

Quantifying humpback whale song sequences to understand the dynamics of song exchange at the ocean basin scale

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Humpback whales have a continually evolving vocal sexual display, or “song,” that appears to undergo both evolutionary and “revolutionary” change. All males within a population adhere to the current content and arrangement of the song. Populations within an ocean basin share similarities in their songs; this sharing is complex as multiple variations of the song (song types) may be present within a region at any one time. To quantitatively investigate the similarity of song types, songs were compared at both the individual singer and population level using the Levenshtein distance technique and cluster analysis. The highly stereotyped sequences of themes from the songs of 211 individuals from populations within the western and central South Pacific region from 1998 through 2008 were grouped together based on the percentage of song similarity, and compared to qualitatively assigned song types. The analysis produced clusters of highly similar songs that agreed with previous qualitative assignments. Each cluster contained songs from multiple populations and years, confirming the eastward spread of song types and their progressive evolution through the study region. Quantifying song similarity and exchange will assist in understanding broader song dynamics and contribute to the use of vocal displays as population identifiers.

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I. INTRODUCTION

Vocal displays can be used to investigate the grouping of individuals into dialect regions, elucidate the directionality in movement of individuals, provide an indication of the amount of contact among populations, and also elucidate the

evolutionary changes to particular vocal displays. Quantification of vocal displays is required to ensure a robust approach to assessment. Typically, individual sounds are measured for various acoustic parameters to allow classification of discrete sounds (e.g., Clemins *et al.*, 2005; Au *et al.*, 2006; Suzuki *et al.*, 2006; Dunlop *et al.*, 2007; Ranjard and Ross, 2008; Rickwood and Taylor, 2008; Stimpert *et al.*, 2011). Vocal displays may also be complex; this requires additional quantification to ensure the complexity is adequately incorporated into analyses. In this paper, we present a quantitative analysis of spatial and temporal variation in the culturally transmitted

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complex songs of humpback whales in the South Pacific Ocean.

Some vocal traits (displays) provide good examples of cultural learning, in which cultural traditions or specific behaviors are learnt from conspecifics (Slater, 1986; Rendell and Whitehead, 2001; Fragaszy and Perry, 2003). Cultural learning of behaviors can occur from various models as behavioral traits can be passed from parents to offspring (vertically), from the previous generation to unrelated younger individuals (obliquely), or within generations or age classes of individuals (horizontally; Rendell and Whitehead, 2001). Song neighborhoods, or dialect areas, occur through song matching in passerine song birds (see Catchpole and Slater, 2008). Most birds' songs do not change substantially with time but there appear to be a few species that show continual cultural evolution and thus learning. The songs of the Panamanian yellow-rumped cacique (*Cacicus cela*) and the village indigobird (*Vidua chalybeate*) appear to continually evolve or change with time (Payne, 1985; Trainer, 1989). Within cetaceans, sperm whales (*Physeter macrocephalus*) form acoustic clans over large geographic areas that are composed of multiple, matrilineal groups that share distinct dialects of patterned clicking sounds (see Whitehead, 2009; Rendell *et al.*, 2012). Killer whales (*Orcinus orca*) are also organized into matrilineal pods, each with a distinct vocal dialect that overlaps to varying degrees with the dialects of other pods in the area to again form acoustic clans (Deecke *et al.*, 2000; Riesch and Deecke, 2011). These dialects can undergo cultural evolution as the call types or sounds have been documented to gradually change over time, with these changes maintained by different matrilines within the acoustic clan (Deecke *et al.*, 2000). The matching of these call types among groups within the clan is an example of horizontal transmission, where learning occurs within a generation or age-classes.

The broadest-scale example of horizontal cultural transmission in cetaceans is the repeated movement of different humpback whale (*Megaptera novaeangliae*) songs between populations within a region (Garland *et al.*, 2011). Male humpback whales have a constantly evolving vocal sexual display, termed "song" (Payne and McVay, 1971; Payne and Payne, 1985). All males within a population conform to the current version of the display (the song type), and due to rapid cultural transmission, similarities exist among the songs of populations within an ocean basin (Payne and Guinee, 1983; Payne *et al.*, 1983; Payne and Payne, 1985; Garland *et al.*, 2011). Within a given population, the song usually changes progressively and gradually over several years or breeding seasons (Payne *et al.*, 1983; Payne and Payne, 1985). This process has been referred to as an example of "cultural evolution" (Winn and Winn, 1978; Payne and Payne, 1985; Cato, 1991; Noad *et al.*, 2000) similar to that seen in some bird species' song (Slater, 1986; Catchpole and Slater, 2008). However, Noad *et al.* (2000) documented a song change in the eastern Australian humpback whale population in which the population's song was replaced rapidly and completely by a song used by the western Australian population two years previously. This change was referred to as "cultural revolution." Thus there appear to be

two forms of cultural change that humpback whales' songs can undergo (progressive evolution and complete revolution), but it remains unclear whether these two forms of change are truly distinct or whether one is simply an extreme form of the other (Noad *et al.*, 2000).

Humpback whales' songs are highly stereotyped, repetitive, and arranged in a nested hierarchy (Payne and McVay, 1971). Multiple sounds or "units" occur in a stereotyped sequence called a phrase, phrases are repeated to make a "theme," and a series of themes, usually produced in a particular order, comprise a song. A song is defined as any complete cycle of themes with no repetition of a theme (Payne and Payne, 1985) as humpback whale song is produced in a highly stereotyped sequence of themes (Payne and McVay, 1971). Songs are repeated multiple times by an individual male to comprise a song session. At the level of the song, different versions of the display are grouped together into song types based on qualitative similarity. Recently, Garland *et al.* (2011) conducted a qualitative study of humpback whale song across the South Pacific Ocean basin. This study involved six populations and 11 years of data, and uncovered a striking pattern of song transmission that was hypothesized to occur through rapid cultural transmission of song types. The spread of song types across the region took approximately 2 years and was hypothesized to occur through the migration of a small number of males and/or song learning on shared migration routes. Photo-identification studies in the region have demonstrated a shared migration route and interchange of whales between populations but with no clear trend in directionality to these movements (Constantine *et al.*, 2007; Garrigue *et al.*, 2011a). We define populations here based on genetic (Olavarria *et al.*, 2007) and extensive photo-identification mark recapture studies (see Garrigue *et al.*, 2011a; Garrigue *et al.*, 2011b), which indicate demographic independence.

Understanding the relationship among songs is important at the levels of both the population and individual singers. To improve on the usual qualitative method of song classification (Garland *et al.*, 2011), our objective was to quantify the relationships among songs over a large geographic scale using multiple years of data. Two levels of analysis were undertaken. The first investigated the similarity of songs at the population level using a representative sequence and the second investigated song sequence similarity at the individual singer level regardless of the populations or years the samples were taken from. To ensure an unbiased quantitative assignment of song type clusters, we removed all information regarding populations, years, and qualitatively assigned song types, and thus all preconceptions of what song types particular songs belonged to, for both levels of analysis. A handful of studies have investigated song sequence similarity in humpback whales using the Levenshtein distance method (Helweg *et al.*, 1998; Eriksen *et al.*, 2005; Tougaard and Eriksen, 2006; Garland *et al.*, 2012). The Levenshtein distance technique and variants of this method provide a quantitative measure to investigate the similarity of multiple song sequences by grouping or clustering similar sequences together. This technique is thus appropriate for assigning a sequence of themes (as this sequence makes up the song) to a cluster based on the

similarity of the sequence to all others investigated. The aims of this study were to (1) use this quantitative analysis to cluster similar songs together and thus assign song types quantitatively, (2) compare the quantitative assignment of songs to the song types assigned based on qualitative assessment (Garland *et al.*, 2011) to test the robustness of such qualitative assignment, (3) test whether evolutionary and revolutionary song changes identified using qualitative analysis are also identified using this quantitative analysis, and (4) identify identical songs at the population level to investigate whether these show any directionality in the transmission of the song among populations.

II. METHODS

A. Field sites

Field sites within the western and central South Pacific region corresponded to the multiple migration and breeding grounds (Fig. 1). Six main locations were the focus: Point Lookout and Peregian Beach in southeastern Queensland, Australia, the southern lagoon in New Caledonia, Vava'u island group in Tonga, the island of Tutuila in American Samoa, the island of Rarotonga in the Cook Islands, and the island of Mo'orea in French Polynesia. Data were also included from other locations (Vanuatu, Fiji, and Niue) when available.

B. Acoustic analysis

Songs were recorded from 1998 through 2008 across the region using a cassette recorder, minidisk, Sony, Japan, Digital Audio Tape (DAT) recorder (recorded digitally but then transferred to computer by digital to analog conversion followed by re-digitizing) or an M-Audio, USA, Microtrack (24/96 and II) digital recorder (WAV files, 16 bit, 44.1 kHz sample rate) and a single hydrophone (High Tech Inc., Long Beach, MS, HTI 96 Min hydrophone; in 2007 and 2008). Recordings in eastern Australia were taken as part of other research (see Noad *et al.*, 2004; Noad and Cato, 2007; Dunlop *et al.*, 2007) using moored hydrophone buoys

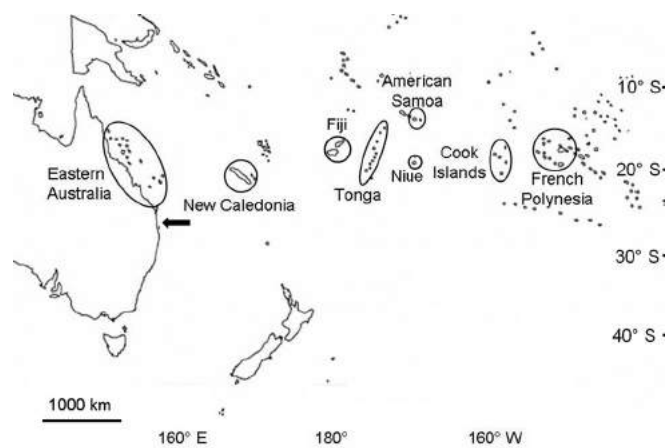


FIG. 1. Map of the western and central South Pacific region. Circles represent the locations of the breeding populations included in this study. Recordings in eastern Australian were taken while the whales were on migration (arrow).

(16 bit, WAV files, 22 kHz sampling rate), and were supplemented by a small number of single hydrophone recordings (Sony DAT recorder or M-Audio Microtrack 24/96 and II digital recorder; Clevite CH17, USA, GEC Marconi SH101X, UK, or High Tec Inc. HTI 96 Min hydrophone; WAV files, 16 bit, 44.1 kHz sample rate) and autonomous bottom-deployed data loggers (16 bit, sampling rate greater than 5 kHz). All recordings adequately covered the frequency range of the whales' songs.

Songs were viewed as spectrograms in Adobe AUDITION (Blackmann-Harris window, fast Fourier transform size 1024 samples). Song was transcribed by human classifiers (M.L.R. for the eastern Australian data and E.C.G. for Oceania) who worked together to ensure consistency. Transcription was based on the visual and aural qualities of the sound and each unit sound type was assigned a descriptive name (e.g., "groan," "squeak"). A discriminant function analysis with cross-validation was performed on a subset of units (400) and resulted in 80% correct classification of sounds, consistent with other studies of humpback whale sound units (e.g., Dunlop *et al.*, 2007; Garland *et al.*, 2011). For each individual singer, a maximum of six songs were transcribed. The majority of singers in this study were not identified; this was because they were not sighted, and therefore not photo-identified or genotyped. When individual identifications were made using photo-identification, only six songs in total from any individual within a season were used in the analysis to avoid bias (over-representation). To test the reliability of our classification of themes, three naïve observers were asked to match 50 themes to 20 of the identified themes in Adobe AUDITION (using the same settings as previously used). Overall, the observers correctly classified over 94% of themes (Garland *et al.*, 2011). Songs were grouped together based on qualitative similarity of themes into song types that were assigned color names as arbitrary labels. If a song was observed to evolve from one type into another through progressive changes to the units within phrases and/or the omission or insertion of themes, the new song was called a different shade of the original color to show that they were related (e.g., Blue to Light Blue). If a new, unrelated song appeared, it was given a completely new color name. As an example, the Yellow (Fig. 2) and Dark Green (Fig. 3) song types are shown [see Garland *et al.* (2011) for Blue, Light Blue, Dark Red, and Light Red song type examples].

C. Levenshtein distance analysis

The quantitative method chosen to assess call sequence similarity was based on the Levenshtein distance technique. The Levenshtein distance (LD) calculates the minimum number of changes (insertions, deletions, and substitutions) needed to transform one string of data into another (Kohonen, 1985; Helweg *et al.*, 1998; Eriksen *et al.*, 2005; Tougaard and Eriksen, 2006; Garland *et al.*, 2012). The LD is calculated as

$$LD(a, b) = \min(i + d + s), \quad (1)$$

where string (*a*) is converted into string (*b*) by the minimum number of insertions (*i*), deletions (*d*), and substitutions (*s*)

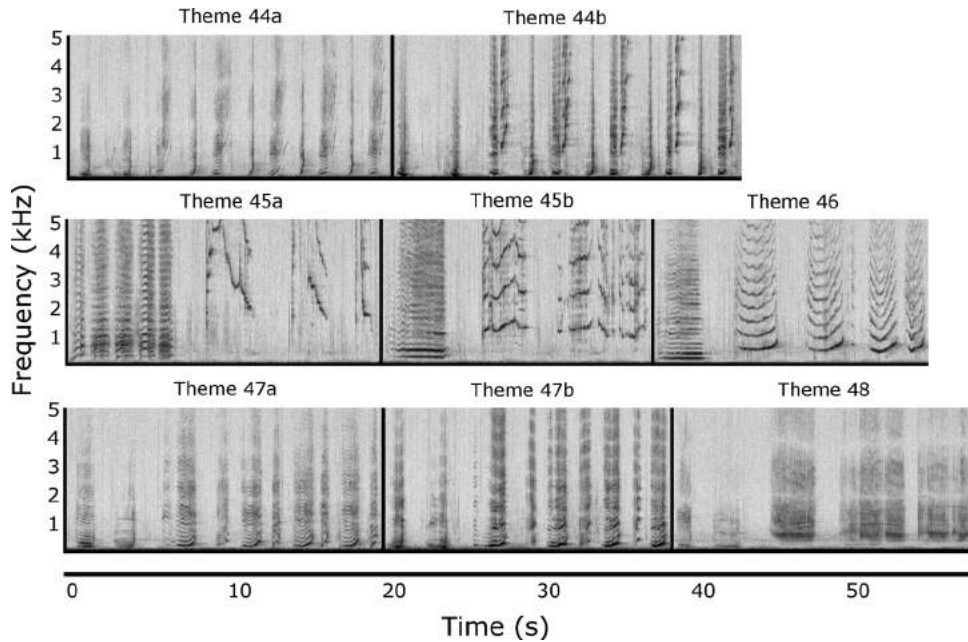


FIG. 2. Spectrograms of the Yellow song type (Themes 44–48). A representative phrase for each theme is shown. Note that some themes contain “a” and “b” phrases. These were all classified as the Yellow song.

(Kohonen, 1985). A string can be anything from a human word to a sequence of behaviors coded out by a researcher. All that is required is a sequence of elements (e.g., letters or numbers) that can be compared to another element sequence. In this study, a string was the typical sequence of themes that made up a song from either an individual singer or from a population. To allow multiple pairwise comparisons, raw LD scores were standardized to allow meaningful comparisons (see Kohonen, 1985; Tougaard and Eriksen, 2006; Garland *et al.*, 2012). Two standardizations of the data were undertaken. The first involved the use of a median or representative string for each group or population/year (called a “Set median”). The second involved normalizing the LD score by incorporating string length into the equation.

The assignment of a median string for each population and year combination (each set) was undertaken to allow

standardization. Data were condensed to a single representative string per individual singer to ensure results were not biased through over-representation from singers with more data. For each singer, up to six songs (depending on the number of songs recorded) were examined to decide which themes were commonly included and their positions in the song. If a theme was present in 50% or more of the songs then it was included in the final sequence. Songs were generally consistent for individual whales and a representative song sequence for each singer in each season was established. Once each singer was represented by a single string ($N=211$), these were grouped into sets ($N=63$) based on the populations and years in which the songs were recorded (Table I). To obtain a representative song sequence or string from a given population and year (the Set median), the representative song sequences (strings) from all individuals in

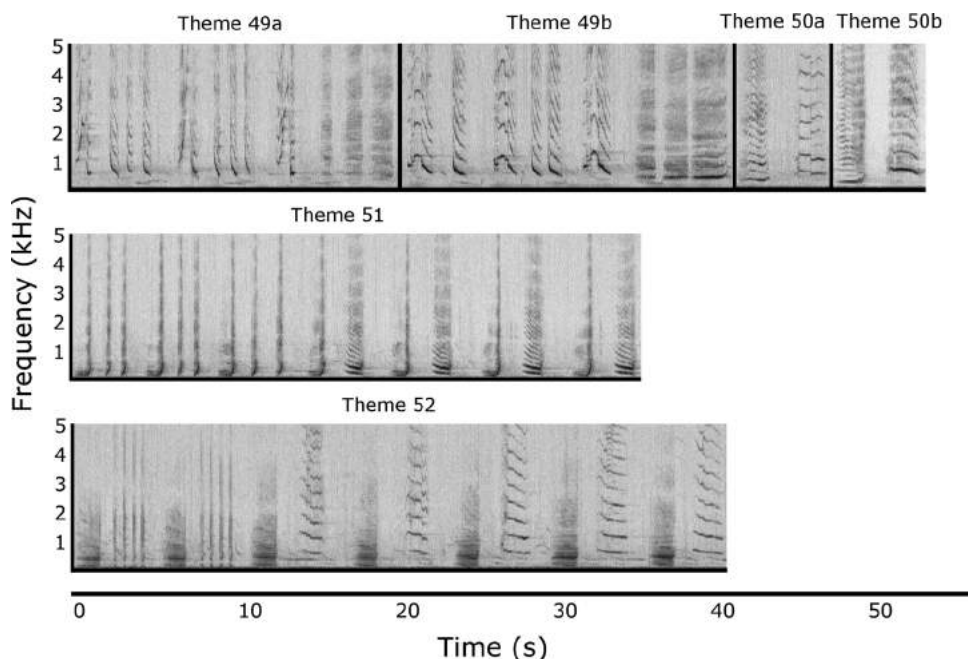


FIG. 3. Spectrograms of the Dark Green song type (Themes 49–52). A representative phrase for each theme is shown. Note that some themes contain “a” and “b” phrases. These were all classified as the Dark Green song.

TABLE I. Number of singers and songs for each location, year, and song type.^a

Year		Eastern Australia	New Caledonia	Vanuatu	Fiji	Tonga	American Samoa	Niue	Cook Islands	French Polynesia
1998	Number of singers	2	5			5		2	1	1
	Number of songs	8	30			9		3	2	4
	Song type	BL	BL			BL		P	P	P
1999	Number of singers	1	6			5				6
	Number of songs	4	22			11				21
	Song type	BL	BL			BL				BL
2000	Number of singers	2	6			2, 4				
	Number of songs	12	24			2, 9				
	Song type	DB	BL			BL, G				
2001	Number of singers	1	6			1, 5			3	2, 2
	Number of songs	2	28			2, 14			13	8, 8
	Song type	DB	DB			G, DB			G	BL, G
2002	Number of singers	6	5		1	6				
	Number of songs	30	17		5	26				
	Song type	BU	BU		BU	BU				
2003	Number of singers	6	6	4		6	1		4	
	Number of songs	36	22	18		14	1		12	
	Song type	DR	BU	BU		BU	BU		BU	
2004	Number of singers	6	1, 3				1		2	3
	Number of songs	35	5, 18				4		8	8
	Song type	DR	BL, DR				BU		BU	BU
2005	Number of singers	5	6				1		1	2, 4
	Number of songs	18	31				2		1	4, 15
	Song type	LR	DR				DR		BU	BL, DR
2006	Number of singers	2	3			6	3		1	5, 1
	Number of songs	9	16			32	4		5	9, 3
	Song type	Y	LR			LR	LR		LR	BL, DR
2007	Number of singers	1	6			6			4, 1	4, 2
	Number of songs	4	27			27			9, 6	17, 10
	Song type	DG	Y			Y			LB, Y	LB, LR
2008	Number of singers	2	6		1	2			1	6
	Number of songs	10	24		1	4			6	9
	Song type	LG	DG		Y	DG			LB	LB
Total number of singers			211			Total number of songs			798	

^aLocations are listed from west to east across the region. Song type color codes: BL = Black, G = Grey, P = Pink, DB = Dark Blue, BU = Blue, LB = Light Blue, DR = Dark Red, LR = Light Red, Y = Yellow, DG = Dark Green, LG = Light Green.

the set were examined. The LD was calculated for every pair of strings within the set. The string with the minimum summed LD to all other strings within the set became the representative sequence or Set median. This string had the highest overall similarity to all other strings within the set. To ensure this sequence was representative of the set, a hypothetical median known as the “Kohonen median” (Kohonen, 1985) was generated to ensure the best representation of all themes. This was done by systematically replacing each theme in the sequence to investigate whether a smaller summed LD could be obtained (Kohonen, 1985). The Kohonen median was used instead of the Set median in 4 out of 63 (6%) population/year/song type combinations as it produced a more representative, although hypothetical, sequence of themes. On a small number of occasions, more than one song type was present within a single population in the same year (as assessed qualitatively). These song types were placed in separate sets to allow the analysis to assess the similarity of these strings and whether they represented a true difference.

D. Matrix of LD similarity

In order to investigate the similarity of multiple sets or groups of data, a variation on the LD equation, called the “Levenshtein distance similarity index” (LSI), was used (Helweg *et al.*, 1998; Eriksen *et al.*, 2005; Garland *et al.*, 2012). This normalized the LD score by the length of the longest string as follows:

$$\text{LSI}(a, b) = 1 - \text{LD}(a, b) / \max(\text{len}(a), \text{len}(b)). \quad (2)$$

This standardized the result of the LD by incorporating string length (len) and produced a proportion of similarity, from 0 to 1, for every pair of strings, which allowed direct comparison of all strings, whether at the individual or set (population) level. The resulting LSI scores formed a matrix of LSI similarity. For each analysis (population and individual), a standardized matrix of similarity was produced and converted to a dissimilarity matrix by subtracting each score from 1. Each matrix was then analyzed using hierarchical

clustering in the statistics program R (The R Foundation for Statistical Computing, 2009, Vienna, Austria).

Hierarchical clustering allowed all components, in our case strings, to be grouped into subsets (or clusters) with similar components. We employed a bottom-up method termed “single-linkage” or “nearest neighbor” clustering. This grouped clusters together based on the members of each group that displayed the highest similarity to each other (Manning *et al.*, 2009). Single-linkage clustering allowed the identification of identical strings as these were placed together and then successively linked to other clusters/strings. We were interested in investigating the similarity of strings and the overall structure based on which individuals or sets (population/year) displayed the highest overall similarity. These groupings help elucidate the movements of particular combinations of themes and thus possible points of acoustic contact within the region.

The matrix of LSI scores represented the strengths of similarity among all components and clusters were based on these scores. To clearly understand the complex groupings produced from clustering, results were displayed in dendrograms, which allowed visual representation of clusters. We then determined whether each cluster represented a song type or lineage of related song types as categorized by qualitative analyses.

III. RESULTS

A. Quantitative assignment of songs to song types

Ten different clusters were identified using this analysis at the set (population/year) level [names correspond to the qualitatively assigned song types in Garland *et al.* (2011);

Fig. 4]. Within each cluster, songs displayed at least 40% similarity to each other, except for the left-most string (in bold) from the Black/Grey cluster, which was a very short sequence and thus possibly aberrant.

At the individual level, nine different clusters were identified as the Red song types formed a single cluster [names correspond to the qualitatively assigned song types in Garland *et al.* (2011); Fig. 5]. This method clustered individuals’ songs based on their display sequence rather than the respective population or year that the individual was sampled from. The majority of individuals within each cluster exhibited 80% or above similarity with their nearest neighbor. Overall, there was 40%–60% similarity within each cluster or song type.

B. Robustness of qualitative assignment

Clusters broadly agree with the song types identified by qualitative analysis at both the population and individual level (Garland *et al.*, 2011). Song types appear to group into separate clusters except for Black, Grey, Dark Red, and Light Red. At both levels, the cluster on the furthest right, which appears to be a complicated cluster, corresponds to two qualitatively assigned song types, Black and Grey (Garland *et al.*, 2011). A connection between the Dark and Light Red song types was present at 15% similarity at the individual level but this connection was absent at the population level.

C. Evolutionary and revolutionary song changes

Evolutionary song changes were identified by the analysis for the Black/Grey and for the Red (Dark and Light)

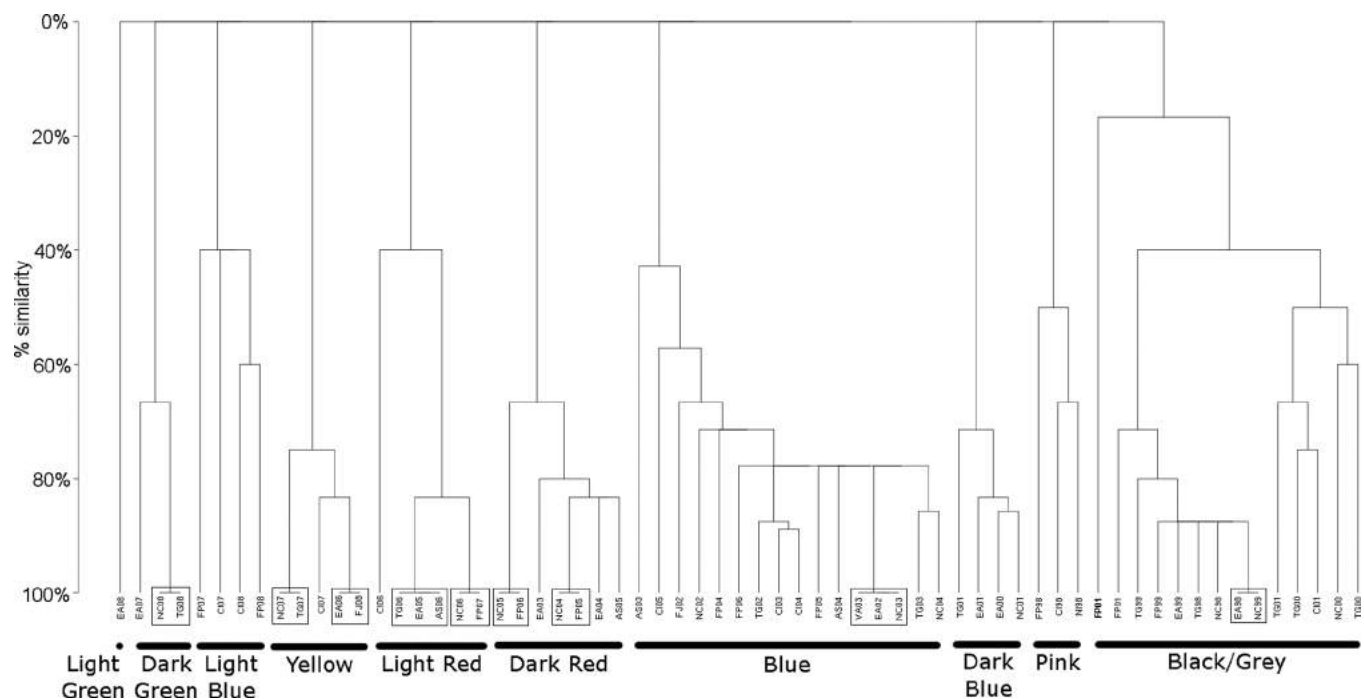


FIG. 4. Population-level Kohonen adjusted Set median dendrogram from single-linkage hierarchical clustering based on LSI scores. Each cluster has the corresponding qualitatively assigned color name from Garland *et al.* (2011) listed. Boxes indicate identical strings within each cluster. FP01 is in bold as it is possibly an aberrant song. Labels for each string indicate population and year (1998–2008). EA = eastern Australia, NC = New Caledonia, VA = Vanuatu, TG = Tonga, AS = American Samoa, FJ = Fiji, NI = Niue, CI = Cook Islands, FP = French Polynesia.

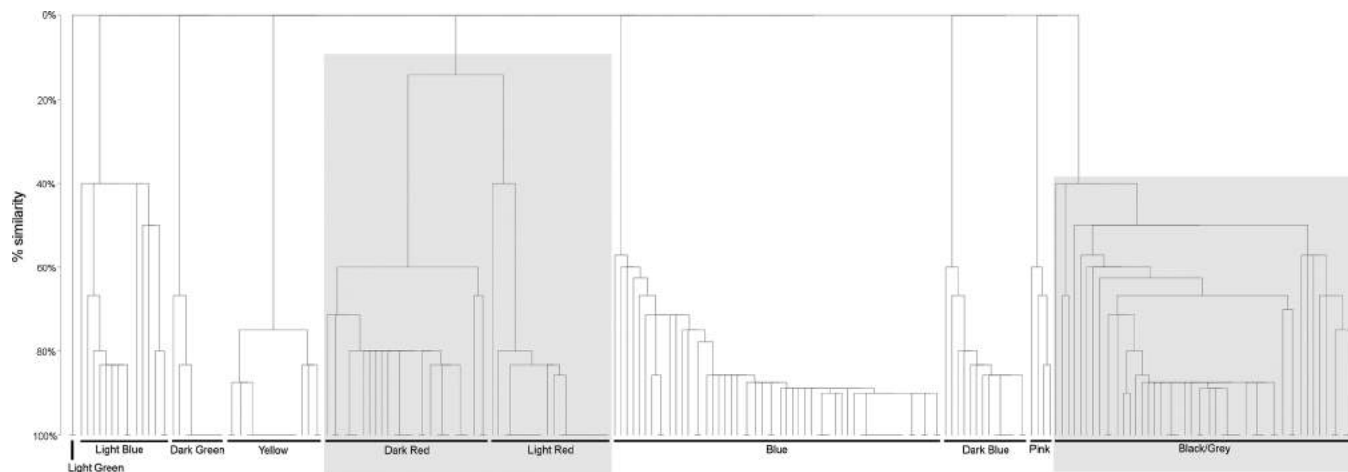


FIG. 5. Individual singer's ($N = 211$) song sequence dendrogram from single-linkage hierarchical clustering using percentage similarity based on LSI scores. Each cluster has the corresponding qualitatively assigned color name from Garland *et al.* (2011) listed. Shaded boxes have been placed around clusters that contain more than one qualitatively identified song type.

lineages, as suggested by qualitative assignment. In contrast, evolutionary progressions in the Blue and Green lineages do not appear clearly in this analysis. The song revolutions identified in Garland *et al.* (2011) from Pink to Black and from Blue to Dark Red appear to be consistent with the current analysis, exemplified by their 0% similarities.

D. Identical songs as indicators of the direction of transmission

Sequences from multiple years and populations were present at the population (set) level within clusters (Fig. 4). Songs that were considered identical are shown with boxes around each group (Fig. 4). These identical groups included: New Caledonia and Tonga 2008; New Caledonia and Tonga 2007; eastern Australia 2006 and Fiji 2008; eastern Australia 2005, American Samoa and Tonga 2006; New Caledonia 2006 and French Polynesia 2007; New Caledonia 2005 and French Polynesia 2006; New Caledonia 2004 and French Polynesia 2005; eastern Australia 2002, Vanuatu and New Caledonia 2003; and eastern Australia 1998 and New Caledonia 1999. Examining these on a west–east line indicated that song types were always first present in western populations (e.g., eastern Australia or New Caledonia) and then subsequently moved to populations further east as time progressed.

IV. DISCUSSION

We have presented a quantitative assignment of humpback whale song types recorded from the western and central South Pacific Ocean, based on the similarity of theme sequences and carried out at both the individual and population level. Clusters represented distinct song types or song lineages, with low levels of similarity differentiating different song types. Our analyses at both the population and the individual singer levels assigned song types without any prior assumptions of similarity by removing information on the location, year, and qualitatively assigned song type. This allowed a comparison with qualitatively assigned song types and also identified identical song sequences that are suggestive of directional

transmission. Some evolutionary changes identified by qualitative analysis were not highlighted by our quantitative analysis. However, all qualitatively assigned song revolutions displayed the predicted 0% similarity in the quantitative assessment.

Evolution of song types can occur through a number of types of changes at all levels within the song. Evolution of song types occurs through progressive change to the units (e.g., stretching, splitting into smaller units), omission or inclusion of units in the composition of the phrases, or, at a higher level, insertion or omission of entire themes (Winn and Winn, 1978; Payne *et al.*, 1983; Payne and Payne, 1985; Cato, 1991). The current analysis focused on the level of the theme and identified differences in the presence/absence of themes through their insertion and/or deletion and their particular position within the song. It has not focused on the small progression of themes from one to the next through changes in units or their composition. Progressive evolution of themes through changes in unit composition would be more difficult to track with this analysis (but see the following for a variation on the method that would allow this). When units have changed (e.g., through splitting of units into two sounds, or completely removing a sound) the theme is considered different and is renamed by the human classifier. The connection between this “new” theme and the “old” version is thus lost. While this information is available to the human classifier in qualitative assignment and is utilized to assign a theme/song evolution, it cannot be utilized in the LSI analysis described here. For example, in Garland *et al.* (2011), all Blue songs form a single lineage comprising three versions or song types (Dark Blue, Light Blue, and Blue) that progressively evolved through changes to units within themes. The Dark Blue song appeared to rapidly evolve into the Blue song, with a few themes showing qualitative similarity. The Blue song evolved into the Light Blue song through very clear and traceable changes in themes (in the qualitative analysis). These changes were not identified by the quantitative analysis as these songs form three different clusters with 0% similarities. Linkages between themes, which are clear to the human classifier, are not as clear in the

quantitative analysis. While there appears to be 0% similarity between some qualitatively similar song types, rapid evolutionary changes may have occurred that could not be differentiated from revolutionary changes. This lack of identifying connections through changes in units also appears to have occurred for the Green lineage (Dark and Light) and to a certain extent the Red lineage (Dark and Light, although see the following).

Despite this, the technique has value and through the weighting of evolutionary transitions or the combination of qualitative and quantitative assessment, a more robust result could be obtained. Previous studies investigating the performance of human classifiers against different quantitative methods have also found that human classifiers performed as well, if not better, at classification than did computer methods (Janik, 1999; Riesch and Deecke, 2011). While there is a need to create more robust methods of analysis, we should not forget that humans are capable of complex categorization, especially when processing graded signals. A combined method is highly desirable to ensure important components of the signal are not missed by either the human classifier or computer method.

Song evolution that occurred through the insertion or deletion of themes appears clearly, but does, however, produce a complex picture of song groupings. The Black and Grey song types clustered together in a single lineage, as was suggested in Garland *et al.* (2011). Themes from both song types were combined by two populations, New Caledonia (2000) and Tonga (2000). In later years, the Black song themes disappeared from the song and only the new Grey themes were sung (Fig. 4). Within the Red lineage (Light and Dark), the majority of changes were to the composition of units within themes, but a few rare theme substitutions occurred. This produced the 15% similarity (Fig. 5) at the individual level due to the inclusion of a Dark Red theme in the Light Red song by one singer in American Samoa (2006).

To trace evolutionary changes through the insertion/omission of themes we have processed a substantial amount of data collected over 11 years to allow the tracing of these evolutionary changes (especially in regards to the Black/Grey lineage). Investigating the similarity of sequences at the theme level produced a variable Black/Grey lineage that relied on the number of themes used, or the combination, to produce the varying similarity within that cluster. The analysis technique that we used in this study was based on common themes and sequences that met a 50% threshold for each individual singer. Rare combinations of themes from evolving song types were typically produced less than 50% of the time, although most singers were very consistent in the themes included in each song. The locations of these emerging themes and their consistency were very unstable. The inclusion of rare themes would require the addition of multiple strings or sequences from each individual singer, which would introduce additional statistical biases.

Song revolutions must, by definition, involve 0% similarity between two song types that occur consecutively or overlap in time. Both revolutions identified qualitatively in Garland *et al.* (2011)—from Pink to Black and from Blue to Dark Red—appear to also have been identified by the current

analysis, exemplified by their 0% similarities. The original cultural revolution identified by Noad *et al.* (2000), which continued spreading across the region [as shown in Garland *et al.* (2011)], is shown by the 0% similarity between the Black and Pink song types at both the population and individual level.

The quantitative analysis of song sequences showed an easterly transmission of identical song types, and thus unidirectional horizontal cultural transmission, as shown by Garland *et al.* (2011). Song transmission between populations is proposed to occur through song learning on shared migration routes or through the movement of a small number of males between populations (Payne and Guinee, 1983; Noad *et al.*, 2000; Garland *et al.*, 2011). In Fig. 4, New Caledonian song periodically displayed 100% similarity with eastern Australian song from the previous year. This indicates that these song types were likely transmitted to New Caledonia (and Vanuatu as it displayed the same pattern of similarity) with high fidelity from eastern Australia in the previous year. This tight relationship broke down as the Black song progressively evolved into Grey. One possible explanation for this breakdown could be a reduction in the number of migrants between these populations.

Song changes spread in an easterly direction (Garland *et al.*, 2011); two types of directional movements are suggested to produce this pattern. New songs could be introduced directly by males moving east to another population. Alternatively, a male could move west, learn the song of a different population, and then return to his natal population to the east taking the new song with him. Movement of individuals between seasons in both directions (east and west) has been documented by photo-identification studies within the western and central South Pacific region (Garrigue *et al.*, 2011a; Garrigue *et al.*, 2011b). Low levels of interchange have been shown between the populations of New Caledonia and eastern Australia (Garrigue *et al.*, 2011b). Four photo-identification matches have been made to date; all individuals were male. These individuals were photo-identified in the New Caledonian population at least once in the late 1990s and/or early 2000s, before three were photographed in the eastern Australia population in 2002. The fourth male was photographed in the eastern Australian population in 2000 and 2001. Thus, all four males moved in a westerly direction. Only one of these males has been photo-identified since 2002; he was photographed in New Caledonia in 2005 (Garrigue *et al.*, 2011b). This represents an east–west–east movement, and while photo-identification data are not robust enough to say more, it is suggestive that one or more other males could have undertaken this movement pattern within the timeframe of the observed song changes. This would have facilitated the transfer of the eastern Australian version of the song to New Caledonia. New Caledonia and eastern Australia also share a portion of their migratory path through New Zealand (Constantine *et al.*, 2007; Garrigue *et al.*, 2011b). This could allow acoustic contact and provide another mechanism for song exchange without any movement of males between populations.

Another example of easterly transmission of identical song types is the similarity of song in French Polynesia to

that of New Caledonia in the previous year (Fig. 4). It is important to note that no data were available from the Tongan population in two of these years (2004 and 2005). Song in Tonga displayed 100% similarity to that in New Caledonia in two years (2007 and 2008), representing a strong connection. The Light Red cluster contained two groups of identical strings; one group contained New Caledonia 2006 and French Polynesia 2007, and the other eastern Australia 2005, Tonga 2006, and American Samoa 2006. The Dark Red songs and the particular combination of Light Red themes were most likely transmitted to French Polynesia from New Caledonia, possibly via Tonga. Recent photo-identification studies in the region have documented a case of easterly movement between years from New Caledonia via Tonga to French Polynesia (Garrigue *et al.*, 2011a). More commonly, there have been photo-identification matches from different years between New Caledonia and Tonga, and Tonga and all other populations including those to the east [American Samoa, the Cook Islands, and French Polynesia; Garrigue *et al.* (2011a)]. These movements would allow acoustic contact and song transmission in a stepwise fashion from one population to the next.

Future song analyses could assign song types based on the LSI. This would group similar songs together and produce a quantifiable way of investigating similarity and the level at which one song type becomes so different it should be assigned as such. However, this only removes one level of subjectivity. Future research should also strive to quantitatively define units and to “match” themes and phrases based on the stereotyped sequence of units using the LD method. This would allow clearer connections between new and old versions of themes. An alternative to this would be to apply varied weightings to the analysis to assign themes as being related. We believe that weighting evolutionary transitions (where there has been clear evolution from one theme into another) with a cost of less than 1 (which is the current cost factor used in the analysis) would provide a robust way to combine both qualitative human classification and quantitative analysis techniques. Rare combinations of themes would also need to be incorporated to further elucidate the connections among song types. This would need to be applied at an intra-individual level to tease apart the complex relationships among song types, but caution is warranted as possible statistical issues may arise when using multiple sequences from the same individual.

We have presented a quantitative analysis of sequence similarity of multiple song types or variants of humpback whale song. Clusters of similar songs were grouped together at both the individual singer and population level to produce song types that were not restricted to any single population or year of data. These, however, did correspond to the qualitatively assigned song types from Garland *et al.* (2011) and therefore provide a robust test of the usual methods of qualitative song assignment. Humpback whale song undergoes continuous evolution (Payne and Payne, 1985) and also rapid revolutionary changes (Noad *et al.*, 2000), and the ability to quantify and trace these changes is important in understanding the differences between them. This technique provides a robust method that combines both qualitatively

and quantitatively assigned songs (at varying levels of the hierarchy) to investigate similarity. A suggested improvement to continue to tease apart the complexities of song is to weight evolutionary changes based on qualitative assessment; this will ensure rapid evolutionary changes are better captured by the analysis. The identification of identical song types at the population level has provided robust evidence for easterly transmission and thus unidirectional horizontal cultural transmission of song types, as suggested in Garland *et al.* (2011). Song is a complex and dynamic display that provides a cultural identity or marker for each population. The use of the LD technique to investigate the dynamics of song propagation and the population connections within an ocean basin allows this acoustic display to provide insights into population structure over a vast scale.

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