Intra-individual variation in the songs of humpback whales suggests they are sonically searching for conspecifics

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Abstract

Observations of animals' vocal actions can provide important clues about how they communicate and about how they perceive and react to changing situations. Here, analyses of consecutive songs produced by singing humpback whales recorded off the coast of Hawaii revealed that singers constantly vary the acoustic qualities of their songs within prolonged song sessions. Unlike the progressive changes in song structure that singing humpback whales make across months and years, intra-individual acoustic variations within song sessions appear to be largely stochastic. Additionally, four sequentially produced song components (or "themes") were each found to vary in unique ways. The most extensively used theme was highly variable in overall duration within and across song sessions, but varied relatively little in frequency content. In contrast, the remaining themes varied greatly in frequency content, but showed less variation in duration. Analyses of variations in the amount of time singers spent producing the four themes suggest that the mechanisms that determine when singers transition between themes may be comparable to those that control when terrestrial animals move their eyes to fixate on different positions as they examine visual scenes. The dynamic changes that individual whales make to songs within song sessions are counterproductive if songs serve mainly to provide conspecifics with indications of a singer's fitness. Instead, within-session changes to the acoustic features of songs may serve to enhance a singer's capacity to echoically detect, localize, and track conspecifics from long distances.

Keywords Acoustic communication · Cetacean · Mysticete · Auditory perception · Bioacoustics

Introduction

Animals use sounds to gain access to opportunities they would not have if they were silent (Owren et al., 2010; Simmons et al., 2003; Surlykke et al., 2014). In some cases, vocalizations serve to facilitate social interactions, while in others they play a more perceptual role. Some sounds can potentially be used for both active perception and communication (Bohn & Gillam, 2018; Clark & Ellison, 2004; Janik, 2013; Jones & Siemers, 2011), making it difficult to determine exactly what outcomes vocalizers are seeking. For instance, bowhead whales produce songs while migrating through areas containing sea ice. Whale songs are generally assumed to be mating displays (Tyack & Clark, 2000),

but they also reflect from ice in ways that can reveal the location and thickness of ice floes (George et al., 1989). Observations that singing bowhead whales avoid swimming under large floes and sometimes increase their rate of calling as they approach floes raises the possibility that bowheads use song-generated echoes to navigate around thick ice (Clark & Ellison, 2004). It remains unclear, however, whether bowhead whales migrating through Arctic waters are singing primarily to communicate with other whales or to perceptually scan their surroundings. Bowhead whales are not the only whales producing functionally ambiguous vocalizations. Recent evidence suggests that other whales may also sing to expand their perceptual horizons, including the most famous cetacean singer of them all, the humpback whale (Mercado, 2018b, 2021b).

Singing humpback whales produce a wide variety of sounds in organized sequences, varying both the repertoire of sounds used and the structural composition of songs throughout their lifespan (Guinee et al., 1983; Payne & Payne, 1985; Winn & Winn, 1978). Whale songs are

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traditionally defined as patterned series of sounds that are repeated over and over (Darling, 2017). The full repertoire of sounds (called units) that humpbacks use within songs is not known, but 100+ distinguishable unit "types" have been identified from whales in the South Pacific alone (Allen et al., 2017; Garland, Rendell, Lamoni, et al., 2017a). Units of each type may vary in duration, bandwidth, intensity, spectral shape, and so on; the boundaries between most unit types are fuzzy with significant overlap, such that the repertoire of units used by humpback whales is graded rather than discrete (Maeda et al., 2000; Mercado et al., 2005; Mercado & Perazio, 2021a; Mercado et al., 2010). Humpback whales within a population appear to collectively and progressively change the repertoire of units that they use within songs across years, suggesting that singers' vocal repertoires are dynamic (Cato, 1991).

Singing humpback whales produce units in patterned sequences (called *phrases* and *themes*; themes typically consist of repeated phrases) that vary over time (Guinee et al., 1983; Payne & McVay, 1971). Sequences can vary in terms of the number and types of units that are included and with respect to how constituent units vary within a song (Cato, 1991; Cerchio et al., 2001; Garland, Rendell, Lilley, et al., 2017b; Payne et al., 1983). The focus of many past studies of humpback whale songs has been on describing how singers vary song structure across years (e.g., Garland et al., 2011). Singers within a particular locale produce similarly structured sequences even as they change the structural features of those sequences over time (Payne et al., 1983), suggesting that the content of songs evolves through processes of cultural transmission (Allen, 2019; Garland & McGregor, 2020). Individual singers also modify the characteristics of songs during periods of continuous song production, referred to as *song sessions*. Song sessions can last many hours, within which humpback whales may produce dozens of songs back to back (Ryan et al., 2019; Winn & Winn, 1978). Songs within such sessions can vary in duration and composition, including variations in the units produced and the persistence with which specific phrases are repeated (Allen et al., 2019; Payne et al., 1983). In some cases, singers repeat the units and sequences within consecutive songs almost exactly (Schneider & Mercado, 2019). Although singers are capable of reproducing multi-minute sequences of units, they often do not do so across consecutive songs within a song session.

Recent acoustic analyses suggest that despite the apparent complexity of song structure, singers may be constrained in terms of the tempo of unit production (Schneider & Mercado, 2019), the overall frequency content of songs (Perazio & Mercado, 2018; Ryan et al., 2019), and the order in which specific unit sequences are produced (Mercado, 2021a; Mercado & Perazio, 2021b). These kinds of constraints or "rules" of song production

may provide important clues about how singers are using songs, as well as about the factors that lead singers to dynamically change both their vocal repertoires and unit sequences over time. Researchers have argued that the primary factors leading to such changes are innovations produced by the most evolutionarily fit singers, or by copying errors that individual singers introduce (Garland & McGregor, 2020; Garland, Rendell, Lamoni, et al., 2017a; McLoughlin et al., 2016). This proposal derives from the widespread belief that the ultimate driver of variation in whale songs is sexual selection, especially female preferences for novelty (for review, see Herman, 2017). The main assumption underlying this belief is that female listeners will favor singers that "demonstrate conformity to the current version of the song as well as display innovation" (Cerchio et al., 2001, p. 326). Evidence that females select mates based on preferences for certain song characteristics is lacking, however, and this hypothesis (hereafter referred to as the *reproductive display hypothesis*, see Fig. 1a) makes no specific predictions about how singers should vary the acoustic features of songs over time to entice females. More generally, the claim that humpback whale songs serve primarily as a sexual display to impress conspecifics (like a peacock's tail) places few constraints either on the form of songs or on the variations that singers might make to either units or sequences of units.

An alternative proposal, hereafter referred to as the *sonar hypothesis* (see Fig. 1b), is that "singing" humpback whales are using sequences of units to actively explore their environments (Frazer & Mercado, 2000; Mercado, 2018b, 2020; Mercado & Frazer, 2001). From this perspective, any variations that a singer introduces into a song may serve to enhance the detectability or interpretability of echoes generated by units, and constraints on both song form and on changes in songs over time are driven by the physical limitations of long-range sound transmission in ocean environments, as well as physiological limits on the perceptual processing of echoic auditory scenes. Consequently, the sonar hypothesis predicts that singing humpback whales will continuously vary their production of unit sequences depending on the strategies that they are engaging in as they actively search for targets (e.g., other whales) at long distances, as is seen in several species of bats (Fawcett & Ratcliffe, 2015; Lewicki et al., 2014; Moss et al., 2014; Moss & Surlykke, 2001). The perceptual task faced by humpback whales searching for conspecifics differs in many respects from the one faced by bats foraging for insects (Mercado, 2018b), because of the aquatic environment, target sizes, and the long distances involved (see Fig. 1c). Nevertheless, like bats, humpbacks can benefit from the echoes generated by the sounds they produce, if those sounds possess suitable spectral and temporal features (Clark & Ellison, 2004; Winn & Winn, 1978; Yi & Makris, 2016).

a) Song as a reproductive display
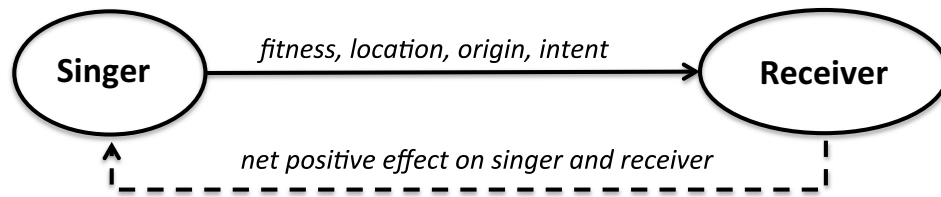
b) Song as sonar
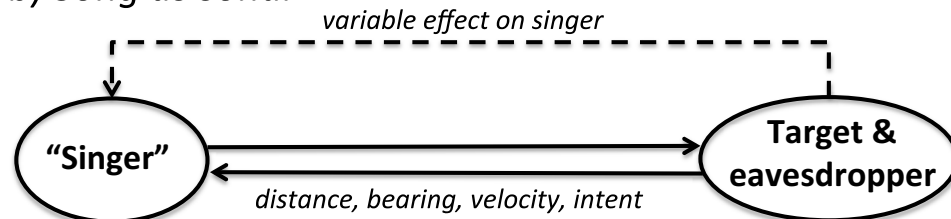
c) Song as a long-range signal

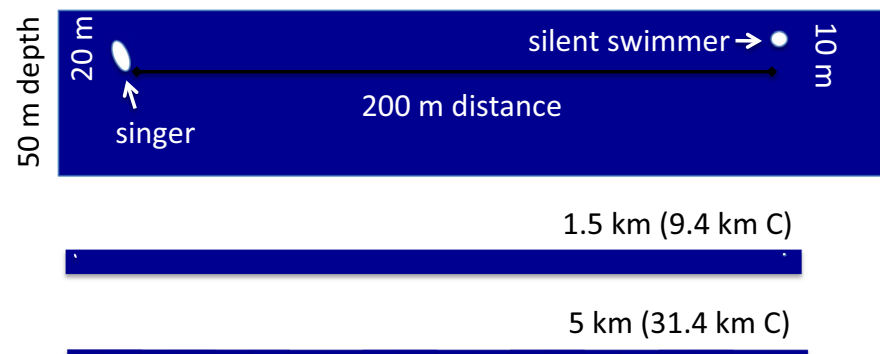**Fig. 1** Two hypotheses for how humpback whale songs function. *Note.* (**a**) For humpback whale songs to function effectively as sexual advertisement displays, they must provide reproductively relevant information to listeners that benefits both the singer and listeners. (**b**) For songs to function as sonar signals, they must generate echoes that provide relevant information to the singer; listeners may also glean relevant information (see also Bohn & Gillam, 2018). (**c**) The environments within which humpbacks sing strongly constrain their capacity to monitor the actions and locations of conspecifics. Singers on breeding grounds are often found ~20 m deep in relatively shallow waters. As the distances between a singer and conspecifics grow, the area the singer will need to monitor increases (C = circumference), and the ratio of water depth to distance shrinks, greatly increasing the complexity of song propagation. Propagation-related distortion changes song features in ways that constrain reliable reception of signals by receivers, and thus confounds listeners' cross-singer comparisons based on those features. This same distortion can enhance the information available to a singer from echoes, however, because the singer can potentially compare the original signal to the distorted echos and extract spatial information based on the differences

Assessing the functional utility of humpback whale songs is logistically challenging. Correlating sound production with social contexts can potentially clarify how vocalizers are using sound (e.g., Clark, 1982), but this approach is often insufficient for resolving competing interpretations (Herman, 2017). In the case of bowhead whales, dynamic changes in vocal timing and frequency during navigation through ice are suggestive of echolocation, but might also be interpreted as social communication (Ellison et al., 1987). Foraging humpback whales are known to vary sound production in ways that match echolocation-related behaviors in dolphins (Stimpert et al., 2007), yet researchers remain reluctant to accept that humpbacks might perceive or attend to any echoes that their sound production generates. The dynamics of humpback whales' vocal actions can provide clues about what they are attempting to do. For instance, the recent discovery that singers produce consecutive units in ways that minimize overlap in the frequency content of resulting echo streams suggests that song phrases may be structured to avoid self-interference (Mercado, 2016, 2021b).

Understanding how singers vary songs over multiple time scales may provide insights into why their songs are so dynamic (Mercado, 2021a), and in particular, can clarify whether singers use songs to explore their surroundings.

Animals engaged in actively exploring their environment show movement profiles that differ systematically from those of animals following chemical trails (Bartumeus et al., 2005) or familiar paths (Atkinson et al., 2002; Hulgard et al., 2016). Vertebrates move their eyes in characteristic patterns while visually inspecting objects and scenes (Collewijn, 1977; Harris et al., 1988; Rayner, 1998; Wallman & Pettigrew, 1985), rodents move their vibrissae differently when they are searching for objects versus interacting socially (Wolfe et al., 2011), and bats vary their vocalizations depending on whether they are searching for targets, attempting to intercept a target, or singing to a conspecific (Seibert et al., 2013; Smotherman et al., 2016; Warnecke et al., 2015). It is thus possible to identify the perceptual functions of some animals' actions by precisely measuring the dynamics of their movements, including vocal dynamics. If singing humpback whales are actively searching their surroundings using sound, then their vocal patterns should vary in ways that are likely to produce informative echoes.

Here, intra-individual variation in the singing behavior of humpback whales was measured to further assess whether singers vary songs in a manner that is conducive to the detection and localization of echoes generated by large, moving targets from long distances. One of the key predictions of the sonar hypothesis is that singers will vary their production of broadband units in ways that differ systematically from their use of narrowband signals. Field studies of bats (*Pipistrellus*) echolocating while actively hunting revealed two main modes of signal production: one in which sequences were composed mostly of narrowband signals, and the other consisting mainly of broadband signals (Kalko & Schnitzler, 1993). Each mode was predominately composed of one or two specific signal types, with types differing significantly across modes. Specifically, narrowband signals were longer in duration, with longer intervals between signals. Bats used different echolocation modes in different environments, suggesting that the efficacy of each mode varies as a function of environmental conditions. Bats echoically search at much shorter ranges (< 10 m) than would be relevant for humpback whales, and are hunting for small targets in air. Consequently, the specific signal frequencies and temporal intervals used by echolocating bats would not be functional for whales. The physical constraints on echo detectability and localizability are conserved across signal wavelengths, however, such that singing humpback whales would face many of the same auditory challenges as echolocating bats when attempting to process echoes. In particular, narrowband and broadband signals vary in their capacity to yield localizable echoes from long ranges underwater, just as they do in air

(Mercado, 2018b). The sonar hypothesis predicts that singing humpback whales will produce sequences of narrowband signals in ways that differ systematically from their production of sequences of broadband signals, because each mode of signal production affords different echoic advantages during long-distance searching.

One way that humpback whale songs differ significantly from the signals used by echolocating bats and dolphins is that singing humpback whales change both their repertoire of units and the patterns of units they produce over time. These changes are clearly evident across years (Cato, 1991; Garland et al., 2011; Mercado et al., 2005; Payne & Payne, 1985; Winn & Winn, 1978), but also can be seen within individual song sessions (Mercado, 2018a; Payne et al., 1983). Changes to song features occur either progressively, through the gradual morphing of units and phrases (Mercado, 2021a; Mercado & Perazio, 2021b; Payne et al., 1983), or rapidly through replacement of units and phrases (Cato, 1991; Noad et al., 2000; Payne & Payne, 1985). The reproductive display hypothesis explains such changes as the result of singers innovating and imitating songs to increase or maintain their attractiveness to females, and thus makes no specific predictions about how song elements should change over time. The sonar hypothesis explains these changes as a side effect of singers changing song features to avoid mutual interference (Mercado, 2018b, 2021a). Consequently, the sonar hypothesis predicts that changes to songs should follow predictably constrained trajectories that maintain the echoic functionality of both narrowband and broadband units. Importantly, the sonar hypothesis predicts that how singers change songs within song sessions should relate to the conditions within which they are singing (as is seen in echolocating bats and dolphins) and to the progress of their search. Given that the time a singer spends producing particular frequencies in either a narrowband or broadband mode will determine what echoes are potentially perceptible, the sonar hypothesis specifically predicts that singers actively searching their surroundings should systematically change these aspects of sound production within song sessions.

The current study examines intra-individual changes in the songs produced by humpback whales within song sessions to answer three questions. First, do songs within a session vary along predictable acoustic dimensions (e.g., frequency bandwidth or time spent producing specific frequencies or unit combinations)? Earlier comparisons of songs across sessions revealed that phrase duration was more consistent across singers than was theme duration (Frumhoff, 1983; Payne et al., 1983), but little attention has been given to describing intra-individual variations in any other song characteristics. The sonar hypothesis predicts that narrowband elements of units provide singers with different information from broadband elements (Mercado, 2018b), and thus may be modified differently over time, as is seen in

echolocating bats (Fawcett et al., 2015; Fawcett & Ratcliffe, 2015). Second, do singers predictably vary their time spent producing different unit sequences or frequencies while singing? If singers consistently devote more time to producing specific sequences within song sessions, then those sequences may be more functionally relevant or strategically advantageous than less extensive sequences. Identifying how singers vary the production of themes within song sessions can also potentially provide clues about the mechanisms that lead singers to change songs in specific ways. For instance, bats vary their use of narrowband versus broadband search signals based on the openness of the environment within which they are searching (Kalko & Schnitzler, 1993). Third, do singers progressively change songs within song sessions (i.e., are the differences between consecutive songs smaller than the differences between more temporally separated songs)? Progressive changes within song sessions might be expected if variations in songs arise when singers intermittently make mistakes as they attempt to copy song variations (e.g., inaccurately imitating specific units or phrases) that they have heard other singers producing, as proposed by the reproductive display hypothesis (Garland & McGregor, 2020; McLoughlin et al., 2018). Alternatively, if song variants within a song session change over time in ways that are less predictable, then this greatly increases the difficulties faced by any females or males attempting to compare the fitness of singers by listening to their songs.

Method

Data set

Song sessions from Google's Pattern Radio online recording database, available at https://patternradio.withgoogle.com/, were manually selected for analysis based on their duration and the extent to which they were occluded by extraneous noise sources (e.g., ships or other whales) in spectrograms. The recordings were originally collected off the coast of Hawaii with a HARP (Wiggins & Hildebrand, 2007). Recordings initially were sampled at 200 kHz, and then later down-sampled to 10 kHz; recordings stored in FLAC format are available at https://doi.org/10.25921/Z787-9Y54. The online database interface displays frequencies between ~55 Hz and 3,200 Hz. Although singing humpback whales are capable of producing units with energy outside of this range (Au et al., 2006; Mercado et al., 2010), spectrograms created with RavenPro software (ver. 1.5) revealed no significant peaks beyond this range for the analyzed song sessions.

The current analyses focused on song sessions recorded between 6 December 2014 and 11 January 2015. During this period, humpback whales were just beginning to arrive in Hawaiian waters after their migration. Consequently, overlapping songs from multiple singers were less likely to be present within recordings; this section of the recordings spanned 888 h. The Pattern Radio database includes indicators of automatically detected humpback whale songs, which can be used to objectively identify times when singers are likely present within recordings (Allen et al., 2020). These indicators, combined with visual inspection of spectrograms (e.g., Fig. 2a), were used to identify song sessions containing a minimum of ten consecutive songs. The ten-song minimum was arbitrarily selected and mainly served to restrict analyses to song sessions produced continuously for more than an hour.

Eighteen song sessions containing at least ten consecutive songs were identified. From these, ten sessions were selected that were recorded on different days (with one exception) to reduce the likelihood of pseudoreplication. It remains possible that a singer was sampled more than once within these ten sessions, although the likelihood is low given that singers typically do not remain in the same location for more than a day (Cerchio et al., 2001; Craig et al., 2001). Each of the ten song sessions was manually divided into overlapping segments spanning ~22 min. The same time scale was used for all segments. Divisions between segments were selected to avoid splitting songs across segments (with an overlap between segments of ~4 min). This segmentation process was the digital equivalent of cutting a continuous printout of a multi-hour spectrogram into similarly sized pieces, replicating the original approach used by Payne and McVay (1971) to analyze humpback whale songs (e.g., see Payne & McVay, 1971; Figs. 2, 3, 4 and 5).

Spectrographic images of segments were screen captured using the "Grab" function from OS X running on a Macintosh computer, such that each selection included the entire spectrogram shown on the screen. Captured spectrographic segments were then imported into ImageJ, which is an open-source image-processing program (https://imagej.nih.gov/ij/download.html). This non-standard methodological approach makes it possible for anyone with a Macintosh computer to exactly replicate the measurements and analyses performed here, without the need for specialized acoustic analysis software, expertise in using such software, or experience working with audio files. Replication of the segmentation process (i.e., partitioning sessions into ~22 min-long segments) is not necessary to obtain the same measurements of songs reported here. All that is necessary is that at least one whole song be visible in each image.

The time-scale within each spectrogram was used to calibrate image measurements along the x-axis. Distances between ticks along the frequency axis were used to create a function (calculated using Matlab's *curvefit* tool) to transform linear image measurements into their corresponding logarithmic frequency values along the y-axis.
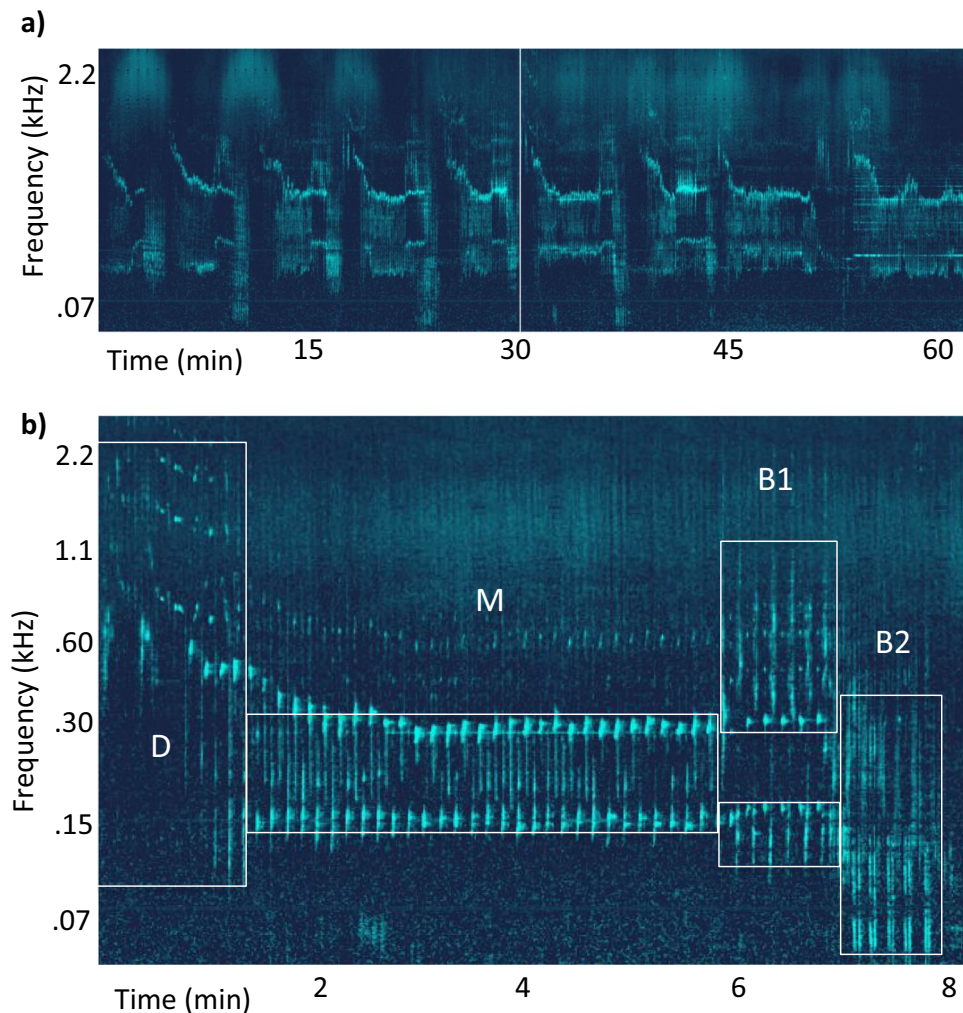
Fig. 2 Spectrograms of a song session segment recorded off the coast of Hawaii. *Note.* (**a**) Nine consecutive songs illustrating variations in song duration and in the distribution of energy across different frequency bands as well as the visual features used to identify humpback whale song sessions within recordings. Note that all nine songs show similar spectrotemporal contours, cycling from higher to lower frequencies, with similar shifts in frequency content over time (corresponding to the predictable ordering of themes). (**b**) A single song selected from the segment shown in (a). Units early in the cycle contain peak frequencies greater than 300 Hz that gradually decrease (D), after which most spectral energy is focused mainly within two narrow bands near 280 Hz and 160 Hz (M). Higher-frequency units in M often ended with a rapid decrease in frequency, while lower-frequency units ended with a rapid increase in frequency, producing interleaved vertical lines between the upper and lower frequency bands. Section B1 contained units with bimodal peak frequencies located close to the peaks in M, alternating with more broadband units with energy spread above or below those peaks. Finally, units in B2 were short-duration, low-register, and broadband. Rectangular measurements of each section characterize the time spent on each section as well as the range of frequencies produced within the section

The sample of song sessions analyzed in the current study was chosen to provide multiple examples of singers producing songs continuously within a specific environment and time period, thereby controlling for variability that might be attributable to large differences in environmental conditions, seasonal changes in behavior, or cross-population differences in song production. Humpback whales producing song sessions in other contexts, years, and locations may vary songs in ways that diverge from the singers considered in the current sample. Although the sample of recordings analyzed here does not represent the full range of singing behavior exhibited by humpback whales, it does provide an unbiased sample of intra-individual variations that singers produced when not singing within groups of chorusing whales.

Data analysis

Humpback whales change the songs they sing within and across years (Guinee et al., 1983; Mercado & Perazio, 2021b; Payne & Payne, 1985). Consequently, any analysis of variations in songs requires characterizing the form of songs being produced within a given year. Traditionally,
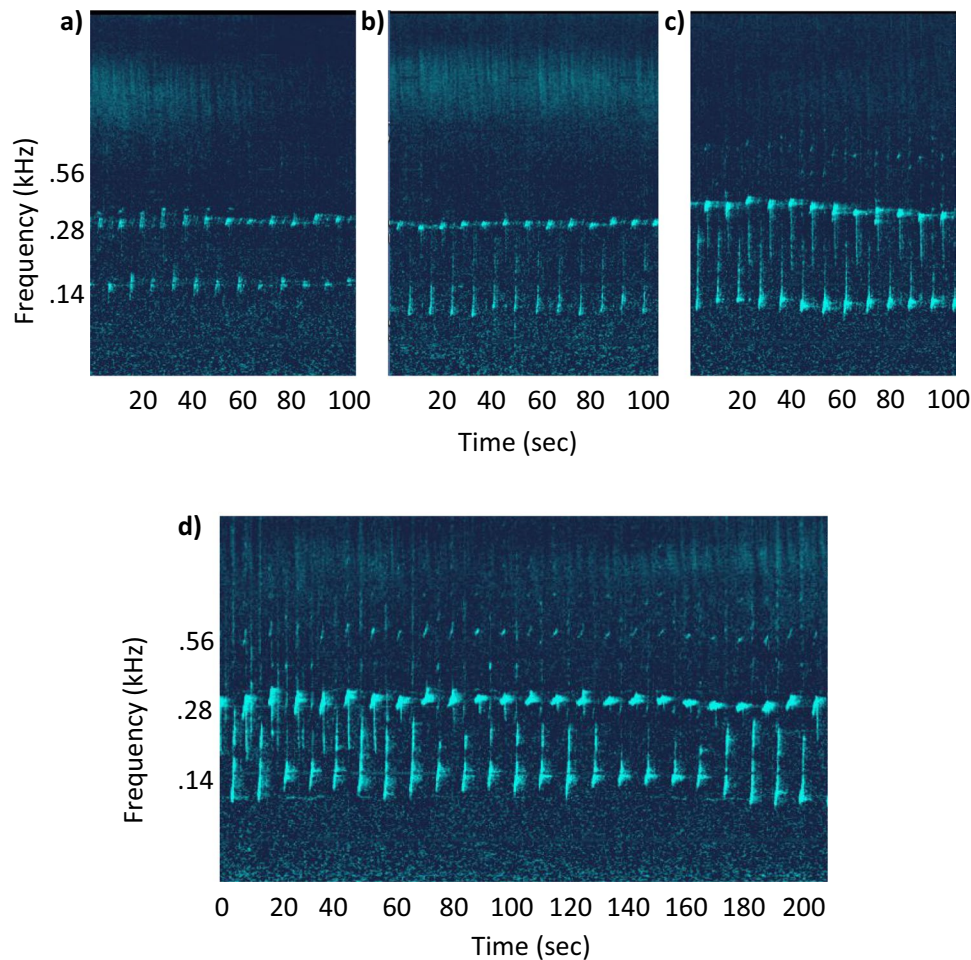
Fig. 3 Sample spectrograms of variation in the M-section. *Note.* (**a**) In this song, M was produced with energy focused within two narrow frequency bands produced by alternating units. (**b**) In a later song, the lower-frequency unit has shifted downward and ends with a rapid increase in frequency (appearing as vertical lines). The higher-frequency unit is unchanged. (**c**) In a third song, rapid decrease in frequency at the end of each higher-frequency unit are evident (all three songs were sampled from a single song session). Some of the acoustic differences shown in (a–c) could potentially be related to variations in the position of the singer relative to the recording hydrophone (e.g., as the distance from the singer decreased, more details of units might have become evident). However, (d) shows that similar variations in the M-section were sometimes evident within a single song (see also Fig. 2b)

descriptions of humpback whale songs have focused on partitioning unit sequences produced by singing humpback whales into discrete sets of repeated patterns; the patterns are typically referred to as phrases, and sets of repeated phrases are called themes (Payne & McVay, 1971). The current analysis instead focused on describing the extent to which singers made use of different acoustic frequencies over time. Spectrograms of all analyzed song sessions were visually inspected and qualitatively analyzed at multiple time scales to identify characteristic visual features that varied within songs (corresponding approximately to different themes).

Four subjectively distinctive sections of songs were apparent (Fig. 2b): a section containing units with gradually decreasing frequencies (D), a section within which medium-frequency (100–500 Hz) units were prevalent (M), a section

in which energy was spread across a much broader range of frequencies (B1), and a section containing broadband units with frequency content less than 150 Hz (B2). Each of these four sections was manually measured for each song within every song session by surrounding the sections with rectangles (e.g., see Fig. 2b). Two rectangles were used to characterize section B1 because of observed variations in how the broadband elements within this section were distributed (see Fig. 2a). The dimensions of each rectangle corresponded to the frequency range and duration of energy concentrations within each of the four sections. This analysis approach is comparable to manually selecting a region of interest within a spectrogram to measure the maximum and minimum frequencies of a recorded sound, as well as its duration, but applied to sections of a song rather than to individual units.
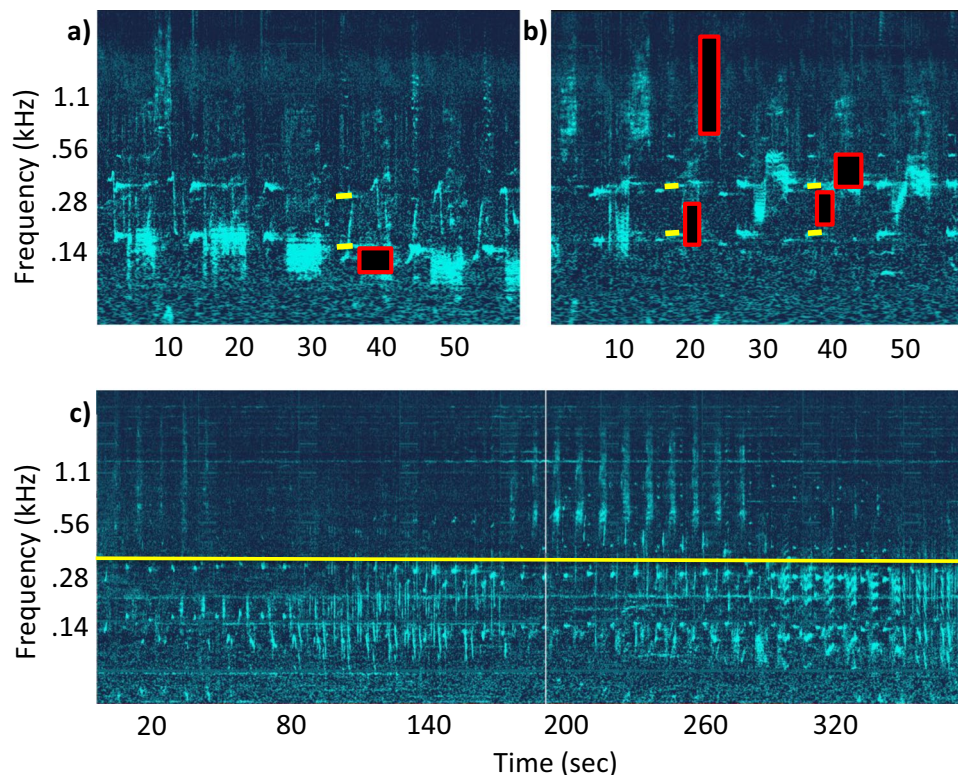
Fig. 4 Sample spectrograms of variation in the B1-section. *Note.* (**a**) In this song, B1 was produced with energy focused within two narrow frequency bands produced by a single unit, alternating with a more broadband unit. These features are highlighted with yellow lines and a red-bordered rectangle for one pair of units. (**b**) In a later song within the same session, the broadband units were more variable, with energy centered in higher frequency bands. The narrowband unit was unchanged. (**c**) Similar variations were sometimes evident within a single song. The yellow line indicates the upper frequency bound for the narrowband unit in this rendition of the B1-section; the range of frequencies spanned by the broadband units varies considerably throughout the section

As illustrated in Fig. 2, transitions between these four sections were typically gradual, preserving a subset of acoustic features across consecutive sections. Consequently, decisions about where to divide each of the four sections were based on subjective visual impressions regarding the point in time were transitions in unit production occurred. The criteria for identifying the duration of a section varied for each section. The start of B2 was identified based on the presence of a sudden transition to production of only broadband units and the end was identified based on the presence of either a silent gap or a sudden transition to higher-frequency units (see Fig. 2b). The start of D was identified based on the presence of higher-frequency units (above 500 Hz) and the end was identified based on a sudden increase in the lowest frequencies being produced and/or a switch to sustained production of units in a lower frequency band near 150 Hz. These latter criteria were also used to identify the beginning of section M. The end of section M and the beginning of B1 were identified based on a sudden transition from alternating tonal units to alternation between a tonal unit and a broadband unit (appearing in spectrograms as a transition in the highest and lowest frequencies produced,

see Fig. 2b). The transition from B1 to B2 was identified using the criteria noted above. Subdivisions of bandwidth within B1 were selected based on the presence of a silent gap between the upper and lower bands. In the current analyses, only the overall bandwidth of B1 was considered. In a few cases where boundaries between sections were not visually obvious, the Pattern Radio website was used to visually inspect spectrograms at a higher temporal resolution and to listen to transitions within songs to verify changes in unit sequences associated with switches between consecutive sections. Dividing sections using the criteria noted above (i.e., determining duration measurements) was more straightforward than selecting the highest and lowest frequency bounds for each section (see Supplementary Fig. 1, Online Supplementary Material (OSM)), because the spectra of some sections tapered off gradually at lower and upper bounds or were time-varying within the section. Because measurements of duration and bandwidth required visual judgments and manual control of the size and placement of rectangles, their precision is limited. However, these simple linear measures are less susceptible to subjective biases than are standard approaches to analyzing humpback whale
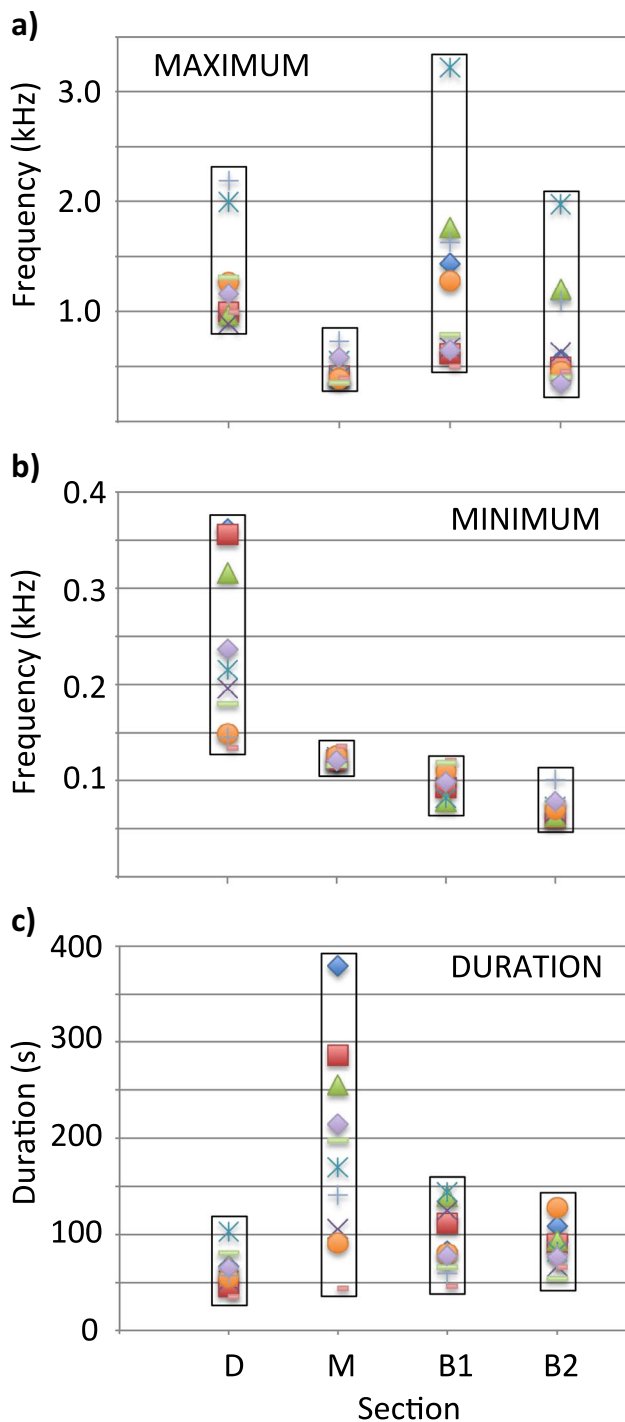
Fig. 5 Mean frequency bounds and durations for sections within each song session. *Note*. Each symbol corresponds to the mean from a single song session produced by a singer (Table 2 lists the numbers of songs averaged within each session). Vertical rectangles highlight the range across all sessions. (**a**) Average highest frequencies for each of the four sections (D, M, B1, and B2) in each of the ten song sessions. (**b**) Mean lowest frequencies produced within each section. The lowest frequencies produced decreased progressively across consecutive sections for all song sessions. (**c**) Mean durations of each section. The M section showed the greatest variation in duration across song sessions and was typically produced for longer periods than other sections

songs, which depend on subjectively identifying and categorizing units, phrases, and themes based on arbitrary perceptual criteria (see Table 1), a process that relies on hundreds of experience-dependent decisions per song.

The low-resolution, image-based analysis used in the current study yielded a conservative measure of the variations that a listening whale would experience if that listener were stationary near the location of the recording hydrophone. The measured variations include not only those generated by singers, but also any variations introduced during the propagation of songs (e.g., frequency attenuation, reverberation, etc.). Comparisons between measurements manually collected from screen-grabbed spectrograms (n = 26 songs from a single song session) and robust measures of duration and bandwidth collected using Raven (ver. 1.5) confirmed that measurements made with these two methods are comparable (see Supplementary Table 1 and Supplementary Fig. 2, OSM), with one exception related to measures of B1 bandwidth. Specifically, in some cases robust measurements of B1 inaccurately characterized the frequency content that singers produced within that section because of large differences in unit intensity (see Supplementary Figs. 3 and 4, OSM). Robust measures of section duration were highly correlated with manual measurements, with Pearson's correlation coefficients varying between 0.96 and 0.99 for the four sections, as were robust bandwidth measures for sections other than B1 (*r* varying between 0.78 and .88).

Rectangular measurements of the four designated sections within each song were used to construct multiple time series for each song session (i.e., corresponding to the sequence of consecutive songs produced by a singer within each session). For instance, if a singer produced 20 consecutive songs, each of which contained a D section, then this would provide 20 × 3 measurements describing how the duration, minimum, and maximum frequency of that section varied within the song session. Means and standard deviations of these measures were calculated for each of the four sections within each song session. Eighteen paired-samples t-tests were conducted to compare these means, providing a quantitative assessment of the extent to which the four sections differed in terms of their temporal and spectral variation across song sessions, with a Bonferroni adjusted alpha level of .00278 per test. Histograms were used to evaluate how much time singers allocated to each of the four sections (D, M, B1, and B2).

As noted earlier, there is no way with this data set to guarantee that each of the ten song sessions analyzed was from a different singer or to determine the exact probability that a singer was recorded more than once, although currently available data suggest the probability of resampling a singer in the same location within a month is low. If the analyzed data represent the performance(s) of less than ten singers, then comparisons between section

Table 1 Comparison of analysis methods for characterizing humpback whale songs

	Hierarchical thematic analysis	Time-bandwidth analysis
Method Summary	1. Songs modeled as a nested hierarchy 2. Recordings transcribed into sequences of symbols 3. Repeated patterns compared using string metrics	1. Songs modeled as repeating spectrotemporal contours 2. Recordings partitioned into sections based on spectrographic transitions 3. Duration and bandwidth of each section measured from spectrograms
Input	Continuous audio recordings converted into spectrograms	Continuous audio recordings converted into spectrograms
Output	Sequences of theme labels	Measures of duration/bandwidth
Subjective Processes	Identification of units vs. subunits Classification of units into types Identification of phrases vs subphrases Designation of start/end of phrases Classification of phrases into types Designation of start/end of themes Designation of start/end of songs	Identification of section "types" Designation of temporal divisions Designation of spectral boundaries Designation of start/end of songs
Strengths	Facilitates comparisons between unit sequences at multiple structural levels using standard methods for analyzing grammars	Facilitates comparisons of song contours and avoids subjective categorization of units/phrases
Limitations	Discards acoustic details related to timing and frequency content; difficult to maintain consistency across studies	Discards structural details of unit patterning and acoustic changes occurring across phrases

Although both methods rely on subjective criteria, time-bandwidth analysis requires fewer subjective assessments based on simpler perceptual judgments. In particular, the designation of spectral boundaries relies on edge detection, and the designation of temporal divisions between sections involves choosing the locations of four to five vertical lines based on the detection of visual discontinuities (see Fig. 2b), both of which rely on low-level visual processes that require no expertise or knowledge of song structure. In contrast, the designation of units alone requires hundreds of subjective decisions about whether the spacing of acoustic energy over time is enough to justify classifying particular events within a song as "a sound that seems continuous," as well as sorting of every identified unit into categories with fuzzy boundaries that have been arbitrarily defined based on the subjective impressions of experts

measures are still relevant for characterizing the consistency with which *some* singers allocate time to different sections and frequency bands across song sessions, as well as for evaluating how systematically song features change within song sessions. The goal of the current analyses was to gain insights into how humpback whales varied songs within song sessions (as opposed to establishing how populations of singers generally vary song production), a goal that can be achieved either by analyzing sessions produced by multiple whales or by analyzing the sessions that a single singer produces on multiple days.

In addition to quantifying how central tendencies of duration and frequency content varied across song sections, 12 F-tests were conducted to compare distributions of coefficients of variation (CV) for each measure across sections, with a Bonferroni-adjusted alpha level of .00426 per test. This analysis was performed to determine whether singers varied the acoustic features of the four sections differently within song sessions. The potential for individual coding (PIC) across sessions was also calculated by dividing the CV measured across sessions by the mean of the CV values for each session (Garcia et al., 2012). A PIC above one suggests that a particular measure varies more across sessions than within them, which could indicate individual differences between singers if each session was produced by a different singer.

Tracking measurements of sections over time made it possible to assess whether the acoustic properties of each section varied along predictable trajectories within sessions (e.g., gradually increasing or decreasing over time). The augmented Dickey-Fuller test (ADF) was used to quantify and assess the degree to which changes across consecutive songs were either progressive or stochastic. Generally, the types of progressive changes that singing humpback whales make to units and phrases, both within songs and across days, are visually evident within time series of acoustic measurements, because they mainly consist of gradual increases or decreases in either duration or frequency content (e.g., see Mercado, 2021a). Consequently, if singers progressively changed the acoustic properties of song sections within sessions in the way that they do across sessions, the direction of progression should be evident from plots of time series (e.g., appearing as linear trends). The ADF test provided a way to statistically assess whether such progressive shifts (e.g., drift) were present by testing whether a time series was nonstationary (Stadnystka, 2010). Any progressive changes to the acoustic features of song sections within a song session will make the time series nonstationary (i.e., changing systematically over time). ADF tests were calculated for each time series in Matlab using the mfile ADFREG (Kanzler, 1998), with zero differenced lags (selected based on visual inspections of time series data). Time series were classified

as stochastic when their probability of being nonstationary was less than .05 (evaluated based on t-ratios calculated by the ADFREG function).

Results

The total duration of the ten song sessions analyzed was 26.7 h; the median duration of these sessions was 153 min (range = 87–272 min). Table 2 summarizes the number of songs present within each analyzed song session (238 songs in total).

Characteristics of songs

Qualitative analyses Song forms within all song sessions were generally comparable to those shown in Fig. 2, consisting of a section containing higher-frequency units that gradually decreased in frequency content (D), followed by a section containing medium-frequency units that were repeated relatively consistently (M), which then transitioned into a section featuring narrowband units alternating with broadband units (B1), followed by a section containing clusters of short-duration, broadband units (B2). Acoustic continuity was consistently maintained during transitions between these four sections in all song sessions analyzed. Specifically, the upper frequency bound for M was a continuation of the frequencies produced within D, the focal narrowband frequencies (i.e., those most visible in spectrograms) within B1 were related to (often matching) the focal frequencies in M, and the range of frequencies present within B2 were a continuation of content from B1 (see Fig. 2). The band of frequencies used by all singers also gradually decreased within each song, as illustrated in Fig. 2b. Consequently, the four identified sections appear to represent periods of either stability or systematic change within a gradually evolving series of units rather than discrete/independent elements within songs (see also Mercado, 2021a; Mercado & Perazio, 2021a, 2021b).

When songs deviated from this generic form, it was typically because one or more of the four sections was not present (n = 19, 8% of songs). However, a subset of songs (n = 7, 3%) included unit sequences that differed qualitatively from the modal forms (i.e., including either unstructured unit sequences or patterns that were not commonly produced). Acoustic properties of D, M, B1, and B2 varied across consecutive songs within each song session. Figure 3 provides an example of intra-individual variation in the M-section that minimally affected the overall bandwidth of the section, and Fig. 4 shows an example of variation in B1 in which bandwidth varied considerably within and across different renditions. Singers never simply repeated songs (or sections) without varying a subset of their acoustic features in any of the sessions analyzed.

Quantitative analyses The specific frequency content of each of the four sections varied across song sessions (Tables 3 and 4; Figs. 5a,b). However, the distribution of frequencies across sections was relatively stereotyped in that later sections (B1, B2) typically included lower frequencies than earlier sections in all song sessions (Table 4; Fig. 5b). The M-section was the least variable across song sessions in terms of bandwidth, but the most variable in terms of duration (Fig. 5). Lower frequency bounds showed less variability across sessions than upper frequency bounds for most sections, and decreased systematically across consecutive sections (in drops of ~30 Hz; Fig. 5b, Table 4). The reduced variability of lower frequency bounds is not simply due to lower frequencies propagating more efficiently, because section D contains lower frequency bounds that were much more variable than the upper frequency bounds of the M-section, despite the fact that both fell within the same frequency range. Additionally, the systematic differences in lower frequency bounds across sections demonstrate that singers can produce a range of lower frequencies, so in principle singers could have included a broader range of lower frequencies within each section (as they did in section D). Finally, the increased variance of higher-frequency bounds across sessions was driven primarily by three song sessions (see Fig. 5a). In most cases, singers produced a subset of sections (M and B2) within predictable lower and upper frequency bounds (Table 3). Thus, the four sections showed predictable spectral and temporal features across song sessions, and different sections varied in distinctive ways.

These findings are consistent with past reports that: (1) humpback whales within a given region and time period typically produce units sequences (phrases and themes) in a predictable order (Payne & McVay, 1971); (2)

Table 2 Number of songs within each song session analyzed

Date	No. of songs analyzed
12/11/14	22
12/14/14	26
12/17/14	35
12/29/14	25
1/4/15	26
1/4/15	33
1/7/15	15
1/9/15	18
1/10/15	12
1/10/15	26
Total	238

Table 3 Spectral variation within and across song sessions

Date	Time	D_L	D_H	D_W	M_L	M_H	M_W	$B1_L$	$B1_H$	$B1_W$	$B2_L$	$B2_H$	$B2_W$
12/11/14	14:15	.09	1.9	.9	.1	2.5	.5	.06	1.6	.6	.06	.9	.3
12/14/14	14:15	.09	3.2	1.1	.09	.4	.2	.04	2.2	.7	.09	.7	.3
12/17/14	12:55	.09	2.4	.9	.09	.6	.3	.07	1.4	.4	.05	.9	.4
12/29/14	15:05	.1	3.2	1.7	.09	.8	.4	.04	3.2	1.4	.05	2.3	1.0
1/4/15	6:00	.1	3.2	1.1	.1	.6	.3	.07	3.2	1.2	.05	.9	.4
1/4/15	23:25	.1	3.4	1.8	.1	3.0	.4	.05	3.5	3.1	.05	3.6	1.9
1/7/15	9:30	.1	1.3	.7	.1	.5	.3	.08	2.1	.6	.05	1.2	.6
1/9/15	9:20	.1	1.9	.7	.1	.7	.3	.05	3.1	1.0	.05	2.2	.8
1/10/15	3:30	.1	2.2	.6	.1	.7	.3	.06	1.9	.5	.05	1.3	.4
1/10/15	11:55	.1	1.3	.6	.1	.6	.3	.06	3.3	1.3	.05	1.0	.5
Median				.9			.3			.9			.5

Each song session can be viewed and heard at https://patternradio.withgoogle.com/ by scrolling to the date and start time indicated. Song sections are denoted as D, M, B1, and B2 as illustrated in Fig. 2; L = lowest frequency bound; H = highest frequency bound; W = mean bandwidth. All values correspond to frequencies in kHz, providing an indication of the frequencies spanned by each section within each song session

Table 4 Statistical comparisons of acoustic variations across song sections

	Sections	Paired-samples tests			sig (two-tailed)
		M	SD	t	
Maximum					
Pair 1	D vs. M	1.3/0.5	0.4/0.1	7.13	**.0000**
Pair 2	D vs. B1	1.3/1.2	0.4/0.8	.068	.9470
Pair 3	D vs. B2	1.3/0.8	0.4/0.5	3.87	.0038
Pair 4	M vs. B1	0.5/1.2	0.1/0.8	3.16	.0116
Pair 5	M vs. B2	0.5/0.8	0.1/0.5	1.96	.0811
Pair 6	B1 vs. B2	1.3/0.8	0.8/0.5	4.00	.0031
Minimum					
Pair 1	D vs. M	.23/.12	.09/.01	3.80	.0042
Pair 2	D vs. B1	.23/.10	.09/.01	4.21	**.0023**
Pair 3	D vs. B2	.23/.07	.09/.01	5.20	**.0006**
Pair 4	M vs. B1	.12/.10	.01/.01	5.06	**.0007**
Pair 5	M vs. B2	.12/.07	.01/.01	11.3	**.0000**
Pair 6	B1 vs. B2	.10/.07	.01/.01	5.29	**.0005**
Duration					
Pair 1	D vs. M	63/185	19/95	4.24	**.0022**
Pair 2	D vs. B1	63/94	19/34	3.23	.0104
Pair 3	D vs. B2	63/84	19/21	2.31	.0463
Pair 4	M vs. B1	185/94	95/34	3.26	.0099
Pair 5	M vs. B2	185/84	95/21	3.45	.0072
Pair 6	B1 vs. B2	94/84	34/21	0.86	.4110

Means and standard deviations were calculated using the means from each song session (shown in Fig. 5), with "value 1/value 2" representing the summary statistic from the first section/second section in the pair respectively. Means of frequencies are given in kHz and means of duration are given in seconds. Statistically significant differences are bolded

singers constantly vary the duration spent producing different themes (Payne et al., 1983); (3) the order in which themes are produced is associated with a systematic, gradual decrease in frequency content (Mercado & Perazio, 2021b); and (4) "themes" within songs represent points along a trajectory of gradually morphing unit sequences (Mercado, 2021a; Mercado & Perazio, 2021b).

Variations within song sessions

Coefficients of variation (CVs) of the time singers spent producing each section revealed substantial variation within sessions for all four song sections (Fig. 6a). Analyses of CVs for the frequency range spanned by each section similarly showed large variations within song sessions (Fig. 6b). The extent to which particular sections varied was not consistent across song sessions. For example, in several song sessions, M was the least variable section in terms of bandwidth, whereas in others it was the most variable (Fig. 6b). In some song sessions, the degree of variation was comparable across sections, but in others it was not. No statistically significant differences were found between the distributions of CVs for either duration or bandwidth across the four sections. The potential for individual coding (PIC) was ≤ 1 for all acoustic properties of all song sections other than the bandwidth of B2 (PIC = 1.4), indicating that most song features varied no more between sessions than within them (Table 5).

Acoustic properties that varied across song sessions also varied within song sessions. For instance, duration for most sections other than the M-section was relatively stable within song sessions (for representative examples, see Figs. 7a and b), and bandwidth varied within song sessions
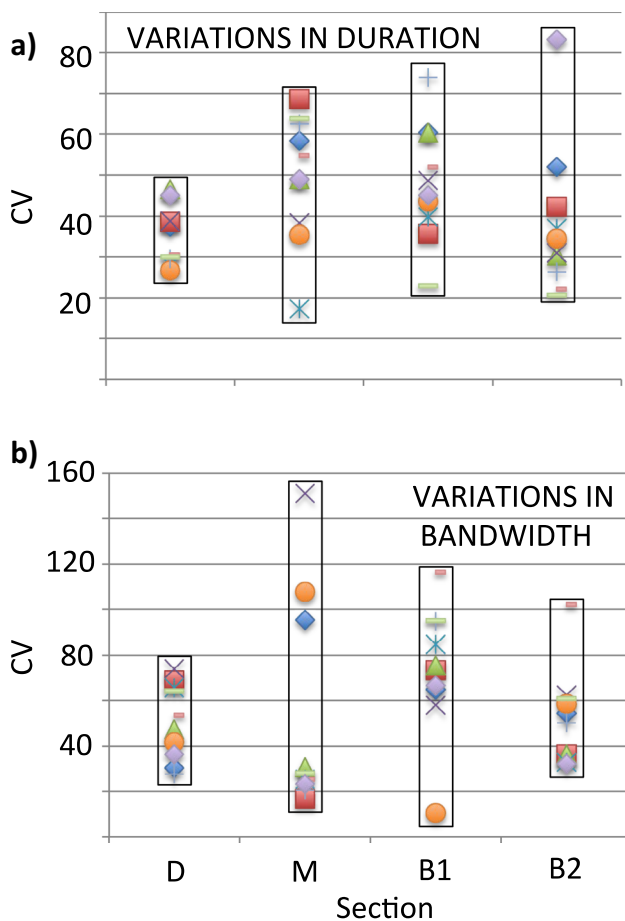
Fig. 6 Coefficients of variation for each section in each song session. *Note*. Each symbol corresponds to the coefficient of variation (CV) from a single song session produced by a singer (Table 2 lists the numbers of songs averaged within each session). Vertical rectangles highlight the range of CVs across all sessions. (**a**) Variations in the time spent on each of the four sections across songs within each song session showed considerable intra-individual variation; specific sections varied much more in duration in some song sessions than they did in others (a possible indication of inter-individual differences). (**b**) Variations in the bandwidth for each section across songs within each song session. The bandwidth of every section varied across songs within a session, with the degree of variation showing large differences across sessions. For instance, the bandwidth of sections M and B1 showed the least variation in some song sessions, but the most variation in others

Table 5 Potential for individual coding values for temporal and spectral measures

	D	M	B1	B2
Bandwidth	0.90	0.68	0.98	1.4
Duration	0.87	1.0	.76	.66

more for D and B1 than for other sections (for examples, compare Figs. 7c and d with Fig. 5a). As illustrated in Fig. 4, some bandwidth variations in sections within song sessions

were a consequence of alterations to constituent units (especially broadband components of units). Changes also could result from the temporary addition of units within sections or from shifts in the distribution of spectral energy within units.

There was little qualitative or quantitative evidence of progressive changes in the amount of time that singers spent producing particular song sections within a session. The time series data plotted in Fig. 7 are representative of most that were analyzed in that changes over time either showed large fluctuations intermittently or smaller fluctuations around a relatively stable baseline. Nonstationary trends in time series were statistically rejected for 83% of duration-based time series (i.e., for 33 of the 40 sequences of section duration measures, the probability that duration of a section changed systematically over time within a session was less than .05 based on the ADF metric). Similarly, 70% of the time series for both upper and lower frequency bounds within song sessions were statistically rejected as showing nonstationary changes over time. Collectively, qualitative and statistical evaluations of consecutive changes to the acoustic features of songs within individual sessions were more consistent with intra-individual variations being stochastic rather than progressive.

Overall distributions of the amount of time singing humpback whales spent producing each section were positively skewed for all four sections (Fig. 8). Skewness of the distribution of B2-section durations was the highest (3.3), followed by the M-section (1.8) and the B1-section (1.5), with the D-section showing the least positive skew (.75). The modal durations for all sections other than the M-section were comparable at ~60 s; the modal duration for M was ~90 s. The distribution of durations that singers spent producing the M-section appeared to be broader than for other sections (see also Fig. 5c). Thus, singers were relatively consistent in spending two minutes or less producing D, B1, and B2 within each song, but varied greatly with respect to the time they spent producing M, both within and across song sessions.

Discussion

Singing humpback whales have captured the interest of researchers because of the apparent complexity (Allen et al., 2018; Suzuki et al., 2006), and variability (Garland et al., 2013; Owen et al., 2019), of the songs they produce. Several past scientific studies have emphasized how populations of humpback whales change the structural properties of songs across years (Cato, 1991; Garland et al., 2011; Maeda et al., 2000; Mercado et al., 2005; Payne & Payne, 1985; Winn & Winn, 1978). The current study is the first, however, to systematically examine how individual whales vary the acoustic features of songs within extended song sessions. Although
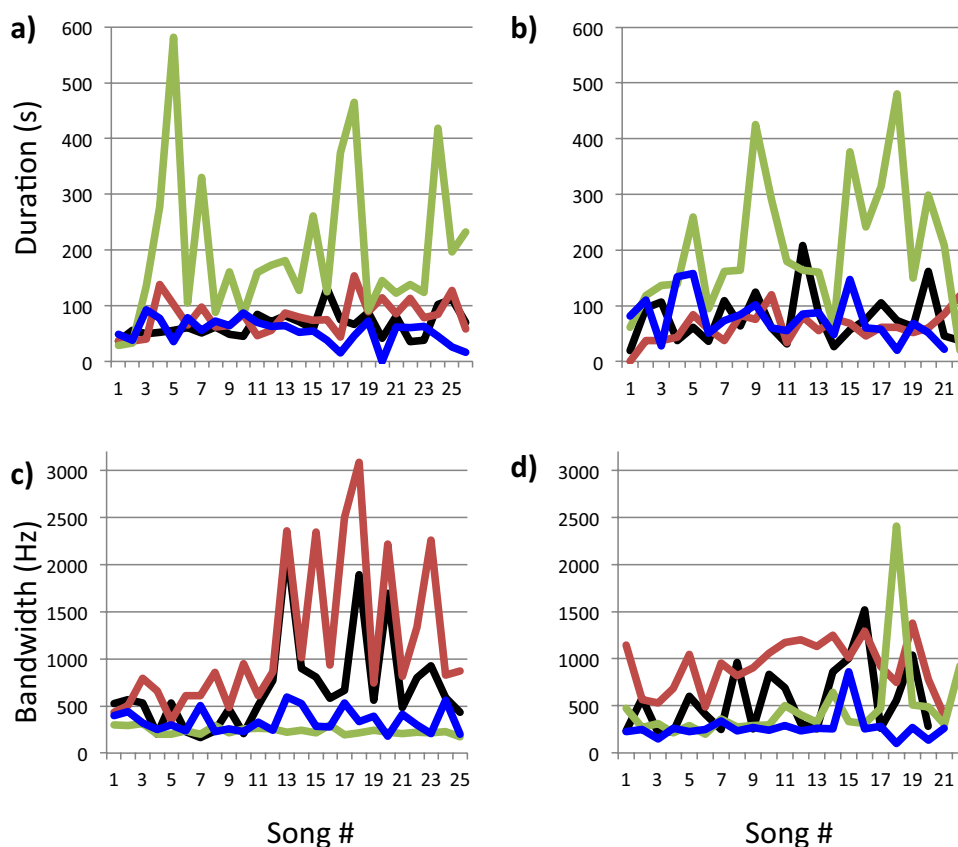
Fig. 7 Example time series of measures from consecutive songs. *Note*. Each line corresponds to a specific section of a song (as designated in Fig. 2): D = red; M = green; B1 = black; B2 = blue. (**a**) This singer consistently spent less than 100 s per song on sections other than M throughout this session recorded on 12/14. The time this whale spent on M varied greatly across consecutive songs, although the singer consistently spent more time producing M than other parts of the song. (**b**) A singer recorded on 12/11 showed a similar trend, with time spent on M varying much more than other sections, and with M often being produced for longer periods. (**c**) The singer recorded on 12/14 produced a consistent range of frequencies in the first ten songs, but then the bandwidth of D and B1 began varying in later songs within the session. M was produced within the narrowest band of frequencies throughout the session and with the least amount of variation across songs. (**d**) The singer recorded on 12/11 also produced a broader range of frequencies during D and B1, with M and B2 showing more stability within a narrower band of frequencies across songs
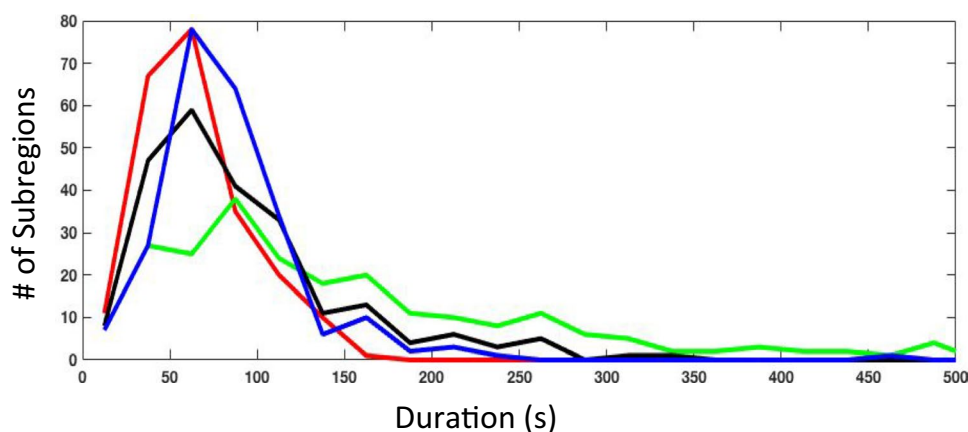

Fig. 8 Histograms of time spent on each section across all song sessions. *Note*. Histograms are plotted as lines to facilitate comparisons across sections: D = red; M = green; B1 = black; B2 = blue. The modal duration for all sections other than M was ~60 s. Distributions of durations for all sections were positively skewed

it was recognized early on that individual singers modified elements of their songs within sessions (Payne & McVay, 1971), changing some elements more rapidly than others (Payne et al., 1983), little effort has been made to understand how and why humpback whales vary content across consecutive songs within a song session. The most commonly proposed explanation is that singers do whatever it takes to compete for mates, and that variety/complexity/novelty must somehow be advantageous in this regard (Garland & McGregor, 2020; Garland, Rendell, Lamoni, et al., 2017a; Noad et al., 2000). This explanation provides a plausible account for why a singer might change characteristics of its songs. It does not explain why whales introduce the specific changes they make to songs, however. In fact, Tyack (1981) argued that the specific changes that singers make are not particularly relevant to song function, as long as those changes make an individual's song stand out.

The current findings suggest that singing humpback whales continuously change acoustic properties of their songs within song sessions even when they are not changing the structural content of songs, and that the changes they make are unlikely to increase song complexity or novelty in ways that can be reliably perceived or assessed by distant listeners. As predicted by the sonar hypothesis, singers varied sections of songs consisting primarily of narrowband units differently from sections composed primarily of broadband units. The kinds of subtle, progressive changes in successive songs predicted by the reproductive display hypothesis (e.g., see McLoughlin et al., 2018) were not evident. Instead, intra-individual variations in the acoustic features of songs within sessions appeared to be stochastic, such that the temporal separation between songs within a session was not predictive of song similarity. The following sections consider what benefits singing humpback whales might gain from varying their songs within sessions in this way.

What information might listeners gain from intra-individual song variations?

Past suggestions regarding the kinds of information that singing humpback whales are attempting to convey to potential listeners focus heavily on indices of a singer's fitness (Adam et al., 2013; Cerchio et al., 2001; Chu, 1988; Darling et al., 2006; Noad et al., 2000; Payne, 2000), such as acoustic markers of a singer's size, sex, dominance, identity, strength, or versatility. Male listeners could potentially use such information to assess potential competitors, while female listeners might use the same information to judge the attractiveness of a potential mate. The basic assumption driving past emphasis on possible fitness indices within humpback whale songs is that humpback songs function like bird songs (Garland & McGregor, 2020; Parsons et al., 2008), an assumption typically justified through qualitative comparisons between

singing humpback whales and singing birds. The shared features most commonly cited as evidence that humpback whale songs function to broadcast reproductively relevant information include: (1) singers are males; (2) singing is seasonal; (3) songs are complex; and (4) songs are learned through cultural transmission. Researchers argue that these cross-taxa similarities suggest comparable song functions (Clapham, 1996). Most descriptions of reproductive ecology in humpback whales acknowledge that physical competitions between males accompanying single females likely play a critical role in mate selection by females (Clapham, 2000; Pack et al., 2009). Specifically, a male that is swimming closest to a female will commonly attempt to maintain his relative proximity by preventing other males from moving to a closer position (Clapham et al., 1992; Tyack & Whitehead, 1983). Such physical competitions, which can become quite violent (Baker & Herman, 1984; Herman et al., 2008), undoubtedly give followed females ample opportunities to determine the sex, size, dominance, and agility of followers in a much more direct way than would be possible through listening to songs from long distances. Because males competing to be close to a female humpback whale rarely sing, some researchers have suggested that singing is a tactic used mainly by immature males that cannot compete physically (Clapham, 1996; however, see Herman et al., 2013).

For songs to provide honest indicators of a singer's reproductive fitness, it is important that the features of a singer's songs be consistently correlated with an individual's qualities. For instance, the frequency content of songs can only provide reliable information about a singer's size if the range or amplitude of produced frequencies is constrained by a singer's size (Adam et al., 2013; Parsons et al., 2008). If each song an individual produces varies in bandwidth and/or intensity, then those cues become unreliable as indicators of size. Similarly, if individuals vary the duration of each song they produce (Fristrup et al., 2003; Miller et al., 2000), then song duration would not be a reliable indicator of a singer's stamina (Chu, 1988). In short, if singers are not consistently demonstrating their vocal prowess (i.e., showing low intra-individual variability), then comparing the physical qualities of different individuals based on songs they produce at different times becomes much more problematic for listeners.

Varying song elements within a song session can potentially increases the acoustic complexity and novelty of a singer's vocal acts relative to simply repeating identical songs. In principle, the range of variations that a singer produces within a song session could provide information about the age, experience, and reproductive fitness of a singer. Several researchers have proposed that listeners judge the relative attractiveness or dominance of singers by evaluating individual differences in song complexity and novelty (Cerchio et al., 2001; Garland & McGregor, 2020; Payne, 2000).

The humpback whale songs analyzed in the current study followed a predictable sequence, glossed here as the DMB song form, in which singers gradually decreased the frequency content of unit combinations before settling into repetitively producing units with spectral content primarily focused within two narrow frequency bands (the M-section), and finally shifting to combinations of shorter duration, broadband units. The DMB song form was ubiquitous across song sessions, appearing in 89% of songs analyzed. This kind of uniformity of song structure within and across whales is the basis for past reports that all humpbacks within a population sing the "same" song within a given year (Payne & McVay, 1971; Winn & Winn, 1978). The DMB form appears to be a common pattern (a modal "song contour"; Mercado, 2021b; Mercado & Perazio, 2021b) produced by many singing humpback whales over long stretches of time and vast geographic distances (Español-Jiménez & van der Schaar, 2018; Helble et al., 2015; Kowarski et al., 2017; Mercado & Handel, 2012; Mercado & Perazio, 2021b; Mercado et al., 2010; Ryan et al., 2019). A whale listening to one or more singers for multiple hours will be exposed to multiple variants of this single song form and possibly to a few deviants from this norm. It is not known how consistently individual singers vary song content within song sessions. If individuals do not vary song elements to the same degree across days, then assessments of reproductive fitness based on such variations (e.g., the relative complexity or novelty of singing) will be unreliable. The current study found low potential for individual coding in the intra-individual variations that singers made within song sessions, suggesting that it would be difficult for listeners to judge differences between sessions (or singers) based on such variations. It thus remains unclear whether listeners comparing either song complexity or novelty across singers would receive or perceive any reliable markers of differences in singer quality based on those features.

A fundamental assumption of the reproductive display hypothesis is that humpback whale song, like bird song, is an acoustic ornament. Specifically, songs are viewed as an elaborate trait with no inherent survival value that has evolved to be extremely complex and variable because of female preferences; what Macdougall-Shackleton (1997) describes as "the acoustic analogue of a peacock's tail." Unlike songbirds, however, humpback whales do not achieve complexity by acquiring larger song repertoires. Humpback whales have been described as "eventual variety" singers, because of the ways in which they repeat phrases (Cholewiak et al., 2018; Cholewiak et al., 2013). But, given that a singer's repertoire size (as perceived by human observers) is effectively a single song on any given day, variety is only "eventual" across a singer's lifespan. Furthermore, the core assumptions that led researchers to hypothesize that humpback whale songs function as reproductive displays are becoming increasingly tenuous. Singing is much less seasonal than was originally thought (Clark & Clapham, 2004; Kowarski et al., 2017). Recent evidence of shared songs across geographically-isolated populations contradicts claims of cultural transmission as a major driver of song change (Mercado & Perazio, 2021b). And, bowhead whales singing off of Greenland were found to be exclusively females (Tervo, 2011). None of these findings preclude the possibility that listeners are judging the attractiveness, virility, or vocal competence of singing humpback whales from their songs. However, given that both males and females can potentially judge each other's fitness and attractiveness during close-proximity physical competitions between males within competitive pods, females should be able to choose fit mates effectively without extracting any information about the qualities of individuals from their songs (Craig et al., 2002; Felix & Novillo, 2015; Lunardi et al., 2010; Pack et al., 2012; Pack et al., 2009).

Listeners can gain information from songs beyond any indices of reproductive fitness or individual differences, including indications of a singer's position, movements, and goals. Some researchers suggest that a primary function of songs may be to reveal the locations of singers (Herman, 2017). Listeners clearly perceive and use the spatial cues available from songs, because males sometimes home in on the positions of speakers playing back songs (Darling & Berube, 2001; Darling et al., 2012), females have been observed avoiding both singers and playbacks of song (Tyack, 1981, 1983), and singers appear to space themselves apart (Frankel et al., 1995). Importantly, the fact that listeners use spatial information garnered from songs does not imply that this is why humpback whales are singing. Eavesdropping listeners (including human researchers) can take advantage of such spatial cues, even if the singer gains no benefits from their reactions.

Intra-individual variations within song sessions could affect the spatial information that listeners can extract from songs. In particular, differential usage of narrowband and broadband units across songs will affect the detectability of singers from different distances, as will variations in the bandwidth of song sections (Mercado & Frazer, 1999; Mercado et al., 2007). Such variations will also affect how precisely listeners can judge a singer's distance and bearing (Mercado et al., 2008; Schneider et al., 2014). How song propagates underwater is determined by numerous factors that a singer can only partly control through selection of the position from which it sings and the frequencies it produces (Clark & Ellison, 2004; Frazer & Mercado, 2000; Mercado & Frazer, 1999; Mercado et al., 2000). As a result, intra-individual variations within song sessions not only will affect what spatial information is available to listening whales, but also will affect which listeners receive specific elements of songs. For example, a listener hearing a song

from 1 km away may be exposed to a different sequence of units/cues than a listener simultaneously hearing that same song from 2 km away (Mercado & Frazer, 1999; Mercado et al., 2007). Such differences further complicate a listener's ability to evaluate reproductive fitness from songs because propagation-related distortion will introduce variations in song complexity and novelty beyond those that a singer produces, reducing the reliability of such cues as fitness indices. In contrast, the distorting effects of shallow water propagation can actually enhance the spatial information available within received songs by providing additional cues to a singer's distance (Mercado et al., 2007), especially within reverberant environments (Mercado, 2016).

How might intra-individual variations contribute to echoic perception?

When considering how song-generated echoes (and variations in those echoes) might contribute to humpback whale behavior, it is important to consider the contexts within which humpbacks sing. Most studies of singing humpbacks have been conducted during times of the year when whales are reproductively active, but humpbacks also sing at times when sexual competitions are rarely seen, during migration, and while foraging (Español-Jiménez & van der Schaar, 2018; Garland et al., 2013; Magnúsdóttir & Lim, 2019; Magnúsdóttir et al., 2015; Stimpert et al., 2012). In regions where mating occurs, singers are known to be primarily males (Glockner, 1983). The number of sexually receptive females present in these regions is much lower than the number of available males (Herman et al., 2011), and multiple males often follow a single female (Baker & Herman, 1984; Clapham et al., 1992; Tyack & Whitehead, 1983). Competition between groups of males vying to associate with a single estrus or pre-estrus female is a common reproductive strategy in several ungulates (some of the closest living relatives of large whales), including mountain sheep (Clapham et al., 1992; Darling & Berube, 2001; Geist, 1971). However, terrestrial mammals that physically compete for mates in this way do not sing. The sonar hypothesis provides a possible explanation for this disparity. When male mountain sheep are motivated to mate with females, step one is to find a potential mate. They do this by travelling around in areas where females historically have been present, and by visually searching for females from high vantage points (Geist, 1971). In other words, male sheep move around and intermittently stop to visually scan for conspecifics over long distances. The sonar hypothesis proposes that when male humpbacks actively seek out mates, they employ the same strategy as their bighorn cousins. However, because visually scanning from high peaks is not an option for humpback whales, they instead scan for conspecifics over long distances using sound. Female sheep in estrus generally do

not climb peaks to scan for randy males because they are not searching for them. Similarly, female humpback whales are unlikely to sing in regions where multiple males are actively searching for them. According to the sonar hypothesis, female humpback whales should be more likely to sing when they can potentially benefit from discovering the locations of other whales that they cannot see (e.g., in some foraging contexts). Of course, any sound that a singer makes will provide information to any whales that hear it (or its echoes). Consequently, the sonar hypothesis does not preclude the possibility that eavesdropping listeners gain reproductively relevant information by listening to individual singers (see Fig. 1).

According to the sonar hypothesis, singers vary the acoustic properties of their songs to facilitate perception of distant conspecifics (Mercado, 2018b). Comparisons with the searching behavior of echolocating bats suggest that intra-individual variations within song sessions may enhance singers' capacity to detect and localize targets from long distances. Unlike songbirds, several species of bats regularly and continuously adjust acoustic characteristics of their vocalizations as they actively search for prey (Fenton et al., 2014; Simmons & Stein, 1980). Some bat species also produce rhythmically alternating sound patterns while searching (Jung et al., 2007; Mora et al., 2011; Obrist, 1995), a strategy that is thought to enhance the detectability of echoes within complex environments (Fenton et al., 2014). Bats vary their sonar signals to account for variations in their distances from potential targets as well as differences in environmental conditions (Moss et al., 2014). Given that the sound field generated by singing humpback whales is more omnidirectional than is true for echolocating bats, intra-individual variations from a relatively stationary position can differentially affect the detectability of echoes received from each direction. For example, the unit sequences that are most likely to yield detectable echoes from distant targets in shallower water will not be the same as those most likely to reveal conspecifics in deeper water, because of differences in propagation. Consequently, intra-individual variations in unit sequences can potentially increase the active space within which a singer can search. Additionally, variations in the time spent on different sequences can determine the locations from which echoes are most likely to be detected, just as the time spent fixating on a particular point in space can affect the likelihood of visually detecting a target near that location (Einhäuser & Nuthmann, 2016; Henderson & Hollingworth, 1999).

Of the four song sections analyzed here, the section most acoustically similar to the search signals used by echolocating bats was the M-section, consisting of alternating CF units, each ending with a steep frequency-modulated (FM) sweep, which are referred to in the bat sonar literature as CF-FM calls. Singers typically spent more time producing

the M-section than other sections, and varied its production in ways that differed systematically from variations in other sections (e.g., consistently keeping energy focused in two narrow bands). Several past reports have noted that singing humpback whales may spend a disproportionate amount of time producing a single theme (Darling et al., 2019; Gill et al., 1995; Mercado et al., 2003), often comprised of alternating CF units with acoustic properties comparable to units within the M-section described here. Acoustic similarities between the M-section and search signals used by echolocating bats (see Fig. 9) suggest that this section may be useful for long-range detection of large targets. Published analyses of songs recorded in Colombia (Mercado & Perazio, 2021b), and off the coast of California (Ryan et al., 2019), suggest that other humpback whales have used similar patterns extensively.

Stable use of frequencies within the M-section shows that singers are capable of producing units within a fixed range of frequencies for long periods (see also Mercado, 2018a; Mercado & Perazio, 2021b). The fact that singers do not always do so suggests that the intra- and inter-individual

variations in frequency observed within other song sections either provide some functional advantages specific to those sections, or that units within those sections are affected more by propagation-related attenuation. For example, units within the D-section previously have been associated with surfacing (Winn et al., 1970); units produced closer to the surface should propagate differently from units produced at depth (Mercado & Frazer, 1999). According to the sonar hypothesis, characterizing the distribution of narrowband and broadband components within songs is particularly relevant to understanding how singers use songs because these elements determine the extent to which echoes from units can be localized from long distances. In particular, by adding or deleting broadband elements in particular frequency ranges, singers can effectively control how precisely echoes generated by those units can be localized – restricting unit bandwidth makes localization increasingly difficult and different frequencies will vary in effectiveness depending on the distance of targets (Mercado & Frazer, 1999). The current findings strongly suggest that singing humpback whales actively control when acoustic energy is focused in one or
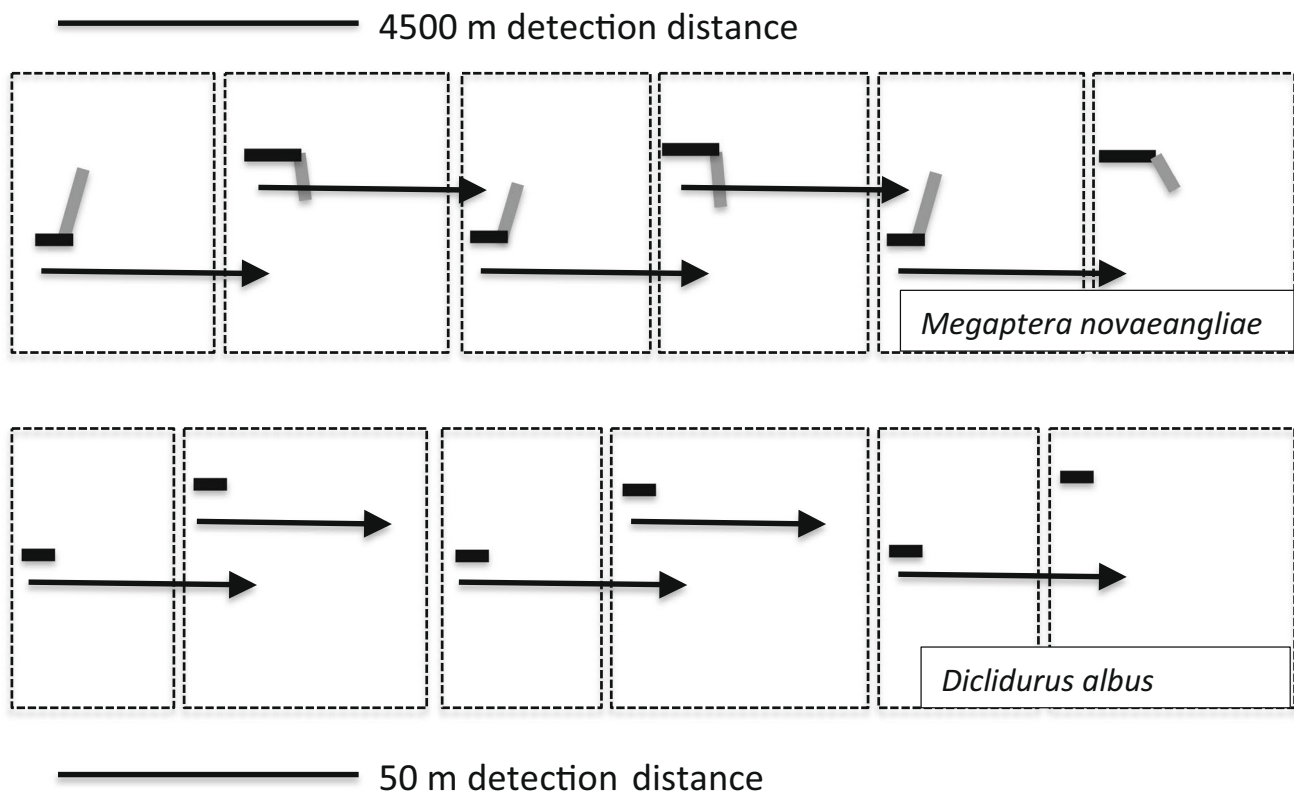

Fig. 9 Comparison of an M-section unit sequence to an echolocating bat's search sequence. *Note*. Traced spectrograms (see Fig. 3) of alternating units from the M-section of a humpback whale song (**top**) show similar temporal and spectral features to the alternating search signals of an echolocating bat (**bottom**; adapted from Jung et al., 2007, Fig. 5). Dotted boxes show "call-to-call" windows for receiving echoes, and arrows show estimated detection distances for perfectly reflecting targets (referenced to scale bars shown above and below each visualization of the sound sequences). Frequency and inter-sound intervals of the spectrograms are not scaled and are provided only to facilitate visualization of the similarities across species

more narrow frequency bands versus spanning a wider band of frequencies. Such precise control of focal frequencies may enable singers to detect or localize targets at many different distances, despite the fact that no one frequency can propagate optimally to all positions within shallow water environments (Mercado & Frazer, 1999; Mercado et al., 2008; Mercado et al., 2007).

Overall, the ways that singing humpback whales vary song elements within song sessions are more similar to the dynamic acoustic adjustments made by echolocating bats than to the variable use of discrete song types typically observed in singing birds (see Table 6). Not only do singing humpbacks gradually shift the acoustic features of units across repetitions (Cato, 1991; Mercado et al., 2005; Payne & Payne, 1985), they do so in ways that maintain concentrations of energy at particular frequencies as well as the temporal patterning of unit production (Mercado & Perazio, 2021b; Schneider & Mercado, 2019). The variety that humpback whales produce within a song session does not relate to switching between different song types (and thus does not serve to reveal a singer's repertoire of songs, as is the case in birds), but does affect the amount of time that a singer can potentially detect or localize echoes from different locations.

An intriguing aspect of the vocal variations revealed through the current analyses is that the distributions of durations of song sections were all positively skewed, with different sections showing different degrees of skew (Fig. 8). These skewed distributions suggest that although individuals varied how long they spent producing particular unit sequences, they did not vary all sections to the same extent. More importantly, how singers distributed their time producing each section closely paralleled the distributions of visual fixation durations observed for animals inspecting visual scenes (Collewijn, 1977; Harris

et al., 1988; Wallman & Pettigrew, 1985). This cross-species, cross-modality congruity suggests that the mechanisms determining when singers switch between sections of a song may operate similarly to the mechanisms that determine when other animals switch their gaze from one point in space to another. In other words, singers switched between specific unit sequences within song sessions in a manner that matched what they would be expected to do if distinctive sequences enabled them to inspect different locations within an auditory scene.

Variations in spatial fixations have been studied most extensively in humans, particularly in cognitive tasks such as reading and visual search (Rayner, 1998; Suppes, 1990). In humans, these variations are used to estimate the amount of processing time required to perform specific cognitive tasks (Nuthmann, 2017; Rayner, 1998). For instance, infants and children show longer overall fixation times than adults, which is thought to reflect the fact that it takes them longer to process what it is that they are seeing (Harris et al., 1988; Suppes, 1990). Similarly, more difficult visual tasks lead to longer fixation durations (Nuthmann, 2017). Across species, ages, and tasks, distributions of fixation durations consistently show a positively skewed shape that deviates from a normal (i.e., Gaussian) distribution. The skewed shape of this distribution is thought to arise from a random-walk process that determines when an observer switches from collecting information at one location to seeking information from a new location (Feng, 2006; Saez de Urabain et al., 2017). Increased processing demands slow down the random-walk process, leading to longer duration fixations. If singing humpback whales use songs to echoically scan their surroundings, then intra-individual variations in the time they spend producing a particular song section may similarly be determined by a random-walk process.

Table 6 Comparison of intra-individual vocal variations across species

Vocal behavior	Stable features	Dynamic features
Eventual variety singing by songbirds (e.g., song sparrows): A song type is repeated multiple times before a singer switches to repeating a different song	Repertoire of songs Repertoire of notes Forms of signals territory/mate	No. of repetitions Order of song usage Duration of bout
Singing by humpbacks: Units are produced within repeated patterns that singers typically cycle through in a predictable order	Order of "themes" Range of frequencies Distribution of durations Pacing of production	No. of repetitions Bandwidth Duration of songs Forms of signals
Echoic searching by bats: Signals are produced repetitively and dynamically adjusted based on the context	Repertoire of signals Range of frequencies Range of durations Temporal patterning	No. of repetitions Bandwidth Patterning of signals Forms of signals

Although different taxa all vary their signals, they do so in differing ways. Eventual variety singing by songbirds is analogous to going through a deck of cards (songs), presenting each one multiple times. Singing humpback whales, in contrast, gradually morph consecutive units and phrases over time in ways that are more analogous to a melting snowman

Limitations of the current analysis

The current study made use of publicly available data recorded for purposes other than the scientific investigation of humpback whale vocal behavior. Consequently, it was not possible to identify the individual whales that were recorded, the social context within which songs were produced, or the positions of singers relative to the recording system. To fully characterize the consistency with which individual singers vary song production would require collecting recordings from close proximity to the singer (e.g., using a tag). Similarly, to assess variations in song characteristics that are actually received by listening whales would require recording songs from close proximity to listeners at the same time recordings of singers are being collected. Sampling a larger number of singers from a broader range of locations and time periods is necessary to determine whether singers might vary song production to different degrees in different circumstances. For example, it is possible that the singers analyzed in the current study were less (or more) experienced than the average humpback whale. Overall, the current findings reveal the kinds of acoustic variations that listening humpback whales may encounter (and produce) over periods of hours, but they cannot address how frequently listeners are likely to produce or experience this level of variation relative to other types of changes that might occur within and across song sessions.

Another limitation of the current analysis is that it does not fully characterize the scope of changes that singers make to songs with song sessions. In particular, no attempt was made to measure variations in the pacing and rhythm of unit production, the time-varying features of individual units, the number of times specific units were produced, the sequencing and durations of units, etc. These properties are clearly varying across consecutive songs and more detailed analyses of such unit-level changes may be critical to understanding song function. Several past studies have attempted to capture variations across units (Allen et al., 2017; Maeda et al., 2000; Mednis, 1991; Ou et al., 2013), as well as intra-individual variations in the production of some unit types (Arraut & Vielliard, 2004; Macknight et al., 2001), but none have quantitatively analyzed changes in unit features across multiple consecutive songs. The method used here of bounding visually salient regions of spectrograms with rectangles cannot capture the intricate vocal variations that singers produce within phrases while singing, and thus only provides a bird's-eye view of the ways that individuals vary their songs.

A final limitation of the current approach to analyzing intra-individual variations is that it requires subjective splitting of songs into sections. Overlapping acoustic features are evident at the boundaries of all the sections analyzed in this study (see Fig. 2b). For instance, the upper frequency band of the M-section is clearly a continuation of elements that were present in the preceding D-section. Partitioning songs into sections (or themes) imposes arbitrary divisions within songs marked by transitions that exceed some subjective threshold of similarity. Whether those divisions are in any way biologically or functionally relevant is unknown. Additional analyses across years and locations are needed to evaluate whether similar partitions are generally possible, or whether alternative methods of characterizing intra-individual variation might better capture the changes that singers make within songs sessions.

A remaining mystery that the current analysis could not solve is how the stochastic changes evident within song sessions might relate to the more progressive changes in songs that have been observed across months and years. One possibility is that singers adjust the properties of their songs depending on the physical environment or social context within which they are singing. Because humpback whales seldom sing in a particular habitat for more than a day, each song session might be slightly different from the one the day before because of daily variations in conditions. Thus, every song session might involve stochastic changes in the bandwidth and/or time spent producing particular unit sequences (i.e., stretching and compressing the "rectangles" within which each section is produced), but the specific sequences produced might change somewhat from one day to the next. Comparing song sessions produced by individual singers across multiple consecutive days will be critical for understanding how within-session variations relate to variations over longer time periods, regardless of whether songs function as sexual advertisement displays and/or as sonar signals.

Conclusions

Historically, explanations for why humpback whales continuously change characteristics of their songs share the assumption that singers modify songs to enhance their communicative value: to avoid boring listeners (Winn & Winn, 1978), to establish a singer's creativity (Garland & McGregor, 2020; Payne, 2000), or to provide an acoustic logo of temporary group membership (Darling et al., 2006; Owen et al., 2019; Rekdahl et al., 2018). This assumption comes from cross-taxa comparisons with songbirds, and from a general belief that whales vary songs to increase the complexity and novelty of those songs, thereby increasing a singer's chances of producing offspring. If singers varied songs in ways that were comparable to how songbirds vary their songs, then these assumptions might be warranted. However, the kinds of intra-individual variations within humpback whale song sessions revealed by the current analyses do not match the ways that songbirds vary songs. Although songbirds sometimes lengthen or shorten their songs within singing bouts (Nelson & Poesel, 2011; Palmero

et al., 2014; Tachibana et al., 2015), they generally do so without varying the spectral characteristics or composition of songs. Sparrows produce multiple variants of individual songs that they change along multiple acoustic dimensions (Lachlan et al., 2018; Lattin & Ritchison, 2009; Nowicki et al., 1999; Podos et al., 1992; Searcy et al., 1999; Searcy et al., 1995), but they do not change the composition of their songs within singing bouts, do not shift the frequency content of song notes within or across consecutive songs, and do not switch between song types in a stereotypical order. To date, no species of songbird has been identified that continuously varies the acoustic properties of its songs in the ways that humpback whales do, despite the wide variety of singing styles and repertoires that songbirds are known to use. One possible explanation for why songbirds are not varying their songs like humpback whales is that birds are using their songs differently from humpback whales (see Mercado, 2018b, for a more extended discussion of bird-whale comparisons).

In reproductive contexts, male humpback whales may be limited to a strategy of searching for and "capturing" individual females (Clapham, 1996; Herman et al., 2011). Female humpbacks could encourage competitions either by making their presence known or by passing through areas where males are located (Clapham, 2000; Herman, 2017). Given that males are likely motivated to physically compete for access to a female, females may indirectly choose a mate based on his ability to consistently outcompete other males. This strategy would not require females to attend to any properties of songs other than perhaps cues that reveal the locations of singers. Indirect mate choice based on physical competitions avoids the complexities associated with comparing songs that vary along multiple dimensions even within a single song session, and that may overlap extensively when multiple singers are simultaneously audible. It is unclear what information about reproductive fitness females or males might gain from comparing singers' songs that they could not also potentially gain from the outcomes of physical contests, or how intra-individual variations in unit sequences could enhance reliable transmission of that information.

In contrast, if songs increase the chances that a singer will succeed in locating and joining an individual female or competitive group (by revealing their presence and swimming trajectory via echoes), then there is no need for any listeners to memorize or compare songs. More importantly, if songs contribute to a singer's ability to find other whales, then intra-individual variations within song sessions can potentially enhance detection and tracking of conspecifics by varying the active space from which echoes are most likely to be detected. This is the primary factor driving intra-individual variation in signal production by both bats and dolphins searching for prey. Singing humpback whales may thus vary the acoustic characteristics of units and sequences

of units for the same reasons that bats and dolphins do – to increase their capacity to detect, localize, and interpret echoes within acoustically complex soundscapes. The distributions of time periods that singers spent producing each song section were similar to distributions of movements previously associated with active perceptual searching (e.g., Saez de Urabain et al., 2017; Suppes, 1990; Wallman & Pettigrew, 1985). Further analyses of longer-duration song sessions are needed to verify that singers consistently vary their usage of sections in ways that produce the kinds of positively skewed distributions associated with fixation durations. Overall, the current findings are more consistent with the proposal that singing humpback whales are actively searching their surroundings than with claims that they are attempting to demonstrate their reproductive fitness.

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Open Practices Statement

All the data analyzed in this study are available at https://patternradio.withgoogle.com/. The original recordings used to construct the spectrograms are available at https://doi.org/10.25921/Z787-9Y54 and the software used to measure spectrographic images is available at https://imagej.nih.gov/ij/download.html.

No experiments or analyses were preregistered.

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