Marine Mammal Science

MARINE MAMMAL SCIENCE, **(*): ***–*** (*** 2012)
© 2012 by the Society for Marine Mammalogy
DOI: 10.1111/mms.12005

Humpback whale song hierarchical structure: Historical context and discussion of current classification issues

DANIELLE M. CHOLEWIAK,[1,2] Department of Neurobiology and Behavior and Bioacoustics Research Program, Cornell University, Ithaca, New York 14850, U.S.A.; RENATA S. SOUSA-LIMA,[3] Field of Zoology and Bioacoustics Research Program, Cornell University, Ithaca, New York 14850, U.S.A. and Instituto Baleia Jubarte, Rua Barão do Rio Branco, 26, Caravelas, Bahia 45900, Brazil; SALVATORE CERCHIO, Wildlife Conservation Society, Global Conservation, Ocean Giants Program, 2300 Southern Boulevard, Bronx, New York 10460, U.S.A.

ABSTRACT

Consistent and well-defined criteria for the classification and measurement of humpback whale song features are essential for robust comparisons between investigators. Song structure terminology has been well-established and used by many authors, though at times inconsistently. This review discusses the development of the nomenclature describing humpback song and explores the potential significance of the often-overlooked variation in song patterns. Within the hierarchical definition of humpback song, the most problematic issues arise from the inconsistent delineation of phrase types, and the use of the metric of song duration without regards to variability in thematic sequence. With regards to the former, a set of guidelines is suggested to facilitate consistent delineation of phrases. With regards to the latter, current research demonstrates that the "song duration" metric has resulted in the disregard of variability at this level, which is more widespread than traditionally reported. An exemplar case is used to highlight the problem inherent in defining and measuring song duration. Humpback song is evaluated within the framework of avian songbird research, and a shift in analysis paradigm is recommended, towards phrase-based analyses in which sequences of phrases are treated as a salient feature of song pattern.

Key words: humpback whale, *Megaptera novaeangliae*, song structure, song classification, eventual variety, avian song.

Variation in a behavioral trait provides the opportunity for selection and evolution, and therefore is of interest to behavioral ecologists. Detailed qualitative description of a species' behavior, such as their sound repertoire, is important. Nevertheless, the questions that drive the advancement of knowledge about a species' communication

[1]Corresponding author (e-mail: danielle.cholewiak@noaa.gov).

[2] Current address: Protected Species Branch, Northeast Fisheries Science Center/NOAA/NMFS, 166 Water Street, Woods Hole, Massachusetts, 02543, U.S.A.

[3] Current address: LaB – Laboratório de Bioacústica/Bioacoustics Lab, Departamento de Fisiologia/Department of Physiology, Centro de Biociências/Biosciences Center, Universidade Federal do Rio Grande do Norte/Federal University of Rio Grande do Norte, C.P. 1511, Natal, RN, Brazil 59078-970,

system are often answered by quantitative analyses of the variation in specific traits. Here we review and discuss the development of the nomenclature describing humpback song and explore the potential significance of the often-overlooked variation in song patterns.

A Short History of the Study of Humpback Whale Song

As recently as the 1940s, scientists did not know whether baleen whales produced sounds. Although cetacean sounds were apparently well known to historic whalers (Aldrich 1889), the early scientific community concluded that cetaceans were mute based upon the discovery that they did not possess vocal chords (Schevill and Watkins 1962). It was not until after the confirmation of sound production by odontocetes (Fraser 1947, Kullenberg 1947, Schevill and Lawrence 1949) that scientists began to realize that mysticetes also produced vocalizations.

The first documentation of humpback vocalizations within the scientific community was presented in 1952, when Schreiber (1952) recorded sounds with a "musical quality" off the island of Oahu, which he attributed to marine life. We now know that these musical sounds were produced by humpback whales. A decade of research after Schreiber's discovery, uncovered the fact that humpbacks produce a wide range of vocalizations on the breeding grounds and en route to them, as well as on the feeding grounds. By 1964 their breeding sounds were becoming well known: "…the sonorous moans and screams associated with the migrations of *Megaptera* past Bermuda and Hawaii may be an audible manifestation of more fundamental vernal urges…" (Schevill 1964). Off the coast of New Zealand, acousticians were making similar discoveries, although they did not positively identify the sounds as humpback in origin. They described how a "…chorus of squeals, creaks, cries, barks, groans, and whoops…" had been labeled the "Barnyard Chorus" by the laboratory staff (Kibblewhite *et al.* 1967). The same author even supposed that one individual might produce all the different sounds in this chorus, though he did not attempt to confirm this. Ironically, these New Zealand researchers may have documented the (near) extirpation of a humpback whale breeding population through acoustic monitoring without realizing it; they described the decline in these sounds from 1960 to 1963, and stated that no positive instances were recorded after 1963. Around the same time, a spectrographic catalog of some of the sounds known to be produced by humpback whales demonstrated the diversity of these vocalizations (Tavolga 1968). In 1970, in a technical report written for the Naval Undersea Research and Development Center, Cummings and Philippi (1970) describe repetitive "stanzas" recorded in late December in the northwest Atlantic. Their low sampling rate precluded the detection of any sounds above 175 Hz, yet the authors were able to identify sound series that lasted 11–14 min, including pulses, blips, and moans. They tentatively identified these sounds as being North Atlantic right whale (*Eubalaena glacialis*) vocalizations; in all likelihood, they were actually listening to humpback whales (Payne and Payne 1971).

It seems that scientists working in every ocean basin were on the verge of a new discovery, but it was not until 1969 that these sounds were finally reported by Roger and Katy Payne as the "song" produced by humpback whales (Anonymous 1969), followed shortly thereafter by a conference presentation by Howard Winn (Winn *et al.* 1970). In 1971 Payne and McVay published a pivotal paper describing the patterned, hierarchical structure of these sounds, making the first connection with bird song. These authors relied on Broughton's (1963) definitions of the term song, including: "… a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time," recognizing that what humpbacks were producing fit into this framework. Winn and Winn (1978) supported this discovery with a separate description of the patterned sequences of sounds recorded from humpback whales in Bermuda and the West Indies, and a slightly different approach towards characterization of song structure than Payne and McVay (1971).

From that time on, investigations regarding the complexity, function, and pattern in humpback whale song have increasingly grown in number. In 1979 the first paper attempting to quantify signature information in song units was published (Hafner *et al.* 1979). The authors did not recognize the significance of the evolving nature of humpback song at this time, and thus variation due to temporal changes was confounded with individual variation. Temporal variation, or rapid cultural evolution, was soon to be described in detail (Guinee *et al.* 1983, Payne *et al.* 1983, Payne and Payne 1985). Singing humpback whales were shown to be males (Glockner 1983), and the function of song within the breeding season was hypothesized to play a role in female attraction (Winn and Winn 1978, Herman and Tavolga 1980, Tyack 1981) or mediate male-male interactions (Darling 1983, Darling *et al.* 2006, Cholewiak 2008). Further studies have compared song patterns across regions (*e.g.*, Payne and Guinee 1983, Helweg *et al.* 1990, Cerchio *et al.* 2001, Darling and Sousa-Lima 2005, Garland *et al.* 2011), or seasons (Winn and Winn 1978; Matilla *et al.* 1987; Noad *et al.* 2000; Eriksen *et al.* 2005; Mercado *et al.* 2003, 2005). This work has repeatedly demonstrated four universally observed features of humpback song: (1) populations or groups of males that are in acoustic contact at some point in time and space sing "similar" songs, which is to say that their songs are comprised of visually and aurally recognizable similarities in pattern that are characteristic of that time/region; (2) the overall hierarchical structure is observed globally, thus a heritable species-level characteristic, although the details of song patterns differ between populations of males that are acoustically isolated during all seasons; (3) song patterns change over time as a result of individual males modifying the spectral and temporal features of song units, as well as their order and repetition; and (4) males in acoustic contact incorporate similar changes into their own songs, maintaining continuity within populations despite progressive temporal changes.

Between the 1970s and early 1980s, the terminology used to describe humpback whale songs was firmly cemented within the scientific literature (Payne and McVay 1971, Payne *et al.* 1983). Other authors occasionally varied this vocabulary (Winn and Winn 1978), but for the most part it has remained in use as originally proposed by Payne and McVay. This terminology is not, however, without complications, and inconsistencies in its application have led to incongruities in the literature (for example, compare Thompson and Friedl 1982 with McSweeney *et al.* 1989).

Despite the consistency of song patterns exhibited among males within a breeding population, researchers have noted a fair amount of variation in humpback whale song, both within the songs of an individual and between the songs of different individuals (first noted by Payne and McVay 1971). Early on, Frumhoff (1983) conducted an extensive review of "anomalous" songs, and while early analyses suggested that song sequence was extremely stereotyped (Payne and McVay 1971, Winn and Winn 1978, Payne *et al.* 1983), later studies have demonstrated that song structure is not always as consistent as was first reported (Helweg *et al.* 1990, 1992, 1998; Eriksen *et al.* 2005). Measurements of variation both on the overall pattern level, as well as on the level of individual song units, are clearly important for understanding the function of song within this species and the influence of sexual selection on singing behavior.

Recently, there has been an increase in attempts to develop automated procedures for the classification of individual song elements, appearing in both refereed (Rickwood and Taylor 2008, Pace *et al*. 2010, Green *et al*. 2011) and nonrefereed literature (Mazhar *et al*. 2008, Picot *et al.* 2008). These procedures range from semi-automated (requiring manual selection of song elements) to fully automated (including both the detection of and classification of song elements). In general, these methodologies are largely still under development and demonstrations of their success are as yet limited. Moreover, for studies of song evolution (rather than song element classification), the variation exhibited at individual, population, and temporal levels will likely present a significant problem for automated classifiers to recognize similar elements as they undergo progressive change over time. Studies assessing song over protracted geographic or temporal scales require the accurate classification and grouping of similar song elements in order to draw valid conclusions regarding song transmission and behavioral processes, and this is often confounded by sparse sampling. There is clearly a need for the development of automated classification systems in order to handle large data sets of recordings; however, no system has yet been demonstrated which compares with the pattern recognition skills of the human brain.

Consistent and well-defined criteria for the classification and measurement of humpback whale song features are essential for robust comparisons between investigators. In humpback song analyses, arbitrary divisions are imposed on what is otherwise a continuous vocal sequence. At times, these divisions are constructed inconsistently. Payne and McVay's (1971) terminology has been established and used by many authors, even though no practical rules were provided to guide the delineation of boundaries between different types of units, phrases, or themes. This lack of specific guidance has contributed to differences among authors in adopting criteria used to partition continuous humpback whale singing sessions. Additionally, in light of ongoing research, it has become clear that the rigid structure suggested by Payne and McVay (1971) is not universally applicable to all songs.

The objectives of this review are to (1) suggest consensus criteria for song structure definitions and discrimination and (2) engage in a discussion on the use of song cycle metrics in the humpback system, with suggestions for revision of the traditional analysis paradigm. While it may not be possible to develop rules that will work universally, we believe that establishing guidelines will be constructive, especially as this field continues to expand rapidly. These suggestions are based upon our combined experience with humpback whale song spanning seven different regions in four ocean basins with recordings collected over three decades. Our aim is to better enable comparable quantitative analyses between investigators. However, we are aware that our suggestions may not be suitable for everyone, therefore we urge future authors to explicitly and thoroughly describe the way they generate the humpback whale song classifications and metrics in their publications.

Review of Song Structure Definitions and criteria

The framework by which humpback whale song is defined and categorized is essentially a model, used to make inference about the singing behavior of humpback whales. As famously noted by Box and Draper (1987), all models are by nature an approximation, and the best models approximate closely enough to be useful in inference; importantly, even the most useful of models should regularly be revisited when new data become available to improve upon them. Payne and McVay (1971), in an effort to describe their observation of predictable, repetitive vocal cycles, described a hierarchical structure that has been widely adopted and utilized by researchers for over 30 yr. The shortest sound is called a *unit*, which may be divided into *subunits* when comprised of pulses that are too rapid to be individually discriminated at real speed. A set of units is combined to form a *phrase*. Similar phrases are repeated to form a *theme*. The *song* is defined as the combination of multiple distinct themes. A *song session* consists of a series of repeated *songs* with silent intervals of less than a minute, which are typically not discernibly longer than those intervals between phrases or themes. Our aim is to assess this framework, identify where it has been useful, and suggest revision where it may be improved.

Subunits and Units

The term *subunit* is one that has multiple uses within the literature. It was originally defined (Payne and McVay 1971) as a component of a sound that is aurally indistinguishable as a discrete vocalization. When examined with appropriate spectrogram parameters or played at a slower rate, seemingly continuous sounds may be shown to be composed of discrete pulses (Fig. 1). Grating or rasping sounds may be considered a single unit, but are actually pulse-trains that are made up of a series of pulses, or subunits. It is important to note that in these cases, spectrogram parameters (such as the number of points in a Fast Fourier Transform (FFT)) will determine the resolution of subunits.

More recently, the term *subunit* has been adopted primarily to refer to the components of a sound distinguished by frequency discontinuities or inflection points. Effort is now being directed towards evaluating whether these sound components can be useful for automatic classification (Pace *et al.* 2010). This effort reflects the progress within the broader field of automated call classification, in which similar analyses are being conducted on odontocete whistles (Shapiro *et al.* 2011).

A *unit* is defined (Payne and McVay 1971) as the shortest sound that seems continuous when evaluated at real speed (Fig. 2). This is analogous to a "note" or "element" in the avian song literature (Issac and Marler 1963). Winn and Winn (1978) called these individual sounds "syllables," which is somewhat confusing, as "syllables" in the avian literature may actually be composed from groups of notes that have internote intervals of silence that are shorter than the duration of the adjacent notes (Isaac and Marler 1963).

We suggest that the hierarchical levels of unit and subunit be maintained. These definitions are simple and unambiguous, allowing robust comparisons. The term *unit* has been more widely used within the humpback literature, and should be used in place of the term syllable.

Subphrases and Phrases

A *subphrase* (Payne *et al*. 1983) is a sequence of one or more units that is sometimes repeated in a series (Fig. 2). These units of repetition were called "motifs" by Winn and Winn (1978), who divided them into two types: similar (containing only one type of unit, repeated several times) or dissimilar (containing two or more different units, which are repeated in combination several times).

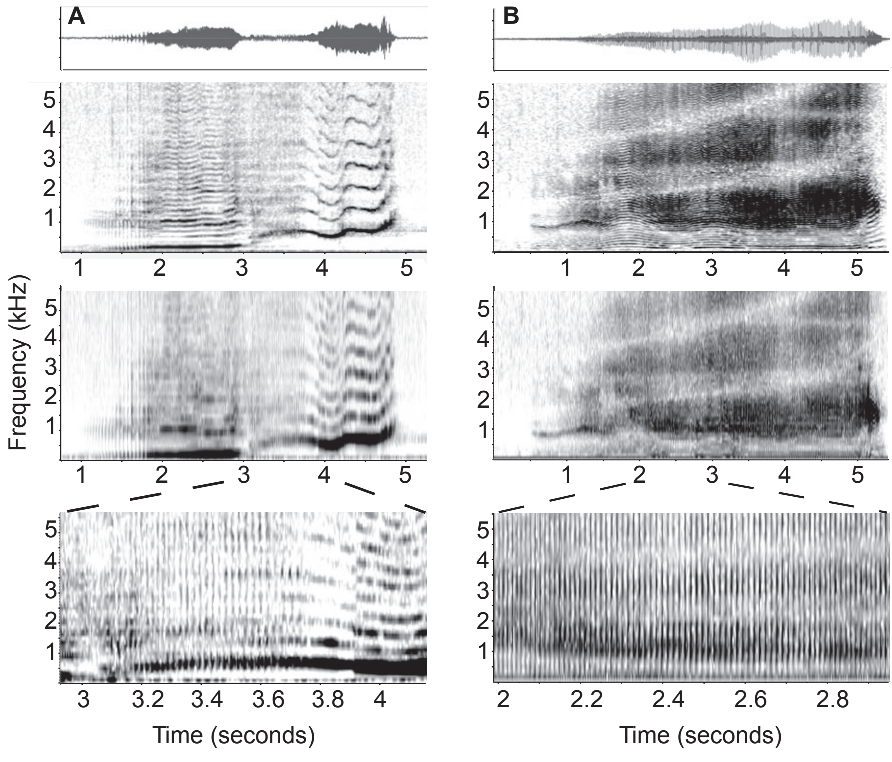

Figure 1. Two different examples of a humpback song unit comprised of subunits, recorded at Isla Socorro, Mexico. The top panel in each column displays the amplitude envelope, and the lower panels display the spectrogram (Hann window, 50% overlap) or part thereof, showing the unit and subunit structure. (A) Recorded 27 March 2006. The middle segment of this song unit is composed of a pulse train of subunits. Top panel: 1024 pt FFT (Fast Fourier Transform); middle panel: 256 pt FFT, bottom panel: 256 pt FFT. (B) Recorded 8 April 2004. Typical "ratchet" sound, in which the entire unit is composed of rapidly produced pulses. Top panel: 1,024 pt FFT; middle panel 256 pt FFT, bottom panel: 128 pt FFT. Note that the full frequency range of these example units exceeds the frequency range chosen for their display in this figure.

Multiple subphrases are grouped into a *phrase* (Payne and McVay 1971). Similar phrases are generally repeated from a few to many times before a different phrase type is introduced (Fig. 2). However, consecutive phrases may have different numbers of units, as well as a change in the spectral and/or temporal characteristics of the units, while still being identifiable as belonging to the same repetitive sequence. As noted by Payne and McVay (1971), phrases are "inexact replicas" of one another. We suggest that the phrase may be considered the salient element of repetition within humpback song. Differing from Payne and McVay's original interpretation (1971), we propose that the phrase hierarchical level is most analogous to the structural level of "song" in the avian literature (see below for further discussion on this topic).

Unfortunately, the delineation of phrases may be difficult and ambiguous. Typically, the intervals between successive phrases are the same as the intervals between units within a phrase (in contrast to most bird song, where intersong intervals are

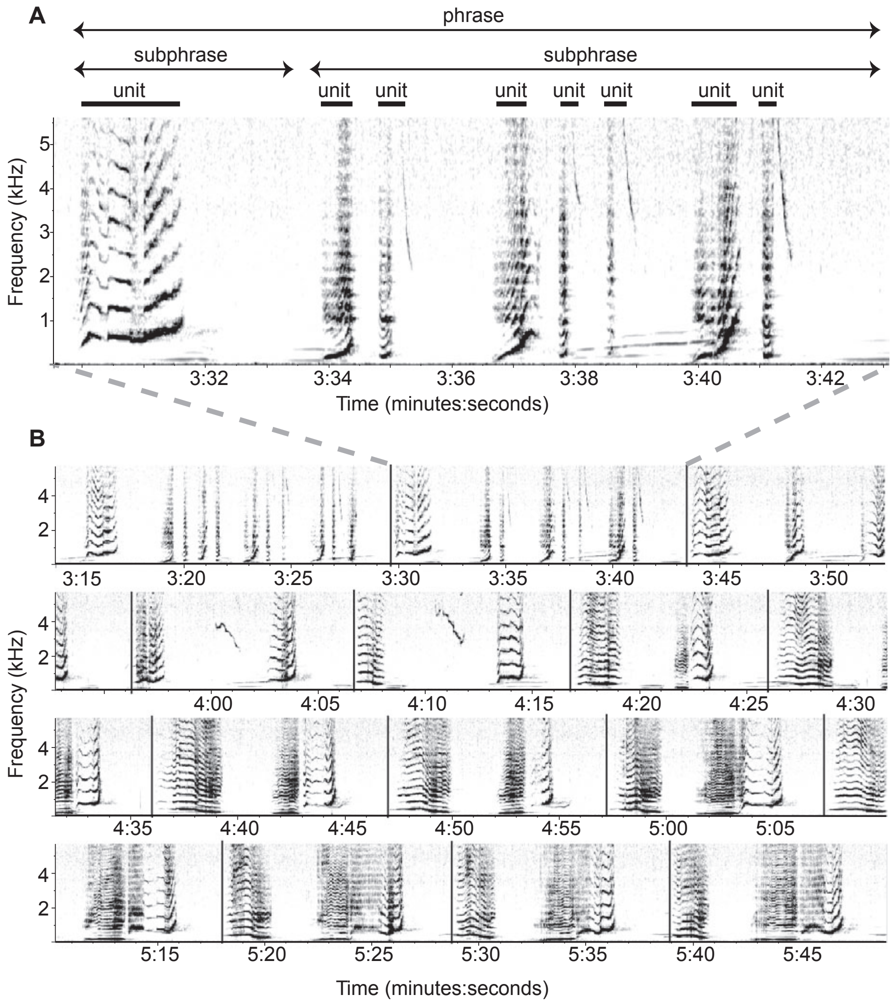

Figure 2. Spectrographic representation of humpback whale song sequence, recorded at Isla Socorro, Mexico, on 27 March 2006 (1,024 pt FFT [Fast Fourier Transform], Hann window, 50% overlap). Time on the x-axis is in minutes:seconds, while frequency on the y-axis is in kHz. (A) One phrase consisting of two subphrases. The first subphrase is composed of one unit, while the second subphrase is composed of a repeating pattern of 2–3 individual units. Note that units 3, 5, 6, and 8 within the example phrase are continuous, although their full frequency range exceeds that chosen for display in this figure. (B) 155 s sequence of song, in which multiple phrases types can be observed. Phrases have been delineated by vertical lines.

noticeably longer than internote intervals [Isaac and Marler 1963]). The delineation of phrase structure is subjective, such that a choice needs to be made about where within a sequence of units one will start a phrase, and at what point variation in phrase structure is significant enough to delineate a new phrase type.

Therefore, differences in methodology between authors make it challenging to compare studies, even of song within the same region. For example, two authors analyzing song recorded off Hawaii in 1979 divided the same sequence into four types of phrases (Thompson and Friedl 1982) and seven types of phrases (McSweeney *et al.* 1989). Irregularities such as these muddle the comparisons.

However, despite challenges in labeling and delineating phrases, multiple authors have recognized that phrase duration is one of the most stable features of humpback whale song, with very low coefficients of variation within and between individuals (Frumhoff 1983, Payne *et al.* 1983, Cerchio 1993, Cerchio *et al.* 2001). This strongly suggests that there is significance to the phrase as an element that is important to humpback whales, and delineation of phrases is not an arbitrary construct of researchers attempting to force organization upon the display. The same does not appear to be true of the "song" measurement that will be detailed below.

In an attempt to partly remedy variability in methodology, we suggest the following simple guidelines for delineating and measuring phrases, which could be adopted in any song:

(1) Consecutive units of similar structure should not be separated within a phrase, but should be kept together as parts of a subphrase.
(2) Phrases should be delineated in a way that minimizes the occurrence of an incomplete phrase at the end of a sequence of similar phrases (also called "hanging" phrases, consisting of only a portion of the repetitive structure, such as one subphrase).
(3) "Transitional" phrases combine units from two different phrase types (Payne and Payne 1985), usually an entire subphrase from the previous and subsequent themes. For example, using letters to indicate subphrases, in the phrase sequence:

ab ab ab **ad** cd cd cd

ad is a transitional phrase, composed of subphrase "a" and subphrase "d." These phrases should be identified as such, and not mistaken for new phrase types.
(4) Care should be taken to recognize inherent variation within phase types, and thereby to distinguish between patterns that are variants of a single phrase type *vs.* completely different phrase types. Variation within a phrase type may involve differences in structure or repetition of units, without a consequent shift in the overall pattern of the subphrase or phrase; conversely, when the pattern, composition and/or number of units in a phrase dramatically differs, and is maintained within the sequence, a completely different phrase type should be defined. This is not necessarily to advocate lumping over splitting, but rather to define different levels of variation. As this process is unavoidably qualitative and somewhat subjective, exemplar spectrograms illustrating different phrases and variants should always be presented in publications, and authors (and editors) should avoid reporting phrase classification only nominally without supporting figures.
(5) Duration of phrases should be measured including the interval between phrases (*i.e.*, measuring from the onset of the first unit in one phrase to the onset of the analogous unit in the subsequent phrase). Measurements made in this way will be robust regardless of how one chooses to delineate phrases. In fact, if measured consistently, phrase duration has the least variation within and between singers of a particular population (Frumhoff 1983, Cerchio *et al.* 2001).
(6) A review of song based on recordings of multiple individuals is essential for appropriately assigning phrase presence and structure; song structure should never be delineated based on recordings from a single individual, and only cautiously for small samples of individuals. When there is ambiguity in the assignment

of units to phrases, we urge authors to search for consistency in interindividual pattern or consistency in subphrase structure.

We suggest that the hierarchical level of the phrase be maintained, with closer attention being given to criteria used to delineate phrases. In addition, the use of recordings that provide adequate signal-to-noise ratio and encompass the entire fundamental frequency bandwidth of the song structure is important, as failure to do so will preclude the detection of some units and may lead to misinterpretation of song structure. When possible, a multiyear review of song, composed of multiple individuals from each year, should be conducted to examine phrase pattern and evolution, which may aid in classification of phrase organization. Although we will not attempt to evaluate or provide guidelines on appropriate sampling protocols, sampling is as critical with humpback whale song as it is with any other data type (*e.g.*, genetic sampling). It is important to optimize both quality of samples (signal-to-noise ratio and recording length) and sample size (number of different individuals recorded) to accurately document population level parameters.

Themes

A sequence of similar phrases is defined as a *theme* (Payne and McVay 1971), and therefore a new phrase type within the song sequence initiates a new theme. Individual males may sing different numbers of phrases, both in different themes and in consecutive renditions of the same theme. Thus, the length of any given theme varies both within and between individuals. Frumhoff (1983) classified *fundamental* themes as those present in all songs in at least 90% of the recordings in both a given season and at least one contiguous season. This concept was driven by the idea that thematic order is fixed (and "aberrant" songs strayed from that order when "fundamental" themes were omitted). Other authors have classified "fundamental" themes as those present in 95% of all recordings within one season (Chu and Harcourt 1986). Due to the evolving nature of humpback song, the concept of a fundamental theme is ephemeral.

Payne and Payne (1985) further classified themes into three different types based on their organization: (1) *Static themes* are those with a sequence of nearly identical phrases. (2) *Shifting themes* are those in which successive phrases evolve progressively from one form to another. Units may gradually change in frequency and/or form, duration, or number of subunits, or be delivered at a slower or faster rate (*i.e.*, variation in interunit interval). Phrases may evolve such that changes are progressive, systematic and irreversible with each successive repetition. (3) *Unpatterned themes* are those in which a variable number of units have no clear organization and thus cannot be subdivided into repeating phrases. The result is a theme composed of one single, long phrase. (Another type of one-phrase theme noted by Payne and McVay (1971) occurs when a single phrase is composed of unique material that does not resemble the previous or next theme but yet occurs consistently.) It should be noted that unpatterned themes appear to be rare, occurring only twice in the cumulative experience of the authors (DMC, RSS-L and SC, unpublished data).

The classification of fundamental themes has not been widely adopted in the literature. The categorization of themes into types has also not been widespread, but Payne and Payne's (1985) proposition of static, shifting, and unpatterned themes does characterize humpback whale singing behavior across many regions and years (DMC, RSS-L and SC, unpublished data).

Because song is constantly undergoing progressive temporal change, the processes by which changes occur can have a profound effect on the structure and classification of song elements. An exploration of all such processes is beyond the scope of this paper, but examples reported in the literature exemplify the phenomenon and underscore the need for consideration of progressive change during classification. Several studies have documented gradual change within and between years (Payne *et al.* 1983; Cerchio *et al.* 2001; Eriksen *et al.* 2005) and have endeavored to maintain the nomenclature for phrases and themes across time despite changes. We emphasize that it is important to maintain the integrity of phrase/theme "lineages" when conducting studies of similarity across time, so as not to confuse the evolution of existing phrases with the introduction of new material (completely different phrases).

Conversely, in some cases, different variants of the same phrase type (as defined above) that are present in the same song and sung in an inconsistent and interchangeable sequence may be indicative of the evolution of a new "theme" (Payne *et al.* 1983). Cerchio (1993) and Cerchio *et al.* (2001) noted that such instances represented the splitting of a theme and "birth" of a new theme over multiple seasons. In the schematic example represented in Table 1, two variants of the same phrase existed in year 1. They shared their second subphrase (d), but their first subphrase represented variants (a or b). They were uttered interchangeably and were considered part of the same theme. In year 2, each variant had evolved and diverged, but subphrase "d" was still similar between the two. The phrase types were no longer sung interchangeably, but had become clearly sequential as typical of consecutive static themes. At this point, they appeared to be treated as two distinct themes. By year 3, subphrase "d" had been dropped completely from the second phrase type, and the two phrases (and consequently, themes) no longer showed any similarity to one another. In this case, the change in phrase structure occurred at the subphrase level. In an analysis of song pattern, Cerchio *et al.* (2001) designated themes in such a way as to follow the changing pattern in subphrase modifications. This convention may reveal rules of change over extended periods of time and extensive geographic scales.

We suggest that the definition of a theme be clarified to emphasize subphrase structure, such that a theme is a repetition of phrases that have similar subphrases in common. Between two phrase types, when one subphrase is similar but another subphrase is consistently different (called "rhyming" phrases in Guinee and Payne 1988), a new theme should be designated based on the sequence consistency of the structural change.

Care should be taken in classifying themes when comparing songs from different regions or time periods. When multiyear samples are available, continuity in naming

Table 1. Example of structural changes occurring at the subphrase level, resulting in the splitting of a single theme into two themes over a 3 yr period. In this schematic representation, subphrase type is indicated by a lower case letter (a, b, or d) and temporal change in the internal structure of the subphrase across seasons is indicated by a prime (a → a' → a"). This process was observed in two sets of themes reported in Cerchio *et al.* (2001), themes 2A/2B and 3A/3B leading up to the year that was analyzed in that study.

Year	Phrase type 1	Phrase type 2	Example sequence
1	ad	bd	…-ad-ad-ad-bd-bd-ad-ad-bd-…
2	a'd'	b'd'	…-a'd'-a'd'-a'd'- b'b'b'd'-b'b'b'd'-…
3	a"d"	b"	…-a"d"-a"d"-a"d"-b"-b"-b"-b"-…

among years should be maintained, so that an individual "lineage" of a theme/phrase type may be followed over time. Similar themes in different adjacent regions (*i.e.,* where the potential for acoustic interaction exists) should be labeled as such, regardless of their position within the song sequence or the presence or absence of other themes. In one study (Maeda *et al.* 2000), what appeared to be similar themes in two different regions were mistakenly treated as different themes; the analyses of theme presence and evolution were therefore incomparable between the two regions, complicating interpretation of the results.

Song

A sequence of themes comprises a *song*, according to the definition proposed by Payne and McVay (1971). This description was further developed by Frumhoff (1983), who described a song as a series of at least three themes, organized in a predictable sequence, repeated in the same order two or more times. The choice of the theme that starts the "song" cycle is considered arbitrary, since males usually sing in a continuous bout without stopping between repeated cycles (*e.g.*, in one famous example, Winn and Winn (1978) report having recorded a humpback whale singing for 22 h). The use of this definition of song will be discussed in detail in the following section.

Discussion of the Hierarchical Level of Song in Humpback whales

Variation in Sequence Consistency

Early studies suggested that humpback song patterns were produced in a fixed and ordered sequence (*i.e.*, a male would sing themes 1 to 2 to 3 and then repeat the same sequence). This observation led to the conclusion that a hierarchical structure existed

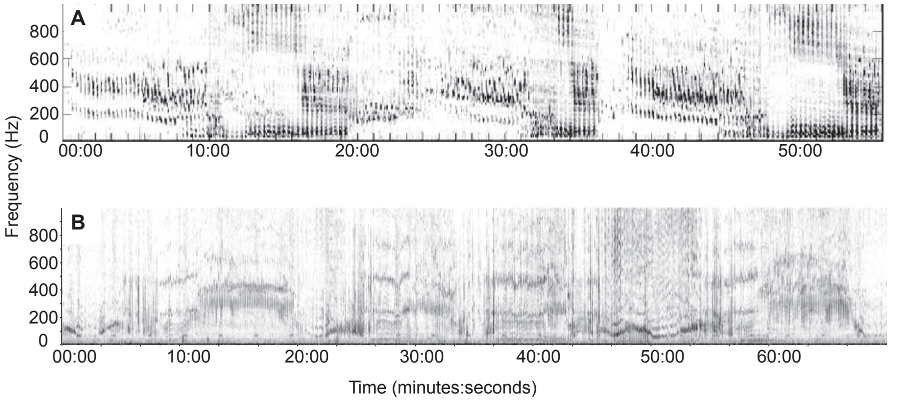

Figure 3. Spectrograms of individual humpback whale song recorded in (A) Brazil and (B) Mexico. The y-axis displays frequency in Hz and the x-axis displays time elapsed (minutes:seconds). (A) Spectrogram of 3500s of song recorded off the coast of Brazil in 2005 (256 pt FFT [Fast Fourier Transform] size, Hann window). Note the cyclical pattern of the signal in the Brazil sample. (B) Spectrogram of 4200s of song recorded from Isla Socorro, Mexico in 2004 (256 pt FFT, Hann window, 50% overlap). The traditional "cyclical" pattern is not observed in this example.

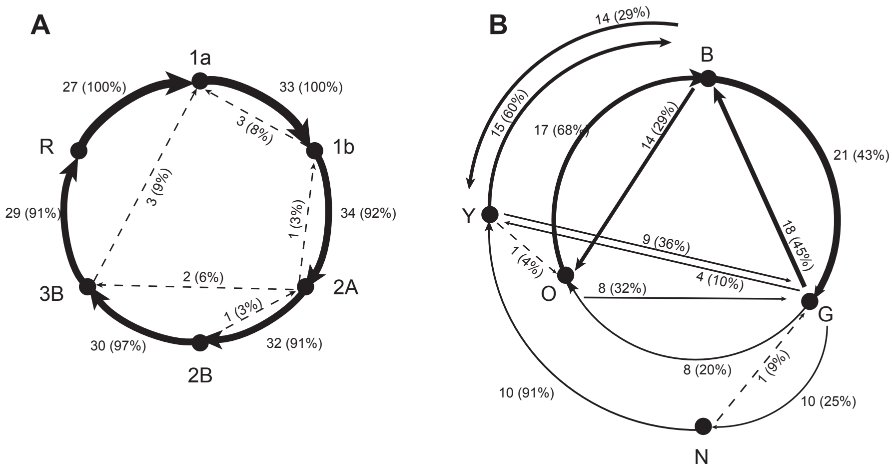

Figure 4. Transition diagrams showing the thematic sequence for multiple singers in two different years, demonstrating (A) "highly invariant" and (B) "highly variable" theme order, respectively. The numbers along each line indicate the number and proportion of total transitions from one theme to another. Note that transitions between phrases within each theme are not represented here. (A) Continuous recordings of five males from Kauai, Hawaii, in 1991 were combined for approximately 7 h of theme sequence analysis. Themes are labeled by sequential numbers and letters. There were a total of 197 theme transitions; thematic sequence may be considered "highly invariant," as 96% of thematic transitions follow the predicted order. (B) Continuous recordings of five males from Isla Socorro, Mexico in 2004 were combined for 5.8 h of theme sequence analysis. Themes were designated by letters, to avoid any unintentional bias associated with designating themes by sequential numbers. There were a total of 150 theme transitions; thematic sequence was quite variable in this year. Some theme transitions were extremely rare or nonexistent, while others were prominent. However, a clear cyclical pattern is not observed, as reversals between themes B & G, O & B, and B & Y are common.

at this level that was extremely stereotyped and rigid (Payne and McVay 1971; Winn and Winn 1978; Winn *et al*. 1981; Payne and Payne 1985; Guinee and Payne 1988).

It is undeniable that there is an overall cyclical pattern at this level of song organization (see Fig. 3A, Brazil and Fig. 4A, Hawaii). However, detailed reviews of the literature reveal that the stereotypy of theme order may vary considerably among and within individuals, or between years. Frumhoff (1983) coined the term "aberrant song session" as one in which a song cycle varied from the "current" norm; specifically, when two themes that are usually separated by a fundamental theme are sung in succession. In general, this was considered uncommon.

Later work, however, suggested a higher degree of variation in theme order. In a small sample of songs recorded in Mexico and Hawaii during 1989–1990, Helweg *et al*. (1990, 1992) reported that the sequence of themes in the songs they recorded was variable (including some theme "reversals"), and suggested that all of their samples would be described as "aberrant" by Frumhoff's classification. Cato (1991) mentioned the existence of "poorly structured" songs in Australia in some years, and in a separate study of South Pacific song (Helweg *et al*. 1998), theme deletions were observed, but theme reversals were not. Additionally, in a multiyear comparison of song evolution in Tonga, Eriksen *et al.* (2005) reported that the order of theme transitions was not consistent from year to year. Although they do not provide data to quantify the number of seemingly "aberrant" song cycles, they graphically demonstrate that the song sequence in particular years of their sample is more variable than others, including a higher degree of theme "reversals" in certain years.

A multiyear study of humpback whale breeding behavior conducted off of Isla Socorro, Mexico, has also resulted in the compilation of many hours of recordings of singing males across years. Recordings of multiple males in 2004 suggest greater variability in theme order than typically expected, or documented in adjacent years (DMC, unpublished data; Smith-Aguilar 2009). Rather than singing each theme in an ordered sequence, males recorded in this period often switch back and forth between themes, including a higher degree of "theme reversals" than previously reported (Fig. 4).

In this situation, defining what constitutes a "song" by the classic definition is extremely difficult. There appears to be no clear, overarching sequence that all males in that region and time period followed while singing. This is not to say that the sequence of themes is random—in fact, examination of the transitions between themes reveals that some transitions are common (*e.g.*, the transition from theme B → G, or theme O → B; Fig. 4), while others are absent (*e.g.*, there is never a transition from theme B → N; Fig. 4). The difference in the loosely structured pattern of songs from males in the Mexico sample, and those singing a more traditionally ordered song, is both visually evident (Fig. 3) and quantifiable (Fig. 4).

Without more detailed study, it is impossible to say whether the variability in theme order observed in the songs of males recorded in Mexico 2004 is a short-term phenomenon or whether it is indicative of a larger-scale process. In an extensive, long-term study conducted on song evolution over many years, Payne and Payne (1985) found that occasionally, the song in a particular year seemed anomalous when compared to previous and subsequent seasons. Similarly, Cato (1991) also found that in some years, song was more poorly structured than others. Possibly, the variability observed in the Mexico 2004 sample can be attributed to a period of rapid song evolution, or it may reflect a broader cycle of the ebb and flow of stereotypy across years. However, regardless of the underlying reason for this variability, its existence (here and in other samples, *e.g.*, Eriksen *et al.* 2005) suggests that, in at least some cases, a different method of considering humpback whale song may be appropriate.

Humpbacks as "Eventual Variety" Singers: An Avian Comparison

There exists terminology in the avian literature that seems to effectively describe the humpback song system. Scholars of avian behavior defined bird song as a series of notes, uttered in such a way as to form a recognizable sequence (Thorpe 1961; Bremond 1963), in which the pauses between notes were shorter than the pauses between songs (Isaac and Marler 1963, Thielcke 1969). Variations on these patterns are called song types. Payne and McVay (1971) drew on this literature when developing their terminology, but equated the entire sequence of themes sung by a humpback whale to a song sung by a bird.

However, we suggest that humpback *phrases* and bird *songs* are analogous. Early scholars of avian song noted different modes of singing behavior, in which an individual may repeat the same song type many times before switching to a different song type (*e.g.*, AAA BBB CCC), or switch immediately between different song types in his repertoire with each consecutive song (*e.g.*, ABCABCABC, Hartshorne 1956). The difference between these modes of singing is often distinguished in the literature as "eventual variety" or "repeat" singing, and "immediate variety" or "serial" singing (Molles and Vehrencamp 1999). These terms may also be used at lower levels of song organization (for example to describe repetition of syllables within songs), but we refer here to their use in describing higher patterns of song presentation. Within the "eventual variety" category, variation may exist between repeats of the same song type, but this variation is less than that between song types (Stoddard *et al*. 1988, Anderson *et al*. 2008).

Not all species fit neatly into one category or the other, in fact there are a wide range of song presentation strategies. Some species may not consistently repeat all song types, and the degree of repetition may vary greatly between individuals (Eens *et al.* 1989). Other species exhibit complex rules for deciding when to repeat song types (Todt and Hultsch 1996). Still others sing extremely long, complex songs, in which even discerning the pattern is challenging, requiring detailed review of syllabic organization (Catchpole 1976).

However, within the broad categories of singing modes, the repeated phrases of humpback song, especially those in "static" themes, would seem to fit well into the "eventual variety" category. In fact, the archetypical song structure described by Payne and McVay (1971) can be considered a specific case of eventual variety singing, in which a singer utters several repetitions of each phrase in his repertoire, passing from one type to another in an invariable order, until he has sung his complete repertoire, and then starts over again without pause. Variations in this paradigm have confounded several investigators and analyses since the original description, and may be better accommodated when considered in the larger paradigm of "eventual variety" singing behavior.

Avian studies that address eventual variety songsters may include analyses of variables such as degree of repetitivity and switching rate—factors shown to be important in interindividual interactions (Molles and Vehrencamp 1999, Molles 2006). Studies of species with more complex song systems incorporate many additional techniques to evaluate song organization, such as syllable organization (Catchpole 1976) or Euclidean distance between songs (Sorjonen 1987). In contrast, most humpback song studies considering the biological significance of song sequence have focused on the broadest level, examining features such as "song duration" (*i.e.,* duration of the entire thematic sequence).

The Problem with Measuring "Song Duration"

Besides limiting the scope of our analyses, why is the present use of the hierarchical level of humpback "song" a problem? Consider the case in which the duration of a "song" is used as a quantitative metric to evaluate the impact of potential acoustic disturbance to singing whales (*e.g.*, low-frequency active sonar experiments: Miller *et al*. 2000, Fristrup *et al*. 2003). Fristrup *et al*. (2003) used a straightforward method to delineate sequential songs: a song was measured as the interval between successive starts of a particular theme (that which was traditionally associated with surfacing), without respect to theme order beyond this "marker" theme. The authors measured "song duration" ranging from 5.5 min to over 33 min in length, and conclude that although songs in general increased in duration in response to the acoustic disturbance, song length was highly variable. Another study (Miller *et al*. 2000) generally agreed that singing humpbacks increased the length of their songs in relation to broadcasts of low-frequency active sonar. Conversely, in a separate study, Sousa-Lima *et al.* (2002) used the number of phrases per theme to assess differences in song length between songs of males before and during boats approaches, and found that song length decreased in response to acoustic disturbance. Given that these studies were all trying to evaluate the potential impact of anthropogenic activity on singing behavior, one might question how to interpret their opposing results.

Interpretation of such changes in song length relative to a stimulus is strongly dependent on the variability of theme order and occurrence in the sequence of themes defined as a song. If theme order is invariant and all themes occur in each cycle of the "song," then a measure of "song duration" as currently defined can be informative, because each repetition through the cycle includes the same number of themes. We can predict that longer songs are achieved in one of several ways (*e.g.*, by increasing the length of particular units or phrases, by increasing the number of phrase repetitions in the theme, *etc.*). Therefore, it is possible that a "longer song" is the result of singers increasing the number of repetitions of phrases within (a) theme(s). Conversely, if theme order and occurrence is variable among consecutive "songs," then it is also possible that males might sing a more "erratic" song, in which they switch back and forth before completing a cycle (*i.e.*, returning to the theme arbitrarily chosen as the song "beginning" without uttering all themes in a sequence). Knowing what type of response led to an increase in "song duration," as well as knowing what constituted a typical "song," would be critical in interpreting the mechanism of the singers' reaction. Biologically, these differences suggest distinct responses to acoustic interference, but none of the studies presented data on variability in thematic composition, nor attempted to quantify the underlying reasons for the large variation or observed change in "song" duration.

In general, when theme order is less stable, consistently defining a sequence that comprises a "song," and consequently measuring "song length," becomes difficult. Consider the following example of an actual theme sequence recorded in Brazil 2002 (Sousa-Lima 2007), when six themes were clearly identified:

...1234124546123465461234546121246...

We may arbitrarily set the beginning of the song to "Theme 1." If we delineate songs in this sample based on the requirement that a "song" includes a complete rendition of all themes, our song sequence would be as follows:

...1234124546/12346546/1234546/121246...

If instead we used Frumhoff's (1983) definition, our "song" could be categorized by the repetition of themes 1-2-3 (since this pattern is repeated more than twice in the song session), perhaps leading to the following:

...1234124546/12346546/1234546121246...

Or, following the precedent of the Fristrup *et al.* (2003) study, we could start a new song each time we encounter Theme 1. Thus our song sequence would be as follows:

...1234/124546/12346546/1234546/12/1246...

Although each of the above examples uses the exact same thematic sequence, different methods of delineating song structure (each published and utilized in different studies) lead to very different results in terms of the number of "songs" in the sequence, in the measured duration of each song, and in the thematic composition and order in each song. As a result, attempts to derive biologically relevant interpretations from analyses at the "song" level become difficult at best, and interpretation of the results is impossible without description of the variability of theme order. This real example demonstrates that the definition of "song," and consequently the metric of "song duration," as currently measured for humpback whales is in some cases problematic, and raises the question as to the biological interpretation of analyses conducted at this hierarchical level.

This is not to say that measures of song cycles, as classically defined for humpback whales, are without significance. When theme order is invariant, dividing sequences into song cycles for analyses may be relevant because the "songs" being compared are true repeats of the same pattern. And clearly, in at least some years, male humpback whales do seem to adhere to a hierarchical sequence at this level, which seems likely to be biologically relevant. However, when individuals incorporate a larger degree of variation into their thematic sequence, trying to force this variation into a structure that is defined by ordered repetition is not appropriate. The outcome is a series of arbitrarily delineated "songs," none of which is like the other.

A final note on song designation: while breathing intervals have sometimes been used as a "convenient way to define a beginning and end" of a song (Winn *et al.* 1970, Payne and Payne 1985), our own observations as well as other studies (Winn and Winn 1978, Winn *et al.* 1981), document individuals breathing during different themes, so the temptation to use breathing cycle as a measure of "song length" should be avoided.

Application of Songbird Metrics to Humpback Whale Song

From a biological perspective, the degree of variation in theme order may be informative. However, many researchers choose to assess effects at the song cycle level, and these potentially relevant differences in singing behavior are consequently ignored. Regrettably, this is likely limiting our understanding of the use of song within the humpback mating system. Instead, if we expand our conceptual framework to learn from studies of song in other taxa, we can consider humpback whales as "eventual variety" singers, and apply established methods for assessing variation and effects within this different paradigm. Some authors have started to move towards quantifying song structure at the level of phrases or repetitions of phrases (Eriksen *et al.* 2005, Tougaard and Eriksen 2006, Cholewiak 2008).

Recent work (Cholewiak 2008) to apply some of the avian song metrics to analyses of humpback whale song have found that males do vary their song presentation in ways that are quantifiable on the level of phrase-based analyses. For example, an analysis of switching rate found that males significantly increase the rate at which they switch between different phrase types in the presence of a second singer, as compared to when they are alone (Cholewiak 2008). This type of analysis provides different and potentially more revealing information than may be obtained, for example from traditional transition matrices or measures of "song" duration. The use of similar metrics in songbirds has revealed that changes in these variables may, for example, indicate an escalation of aggression between males (Krebs *et al.* 1981, Vehrencamp 2001). Further applications of these types of methods to humpback whale songs, such as using quantitative metrics to measure the degree of repetition over time rather than across song cycles, may be important in advancing our understanding of the complex nature of humpback whale vocal behavior.

Conclusions and Recommendations

Investigations of humpback whale song have spanned over four decades, yet there are still many unanswered questions regarding the degree of variation within and between individuals, the ways in which changes in song structure are transmitted over space and time, and the role of song within the breeding system. Pioneering work in the 1970s and 1980s developed a framework within which to analyze and understand humpback song structure, which was later reinforced and expanded by further studies. Humpback whale song is a constantly changing phenomenon, which has captured the interest of many students of animal behavior, while also presenting challenges with respect to qualitative and quantitative analyses.

At the lower hierarchical levels within the humpback song framework, traditional definitions have worked well to identify song elements for analyses. At the middle levels, however, delineation of "phrases" and "themes" has been complicated both by the lack of well-defined time intervals between repetitive sequences, as well as by the ever-changing nature of song features. At the highest hierarchical level within this framework, the application of song cycle measures has obscured the degree of variation in theme order that exists between males, and has made interpretation and comparison of studies using different classification schemes problematic at best. While individuals have been shown to often sing themes in a relatively fixed order, it appears that in some regions (and/or time periods) there is variation in the consistency with which individual males adhere to a strict sequence. In the majority of studies to date, the potential biological relevance of this variability has been overlooked, because it is difficult to quantify within the traditional framework. In these situations, we suggest that the measures at the level of "song" (as a fixed sequence of themes) be used with extreme caution, and that alternative analyses be considered. In light of the burgeoning body of work on humpback whale singing behavior, we hope that this review will enable more consistent, meaningful comparisons across studies.

Recommendations

Given the analytical approaches that have become common in studies of humpback whale song, and our assessment of the inherent variation in song behavior and associated problems, we make the following recommendations for studies of humpback whale song patterns:

(1) Maintaining the use of "units" and "subunits" in song description and measurements.
(2) Use of a consistent set of criteria for delineation of phrases, as described in this review.
(3) Maintaining and using vocabulary describing different theme types, as described in Payne and Payne (1985).
(4) Abandonment of the classical use of the "song duration" metric as a response variable, and except in the specific case in which theme order and occurrence within and between singers is demonstrated to be invariable or nearly invariable.
(5) Adoption of the "phrase" as the salient level of repetition, as analogous to a bird "song" in the avian literature, and consequent exploration of analysis approaches that focus on sequences of phrases, following the birdsong paradigm for analysis of song sequences.

Acknowledgments

For assistance in the field off the Brazilian coast, we thank Alexandre Paro, Márcia Freitas Araújo, Lucas Goulart Collares, Bruna Mazoni Guerra, Roberto Caçonia Fortes, and Carlo D'Angelo, and the crews of the boats *Tomara*, *Coronado*, and *Piloto*. For assistance in the field and laboratory related to data collected off Isla Socorro, Mexico, we thank Sergio Martinez Aguilar, Hiram Rosales Nanduca, Sandra Smith Aguilar, Gloria Panecatl, Tom Turowski, Joe Kaplan, Melissa Crawford, Jenny Gerding, Axa Brambila Villasenor, and Risa Kohara. The authors would also like to extend a special thanks to Jeff Jacobsen, Jorge Urbán-Ramírez and to the Armada de México for making the work at Isla Socorro possible. We thank Tom Norris for assistance with data collected off Kauai, Hawaii. Sandra Smith Aguilar, Christopher Clark, Stephen Morreale, Milo Richmond, and John Hermanson provided helpful comments on early versions of this manuscript. We also thank three anonymous reviewers for their helpful comments on this manuscript. Funding and support were provided by the EPA STAR fellowship (funding provided to DMC), Brazilian Government (CAPES BEX 1523-01-5 scholarship to RSSL), the Society for Marine Mammalogy's Grant-in-Aid of Research, the Animal Behavior Society's Cetacean Behavior and Conservation Award (to both DMC and RSSL); Petróleo Brasileiro S. A., and The Canon National Parks Science Scholars Program.

Literature Cited

Aldrich, H. L. 1889. Arctic Alaska and Siberia, or, Eight months with the Arctic whalemen. Rand McNally, Chicago, IL.

Anderson, R. C., W. A. Searcy, S. Peters and S. Nowicki. 2008. Soft song in song sparrows: Acoustic structure and implications for signal function. Ethology 114:662–676.

Anonymous. 1969. Singing whales. Nature 224:217.

Box, G. E. P., and N. R. Draper. 1987. Empirical model-building and response surfaces. John Wiley & Sons, New York, NY.

Bremond, J. C. 1963. Acoustic behavior of birds. Pages 709–750 *in* R. Busnel, ed. Acoustic behavior of animals. Elsevier, New York, NY.

Broughton, W. B. 1963. Glossarial index. Pages 824–911 *in* R. Busnel, ed. Acoustic behavior of animals. Elsevier, New York, NY.

Catchpole, C. K. 1976. Temporal and sequential organization of song in the sedge warbler (*Acrocephalus schoenobaenus*). Behaviour 59:226–246.

Cato, D. H. 1991. Songs of humpback whales: The Australian perspective. Memoirs of the Queensland Museum 30:277–290.

Cerchio, S. 1993. Geographic variation and cultural evolution in songs of humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific. M.Sc. thesis, Moss Landing Marine Laboratories, Moss Landing, CA and San Jose State University, San Jose, CA. 72 pp.

Cerchio, S., J. K. Jacobsen and T. F. Norris. 2001. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: Synchronous change in Hawaiian and Mexican breeding assemblages. Animal Behaviour 62:313–329.

Cholewiak, D. 2008. Evaluating the role of song in the humpback whale (*Megaptera novaeangliae*) breeding system with respect to intra-sexual interactions. Ph.D. thesis, Cornell University, Ithaca, NY. 159 pp.

Chu, K., and P. Harcourt. 1986. Behavioral correlations with aberrant patterns in humpback whale songs. Behavioral Ecology and Sociobiology 19:309–312.

Cummings, W. C., and L. A. Philippi. 1970. Whale phonations in repetitive stanzas. Technical Publication 196, Naval Undersea Research and Development Center, San Diego, CA.

Darling, J. 1983. Migrations, abundance and behavior of "Hawaiian" humpback whales (*Megaptera novaeangliae*). Ph.D. thesis, University of California, Santa Cruz, CA. 147 pp.

Darling, J. D., and R. S. Sousa-Lima. 2005. Songs indicate interaction between humpback whale (*Megaptera novaeangliae*) populations in the western and eastern South Atlantic Ocean. Marine Mammal Science 21:557–566.

Darling, J. D., M. E. Nicklin and C. P. Nicklin. 2006. Humpback whale songs: Do they organize males during the breeding season? Behaviour 143:1051–1101.

Eens, M., R. Pinxten and R. F. Verheyen. 1989. Temporal and sequential organization of song bouts in the starling. Ardea 77:75–86.

Eriksen, N., L. A. Millar, J. Tougaard and D. A. Helweg. 2005. Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. Behaviour 142:305–328.

Fraser, F. C. 1947. Sound emitted by dolphins. Nature 160:759.

Fristrup, K. M., L. T. Hatch and C. W. Clark. 2003. Variation in humpback whale (*Megaptera novaeangliae*) song length in relation to low-frequency sound broadcasts. Journal of the Acoustical Society of America 113:3411–3424.

Frumhoff, P. 1983. Aberrant songs of humpback whales (*Megaptera novaeangliae*): Clues to the structure of humpback songs. Pages 81–127 *in* R. Payne, ed. Communication and behavior of whales. AAAS Selected Symposium 76. Westview Press, Boulder, CO.

Garland, E. C., A. W. Goldizen, M. L. Rekdah, *et al*. 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Current Biology 21:687–691.

Glockner, D. A. 1983. Determining the sex of humpback whales (*Megaptera novaeangliae)* in their natural environment. Pages 447–464 *in* R. Payne, ed. Communication and behavior of whales. AAAS Selected Symposium 76. Westview Press, Boulder, CO.

Green, S. R., E. Mercado III, A. Pack and L. M. Herman. 2011. Recurring patterns in the songs of humpback whales (*Megaptera novaeangliae*). Behavioural Processes 86:284–294.

Guinee, L. N., and K. Payne. 1988. Rhyme-like repetitions in song of humpback whales. Ethology 79:295–306.

Guinee, L. N., K. Chu and E. M. Dorsey. 1983. Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). Pages 59–80 *in* R. Payne, ed. Communication and behavior of whales. AAAS Selected Symposium 76. Westview Press, Boulder, CO.

Hafner, G. W., C. L. Hamilton, W. W. Steiner, T. J. Thompson and H. E. Winn. 1979. Signature information in the song of the humpback whale. Journal of the Acoustical Society of America 66:1–6.

Hartshorne, C. 1956. The monotony-threshold in singing birds. Auk 73:176–192.

Helweg, D. A., L. A. Herman, S. Yamamoto and P. H. Forestell. 1990. Comparison of songs of humpback whales (*Megaptera novaeangliae*) recorded in Japan, Hawaii, and Mexico during the winter of 1989. Scientific Reports of the Cetacean Research Institute 1:1–20.

Helweg, D. A., A. S. Frankel, J. R. Mobley Jr and L. A. Herman. 1992. Humpback whale song: Our current understanding. Pages 459–483 *in* J. Thomas, R. Kastelein and A. Supin, eds. Marine mammal sensory systems. Plenum Press, New York, NY.

Helweg, D. A., D. H. Cato, P. F. Jenkins, C. Garrigue and R. D. McCauley. 1998. Geographic variation in South Pacific humpback whale songs. Behaviour 135:1–27.

Herman, L. M., and W. N. Tavolga. 1980. The communication systems of cetaceans. Pages 149–209 *in* L. M. Herman, ed. Cetacean behavior: Mechanisms and function. John Wiley and Sons, New York, NY.

Isaac, D., and P. Marler. 1963. Ordering of sequences of singing behavior of Mistle thrushes in relationship to timing. Animal Behaviour 11:179–188.

Kibblewhite, A. C., R. N. Denham and D. J. Barnes. 1967. Unusual low-frequency signals observed in New Zealand waters. Journal of the Acoustical Society of America 41:644–655.

Krebs, J. R., R. Ashcroft and K. V. Orsdol. 1981. Song matching in the great tit *Parus major* L. Animal Behaviour 29:918–923.

Kullenberg, B. 1947. Sound emitted by dolphins. Nature 160:648.

Maeda, H., N. Higashi, S. Uchida, F. Sato, M. Yamaguchi, T. Koido and A. Takemura. 2000. Songs of humpback whales *Megaptera novaeangliae* in the Ryukyu and Bonin regions. Mammal Study 25:59–73.

Matilla, D. K., L. N. Guinee and C. A. Mayo. 1987. Humpback whale songs on a North Atlantic feeding ground. Journal of Mammalogy 68:880–883.

Mazhar, S., T. Ura and R. Bahl. 2008. Effect of temporal evolution of songs on Cepstrum-based voice signature in humpback whales. IEEE Oceans Conference Proceedings 1–8.

McSweeney, D. J., K. C. Chu, W. F. Dolphin and L. N. Guinee. 1989. North Pacific Humpback whale songs: A comparison of Southeast Alaskan feeding ground songs with Hawaiian wintering ground songs. Marine Mammal Science 5:39–148.

Mercado, E. III, L. H. Herman and A. A. Pack. 2003. Stereotypical sound patterns in humpback whale songs: Usage and function. Aquatic Mammals 29:37–52.

Mercado, E. III, L. H. Herman and A. A. Pack. 2005. Song copying by humpback whales: Themes and variations. Animal Cognition 8:93–102.

Miller, P. J. O., N. Biassoni, A. Samuels and P. L. Tyack. 2000. Whale songs lengthen in response to sonar. Nature 405:903.

Molles, L. E. 2006. Singing complexity of the banded wren (*Thryothorus pleurostictus*): Do switching rate and song-type diversity send different messages? Auk 123:991–1003.

Molles, L. E., and S. L. Vehrencamp. 1999. Repertoire size, repertoire overlap, and singing modes in the banded wren (*Thryothorus pleurostictus*). Auk 116:677–689.

Noad, M. J., D. H. Cato, M. M. Bryden, M. N. Jenner and C. S. Jenner. 2000. Cultural revolution in whale songs. Nature 408:537.

Pace, F., F. Benard, H. Glotin, O. Adam and P. White. 2010. Subunit definition and analysis for humpback whale call classification. Applied Acoustics 71:1107–1112.

Payne, R., and L. N. Guinee. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of "stocks." Pages 333–358 *in* R. Payne, ed. Communication and behavior of whales. AAAS Selected Symposium 76. Westview Press, Boulder, CO.

Payne, R. S., and S. McVay. 1971. Songs of humpback whales. Science 173:585–597.

Payne, R., and K. Payne. 1971. Underwater sounds of southern right whales. Zoologica 58:159–163.

Payne, K., and R. Payne. 1985. Large scale changes over 19 years in songs of humpback whales in Bermuda. Zeitschrift für Tierpsychologie 68:89–114.

Payne, K., P. Tyack and R. S. Payne. 1983. Progressive changes in the song of humpback whales songs (*Megaptera novaengliae*): A detailed analysis of two seasons in Hawaii. Pages 9–57 *in* R. Payne, ed. Communication and behavior of whales. AAAS Selected Symposium 76. Westview Press, Boulder, CO.

Picot, G., O. Adam, M. Bergounioux, H. Glotin and F-X. Mayer. 2008. Automatic prosodic clustering of humpback whales song. New Trends for Environmental Monitoring Using Passive Systems, 14–17 October 2008, French Riviera.

Rickwood, P., and A. Taylor. 2008. Methods for automatically analyzing humpback song units. Journal of the Acoustical Society of America 123:1763–1772.

Schevill, W. E. 1964. Underwater sounds of cetaceans. Pages 307–316 *in* W. N. Tavolga, ed. Marine bio-acoustics. Pergamom, Oxford, U.K.

Schevill, W. E., and B. Lawrence. 1949. Underwater listening to the white porpoise (*Delphinapterus leucas*). Science 109:143–144.

Schevill, W. E., and W. A. Watkins. 1962. Whale and porpoises voices: A phonograph record. Contribution Number 1320, Woods Hole Oceanographic Institution, Woods Hole, MA. 24 pp. + phonograph record.

Schreiber, O. W. 1952. Some sounds from marine life in the Hawaiian area [Abstract]. Journal of the Acoustical Society of America 24:116.

Shapiro, A. D., P. L. Tyack and S. Seneff. 2011. Comparing call-based versus subunit-based methods for categorizing Norwegian killer whale, *Orcinus orca*, vocalizations. Animal Behaviour 81:377–386.

Sorjonen, J. 1987. Temporal and spatial differences in the traditions and repertoires in the song of the thrush nightingale (*Luscinia luscinia*). Behaviour 102:196–212.

Sousa-Lima, R. S. 2007. Acoustic ecology of humpback whales (*Megaptera novaenagliae*) in the Abrolhos National Marine Park, Brazil. Ph.D. thesis, Cornell University, Ithaca, NY. 179 pp.

Sousa-Lima, R. S., M. E. Morete, R. C. Fortes, A. C. Freitas and M. H. Engel. 2002. Impact of boats on the vocal behavior of humpback whales off Brazil. The Journal of the Acoustical Society of America 112:2430–2431.

Smith-Aguilar, S. 2009. Análisis estructural de la canción de la ballena jorobada (*Megaptera novaeangliae).* Variación individual, temporal y geográfica en la Bahía de Banderas y alrededores de la Isla Socorro, México. M.Sc.thesis, Universidad Nacional Autónoma de México. 99 pp.

Stoddard, P. K., M. D. Beecher and M. S. Willis. 1988. Response of territorial male song sparrows to song types and variations. Behavioral Ecology and Sociobiology 22:125–130.

Tavolga, W. N. 1968. Marine animal data atlas. Naval Training Device Center. Technical Report: NAVTRADEVCEN 1212-2. pp. 170–185.

Thompson, P. O., and W. A. Friedl. 1982. A long term study of low frequency sounds from several species of whales off Oahu, Hawaii. Cetology 45:1–19.

Thielcke, G. 1969. Geographic variation in bird vocalizations. Pages 311–330 *in* R. A. Hinde, ed. Bird vocalizations: Their relations to current problems in biology and psychology. Cambridge University Press, Cambridge, U.K.

Thorpe, W. H. 1961. Bird-song: The biology of vocal communication and expression in birds. Cambridge University Press, Cambridge, U.K. p. 15.

Todt, D., and H. Hultsch. 1996. Acquisition and performance of song repertoires: Ways of coping with diversity and versatility. Pages 79–96 *in* D. E. Kroodsma and E. H. Miller, eds. Ecology and evolution of acoustic communication in birds. Comstock Publishing, Ithaca, NY.

Tougaard, J., and N. Eriksen. 2006. Analysing differences among animal songs quantitatively by means of the Levenshtein distance measure. Behaviour 143:239–252.

Tyack, P. 1981. Interactions between singing Hawaiian humpback whales and conspecifics nearby. Behavioral Ecology and Sociobiology 8:105–116.

Vehrencamp, S. L. 2001. Is song-type matching a conventional signal of aggressive intentions? Proceedings of the Royal Society of London Series B-Biological Sciences 268:1637–1642.

Winn, H. E., and L. K. Winn. 1978. The song of the humpback whale (*Megaptera novaengliae*) in the West Indies. Marine Biology 47:97–114.

Winn, H. E., P. J. Perkins and T. C. Poulter. 1970. Sounds of the humpback whale. 7th Annual Conference on Biological Sonar and Diving Mammals, Stanford Research Institute, Menlo Park, CA. pp. 39–52.

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. Behavioral Ecology and Sociobiology 8:41–46.

Received: 1 April 2011
Accepted: 27 August 2012