also tended to be unimodal both within years (see S4), and across years (Fig. 3). As might be expected, the distribution of minimum sound frequency was similar to the distribution of mean pulse-repetition rate, ranging between 0.0 and 3.97 kHz (where 0 kHz represents the limit at the bottom of the spectrographic display), with most units having a minimum frequency below 400 Hz. Maximum frequency varied greatly, with most units having a maximum frequency above 3 kHz but

**Fig. 3** Overall frequency distributions of spectral characteristics, including sounds sampled from 1981 to 1995. See Table 1 for abbreviations.



below 8 kHz. The distribution of frequencies with peak energy was broad, with a large peak at around 200 Hz, and a substantial number of units with peak frequencies between 500 and 2,000 Hz. Changes in peak frequency paralleled those seen for changes in pulse-repetition rate. Most changes were less than  $\pm 400$  Hz, suggesting that peak frequencies typically were constant from the beginning to the end of most units. The change in energy from the lower to the middle frequency band was highly variable, ranging from a halving in energy to a doubling. Overall, units typically had less energy in the middle band than the lower band. About one-third of the units, however, had greater energy in the middle band than in the lower band. Changes in energy from the middle to the upper band were less variable, with most units showing decreased energy in the upper band compared to the middle band.

Distributions of temporal descriptors subjectively were less variable across years than distributions of spectral descriptors (compare S3 and S4). Statistical tests performed on distance measures characterizing differences in frequency distributions (summarized in Table 3) confirmed that spectral descriptors were more variable than temporal descriptors ( $t_{39} = -10.4$ ,  $p = 1.0 \times 10^{-12}$ ; see Fig. 4). Differences between distributions from different years did not vary consistently as a function of the span between the years being compared (i.e., increasing the number of years separating the samples did not increase the difference between distributions of the sound features measured from those samples).

## Discussion

Humpback whales appear to copy features of songs they are exposed to (Guinee et al. 1983; Payne and Payne 1985) and occasionally may copy entire songs (Noad et al. 2000). Unlike singing birds, adult humpback whales progressively modify their songs on a yearly basis (Payne and Payne 1985), never settling either on a predictable song structure or on a stable sound repertoire. Past studies have described how the structural features of

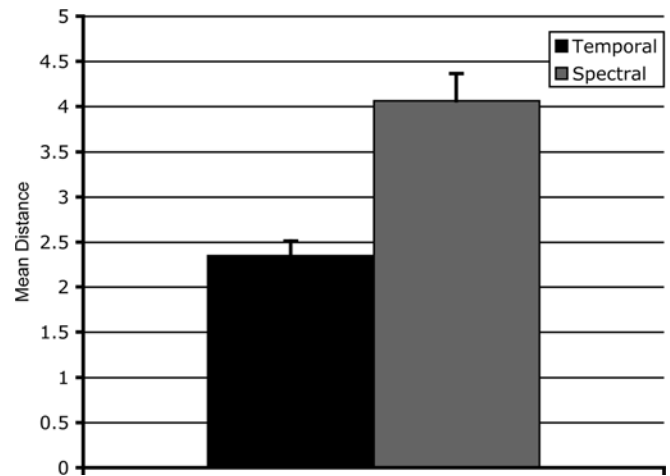


Fig. 4 The distance between frequency distributions from individual years was greater for spectral descriptors ( $t_{39} = -10.4$ ,  $P < 0.001$ ) than for temporal descriptors. Bars represent the mean distance, and error bars represent standard error

humpback whale songs change over time (Winn and Winn 1978; Payne and Payne 1985; Cato 1991). Our results provide the first quantitative assessment of cross-year variability in the sound repertoire used by singing humpback whales. Although singing humpbacks continuously modify the repertoire of units they use (Winn and Winn 1978; Guinee et al. 1983; Payne et al. 1983; Payne and Payne 1985; Cato 1991), they appear to do so within the boundaries of acoustic constraints that are stable for at least a decade.

Because we used purposive sampling techniques to characterize units produced by humpback whales from a restricted locale, we cannot yet determine whether the variability that we observed is representative of humpback whales around the world. Our main goal in using this technique was to characterize repertoire variability over time within a subpopulation of whales. Past analyses of humpback whale songs have been limited to structural analyses in part because when recordings are made from a distance, propagation within complex shallow water environments distorts the acoustic properties of individual

Table 3 Distance between overall distribution and distribution for each year

Descriptor	Distance from										Mean $\pm$ SD
	1995	1994	1993	1992	1989	1988	1987	1986	1985	1981	
DNRG1	5.2	2.7	4.4	6.5	4.4	7.4	8.3	5.0	4.3	7.1	5.5 $\pm$ 1.7
MAXHZ	5.4	4.3	4.4	4.7	5.8	4.7	4.9	4.8	5.9	8.0	5.3 $\pm$ 1.1
TIMPK	3.7	3.5	2.7	4.7	3.3	4.3	3.2	4.2	4.9	3.8	3.8 $\pm$ 0.7
PKHZ	2.7	3.8	2.9	3.0	3.3	4.7	5.6	3.2	3.0	3.4	3.6 $\pm$ 0.9
DNRG2	1.7	1.0	1.2	8.1	1.0	3.1	5.7	1.2	1.6	3.3	2.8 $\pm$ 2.4
PRRMN	2.4	1.5	1.8	1.5	2.1	3.2	2.0	1.9	2.6	2.9	2.2 $\pm$ 0.6
MINHZ	1.5	1.3	1.5	1.2	1.2	1.9	2.4	2.7	1.7	3.4	1.9 $\pm$ 0.7
DUR	1.6	1.2	2.1	0.7	2.3	1.7	2.5	1.6	1.7	2.1	1.8 $\pm$ 0.5
INT	1.9	1.7	1.5	1.0	1.3	2.1	1.6	1.2	2.4	1.6	1.6 $\pm$ 0.4
DPKHZ	0.6	0.7	0.7	0.7	0.6	0.9	0.7	0.6	0.9	1.4	0.8 $\pm$ 0.3
DPRR2	0.6	0.4	0.9	0.7	0.7	0.5	0.7	1.2	0.9	0.7	0.7 $\pm$ 0.2
DPRR1	0.7	0.8	0.9	0.6	0.4	0.8	0.6	0.3	1.1	0.7	0.7 $\pm$ 0.2

units (Mercado and Frazer 1999; Mercado et al. 2000). When recordings are made from nearby whales, as in the current study, more veridical records of the units produced within songs can be obtained, facilitating detailed quantitative comparisons between units. Because humpback whale song units are loud, reaching levels of 155–189 dB re 1  $\mu$ Pa (Richardson et al. 1995; Au et al. 2001; Pack et al. 2003), signal-to-noise levels within a 50-m radius of a solo singer are quite high.

Given that singing humpback whales are continuously modifying the repertoire of sounds they use, it is tempting to infer that they are continuously copying the units that they hear being produced by other whales. An alternative possibility, however, is that the acoustic morphology of units that are suitable for use in songs is constrained by preexisting circuitry within the humpback whale brain, and that the sound repertoire singers use within a particular year represents a selected subset of this repertoire. Marler (1997) suggested that such “learning by selection” can explain how most birds learn their songs. Behavioral evidence supportive of this neuroselective model in birds includes the facts that (1) few experiences are needed for birds to memorize a song; (2) birds favor conspecific songs; and (3) large-scale analyses of song variation show evidence of acoustic universals (Marler 1997). Although it is not known how many times a whale needs to hear a song (or song components) before being able to reproduce it, or how many different songs an adult whale hears in any given year, recent reports suggest that whales can learn entire songs after minimal exposure (Noad et al. 2000). There are no reports of humpbacks producing the songs or sounds of other species. Recent large-scale analyses of song structure have revealed universal phrase structures that are used by whales across years and populations (Mercado et al. 2003). Our findings here suggest that temporal features of individual units used by humpback whales singing in Hawaii are highly stable across years and thus may reflect innate constraints on the phonology of song elements.

We found several properties of humpback whale song units not noted in prior reports: (1) the pacing of unit production within humpback whale songs is consistent across years; (2) units are most likely to reach peak amplitude halfway through production of the unit, rather than at the beginning or end; (3) the frequency with peak energy within a unit is often in the middle of the band of frequencies spanned by the unit and is only weakly constrained by the position of the fundamental frequency; (4) temporal features of sound types and subsequent silent intervals may be progressively modulated within individual songs; and (5) distributions of spectral characteristics vary more than distributions of temporal characteristics both within and across years.

It is unclear whether spectral variability within and across years reflects individual differences in sound production, individuals modulating the spectral features of their sounds to accommodate the particular environmental context within which they are singing, an artifact of the position of the recording hydrophone relative to the

orientation and depth of the singing whale (Au et al. 2003), or some combination of these factors. What is clear is that humpback whales listening to songs from distances of more than 100 m will experience even greater spectral variability, because of distorting propagation (Mercado and Frazer 1999; Frazer and Mercado 2000). Listening whales hear songs in a wide variety of locations and from various distances. Consequently, the spectral features of song units that listening whales receive will be less predictable than the temporal characteristics.

Singing humpback whales probably do not attempt to replicate the distorted versions of song units that they receive. The existence of predefined phonological templates would greatly ease the reconstruction of distorted song units. If such templates are represented within humpback whales’ auditory processing systems, then they do not appear to constrain song units to contain particular frequencies. Singing birds are known to produce sounds with stereotypical spectral features (reviewed by Catchpole and Slater 1995), and to be highly sensitive to absolute differences in frequency content (Weisman et al. 1998). Birds do not easily recognize sounds transposed across frequency ranges (Hulse and Cynx 1985), whereas humans and bottlenose dolphins are known to be able to transpose complex sounds immediately from one frequency range to another (Richards et al. 1984; Ralston and Herman 1995). The ability to recognize and classify sounds independent of their specific spectral content may thus play a more important role in song learning by humpback whales than in song learning by birds.

Singing humpback whales use a graded repertoire of units that they continuously modify over time and vary their song sound repertoire in such a way that the distributions of temporal acoustic features within the repertoire remain stable. Humpback whale songs include several universal features including sequential ordering of phrases, stereotypical structuring of certain phrases, and stereotypical timing of unit production. Spectral features of distinctive units within songs are only weakly constrained, whereas frequency and amplitude modulation within sound types is more predictable. These properties of humpback whale song suggest that individual whales select patterns and units to include in songs based on their recent experience. Song copying by humpback whales appears to be an open process in the spectral domain in that specific frequencies are not used by all individuals within or across years. In contrast, the temporal and structural stability of humpback whale songs suggests that species-specific constraints on these properties strongly determine song form. These constraints likely relate to the function(s) of humpback whale songs, which remain unknown.

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## References

- Au WWL, Darling J, Andrews K (2001) High-frequency harmonics and source level of humpback whale songs. *J Acoust Soc Am* 110:2770
- Au WWL, Pack AA, Lammers MO, Herman LM, Andrews K, Deakos M (2003) The acoustic field of singing humpback whales in the vertical plane. *J Acoust Soc Am* 113:2277
- Caldwell CA, Whiten A (2002) Evolutionary perspectives on imitation: is a comparative psychology of social learning possible? *Anim Cogn* 5:193–208
- Catchpole CK, Slater PJB (1995) *Birdsong: themes and variations*. Cambridge University Press, Cambridge
- Cato DH (1991) Songs of humpback whales: the Australian perspective. *Mem Queensl Mus* 30:323–332
- Cerchio S, Jacobsen JK, Norris TF (2001) Temporal and geographic variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Anim Behav* 62:313–329
- Clark CW (1990) Acoustic behavior of mysticete whales. In: Thomas J, Kastelein RA (eds) *Sensory abilities of cetaceans*. Plenum, New York, pp 571–583
- Corey D, Dunlap W, Burke M (1998) Averaging correlations: expected values and bias in combined Pearson *r*s and Fisher's *z* transformations. *J Gen Psychol* 125:245–261
- Edds-Walton PL (1997) Acoustic communication signals of mysticete whales. *Bioacoustics* 8:47–60
- Frazer LN, Mercado E III (2000) A sonar model for humpback whale song. *IEEE J Ocean Eng* 25:160–182
- Frumhoff P (1983) Aberrant songs of humpback whales (*Megaptera novaeangliae*): clues to the structure of humpback whale songs. In: Payne R (ed) *Communication and behavior of whales*. Westview, Boulder, Colo., pp 81–127
- Gray PM, Krause B, Atema J, Payne R, Krumhansl C, Baptista L (2001) Biology and music. *The music of nature*. *Science* 291:52–54
- Guinee LN, Chu K, Dorsey EM (1983) Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). In: Payne R (ed) *Communication and behavior of whales*. Westview, Boulder, Colo., pp 59–80
- Helweg DA, Herman LM, Yamamoto S, Forestell PH (1990) Comparison of songs of humpback whales (*Megaptera novaeangliae*) recorded in Japan, Hawaii and Mexico during the winter of 1989. *Sci Rep Cetacean Res Inst* 1:1–20
- Helweg DA, Cato DH, Jenkins PF, Garrigue C, McCauley RD (1998) Geographic variation in South Pacific humpback whale songs. *Behaviour* 135:1–27
- Herman LM (2002) Vocal, social, and self-imitation by bottlenose dolphins. In: Nehaniv C, Dautenhaun K (eds) *Imitation in animals and artifacts*. MIT Press, Cambridge, Mass., pp 63–108
- Hulse SH, Cynx J (1985) Relative pitch perception is constrained by absolute pitch in songbirds (*Mimus*, *Molothrus*, and *Sturnus*). *J Comp Psychol* 99:176–196
- Janik VM, Slater PJB (1997) Vocal learning in mammals. *Adv Study Behav* 26:59–99
- Marler P (1997) Three models of song learning: evidence from behavior. *J Neurobiol* 33:501–516
- McSweeney DJ, Chu K, Dolphin WF, Guinee LN (1989) North Pacific humpback whale songs: a comparison of southeast Alaskan feeding ground songs with Hawaiian wintering ground songs. *Mar Mamm Sci* 5:139–148
- Mednis A (1991) An acoustic analysis of the 1988 song of the humpback whale, *Megaptera novaeangliae*, off Eastern Australia. *Mem Queensl Mus* 30:323–332
- Mercado E III, Frazer LN (1999) Environmental constraints on sound transmission by humpback whales. *J Acoust Soc Am* 106:3004–3016
- Mercado E III, Michalopoulou Z-H, Frazer LN (2000) A possible relationship between waveguide properties and bandwidth utilization in humpback whales. *OCEANS 2000 MTS/IEEE Conf Proc*, pp 1743–1747
- Mercado E III, Herman LM, Pack AA (2003) Stereotypical sound patterns in humpback whale songs: usage and function. *Aquat Mamm* 29:37–52
- Noad MJ, Cato DH, Bryden MM, Jenner MN, Jenner KCS (2000) Cultural revolution in whale songs. *Nature* 408:537
- Pack AA, Au WWL, Lammers MO, Herman LM, Deakos MH (2003) Determining the acoustic field and transmission characteristics for singing humpback whales on the Hawaiian winter grounds. *15th Biennial Conf Biol Mar Mamm*, pp 125–126
- Payne R, Guinee L (1983) Humpback whale (*Megaptera novaeangliae*) songs as an indicator of “stocks”. In: Payne R (ed) *Communication and behavior of whales*. Westview, Boulder, Colo., pp 333–358
- Payne RS, McVay S (1971) Songs of humpback whales. *Science* 173:585–597
- Payne K, Payne R (1985) Large scale changes over 19 years in songs of humpback whales in Bermuda. *Z Tierpsychol* 68:89–114
- Payne K, Tyack P, Payne R (1983) Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): a detailed analysis of two seasons in Hawaii. In: Payne R (ed) *Communication and behavior of whales*. Westview, Boulder, Colo., pp 9–57
- Ralston JV, Herman LM (1995) Perception and generalization of frequency contours by a bottlenose dolphin (*Tursiops truncatus*). *J Comp Psychol* 109:268–277
- Reiss D, McCowan B (1993) Spontaneous vocal mimicry and production by bottlenose dolphins (*Tursiops truncatus*): evidence for vocal learning. *J Comp Psychol* 107:301–312
- Richards DG, Wolz JP, Herman LM (1984) Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenose dolphin, *Tursiops truncatus*. *J Comp Psychol* 98:10–28
- Richardson W, Greene C, Malme C, Thomson D (1995) *Marine mammals and noise*. Academic, San Diego
- Tyack P (1981) Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav Ecol Sociobiol* 8:105–116
- Weisman R, Njegovan M, Sturdy C, Phillmore L, Coyle J, Mewhort D (1998) Frequency-range discriminations: special and general abilities in zebra finches (*Taeniopygia guttata*) and humans (*Homo sapiens*). *J Comp Psychol* 112:244–258
- Whiten A (1992) On the nature and evolution of imitation in the animal kingdom—reappraisal of a century of research. *Adv Study Behav* 21:239–283
- Winn HE, Winn LK (1978) The song of the humpback whale *Megaptera novaeangliae* in the West Indies. *Mar Biol* 47:97–114
- Winn HE, Perkins PJ, Poulter TC (1970) Sounds of the humpback whale. Paper presented at proceedings of the seventh annual conference on biological SONAR and diving mammals. Stanford Research Institute, Menlo Park
- Winn HE, Thompson TJ, Cummings WC, Hain J, Hudnall J, Hays H, Steiner WW (1981) Song of the humpback whale: population comparisons. *Behav Ecol Sociobiol* 8:41–46