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INTERNATIONAL
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Abstract

Humpback whale song recorded off the coast of Oman between 2011 and 2020 was used to assess the degree of change over a ten year period, and whether there was indication of novel song introduction that would imply connectivity with Southern Hemisphere populations. During the first eight years of the study period (2011-2018), Oman song maintained an atypically slow and gradual change compared to other populations of humpback whales, with only a few exceptions in three phrase lineages. Between 2018 and 2020 (noting that there no samples from 2019), there was a complete shift from long complex phrases to short simple phrases; however, in all cases the new, short phrase variants represented elements of the previous, parent phrases from 2018. There were no large-scale introductions of new phrase-types, or replacement of phrases across the ten years. In all but one instance, new phrases resulted from the splitting of existing lineages and formation of new variants of an existing phrase-type. There was only one example of a potentially novel phrase-type being introduced during 2017. Therefore, we observed no cultural diffusion events as has been described in Southern Hemisphere populations, in which the entire song is replaced by the song of immigrant whales. Comparison of a small sample of songs recorded off western India in 2011 and 2017 indicated that all phrases diagnosed in the India sample (2 phrases in 2011 and 6 phrases in the 2017 sample) were also present in the Oman songs, indicating a close connection between whales found in both the western and eastern Arabian Sea. These results reinforce the understanding that the Arabian Sea humpback whale population is isolated as indicated by population genetic studies and the lack of photographic matches to date, and unique on multiple levels of its behaviour and life history patterns.

Introduction

Existing genetic, demographic and behavioural evidence indicates that Arabian Sea humpback whales (*Megaptera novaeangliae*, from here on referred to as ASHW) represent an isolated and unique population (Minton et al 2011, Pomilla, Amaral et al. 2014, Willson et al. 2018, Willson 2021). ASHWs exhibit a Northern Hemisphere breeding cycle and do not undergo the typical

latitudinal migrations and seasonal separation of breeding and feeding ecology exhibited by other populations of humpback whales globally. The population is the subject of a standing Scientific Committee (SC) agenda item and numerous recommendations for research and conservation actions in the IWC's SC since 2010. These recommendations include the implementation of a Conservation Management Plan (CMP) for the population (e.g. IWC, 2016).

A key feature of humpback whale breeding behaviour is the male acoustic breeding display, a hierarchically structured song (Payne & McVay 1971), studied extensively around the world. Characteristics of humpback whale song include: all males within a population share the same song patterns (phrases); a population's song changes progressively over time with all individuals in a population incorporating changes; and populations that do not overlap or exchange individuals have distinctly different songs, whereas populations in contact share some or all phrases (Payne et al. 1983, Payne & Guinee 1983, Payne & Payne 1985, Cholewiak et al. 2013, Cholewiak and Cerchio 2022). This makes studies of geographic variation in song an ideal method to assess connectivity and interaction between populations on a broad scale, as has been used in all ocean basins globally (Winn et al. 1981, Payne & Guinee 1983, Noad et al. 2000, Cerchio et al 2001, Garland et al. 2011).

Cerchio et al. (2018) compared song samples collected through long-term acoustic monitoring off the coast of Oman from 2011-2013 with song samples collected in the Southwest Indian Ocean (SWIO) and off the west coast of India. There were four major findings of consequence from the results of this previous study:

(1) Assessment of an extensive sample revealed that songs recorded off Oman during the Boreal winter were distinctively different from songs recorded in the SWIO during the Austral winter, with no phrases shared between the regions. In contrast to this finding, a small sample of song fragments recorded in 2011 from India revealed only two phrase types, both of which matched phrases from Oman in the same year.
(2) Oman singers exhibited a globally unique temporal stasis in their songs over the three monitored years, displaying very little of the progressive change that is typical of all previously studied humpback whale populations.
(3) The presence of SWIO song was documented off Oman during August of 2012, indicating that SWIO males had travelled into the Arabian Sea during at least one month of their Austral winter breeding season.
(4) Despite the presence of SWIO singers in 2012 and the opportunity for exchange of song material, there was no diffusion of SWIO song into the Arabian Sea population's song.

These results support previous findings of both the isolation of ASHWs and potential continuity / connectivity across the Arabian Sea between Oman and India. Somewhat incongruent to this finding, the presence of SWIO whales off Oman indicates that there is an opportunity for cultural transmission and mixing of populations. It was proposed that behavioural isolation mechanisms may exist that maintain the isolation of the ASHW, as exhibited by the lack of song diffusion which might otherwise be expected (Noad et al. 2000, Garland et al. 2011) and relative temporal stasis of Arabian Sea song.

This study seeks to build on the findings from the 2011-2013 dataset to further assess the isolation and behaviour of humpback whales in the Arabian Sea using a larger dataset collected over a 10-year time frame. A series of song samples recorded off Oman between 2010 and 2020 were examined to assess whether the relative temporal stasis observed in 2011-2013 was maintained over a decade, or if there is any evidence of complete replacement of song phrases

suggesting song diffusion from another population (i.e., SWIO). In addition, the long-term series from Oman was compared to a much smaller sample of songs recorded off the west coast of India in the years 2011 and 2017, to assess similarities between songs recorded in the western and eastern Arabian Sea.

Methods

Sample - Oman

The sample of songs from the 2011/2012 and 2012/2013 breeding seasons was collected primarily from autonomous archival recorders that were deployed in Hallaniyats Bay and the Gulf of Masirah on stationary mounts at approximately 20 to 30 m depth (Cerchio et al. 2018). These acoustic data were recorded throughout the breeding season and provided relatively large samples of individual song sessions for each season. This also allowed selection of samples from the early (December to February) and late (Mar to May) periods of the seasons, to assess change in songs over the course of the breeding season. Additional acoustic data from autonomous archival recorders deployed in Hallaniyats Bay were also available for the late 2010/2011 and late 2019/2020 seasons and were used to supplement song samples from those seasons. The current study also includes song samples collected in 2010, 2011 and from 2014 to 2019 through opportunistic boat-based recordings in either Hallaniyats Bay or the Gulf of Masirah. These were collected by deploying a dipping hydrophone connected to a digital recorder (various models and combinations, all with sample rates of 44.1kHz, 48kHz or 96kHz). Due to the competing objectives (normally including photo-ID, biopsy, and satellite tagging) and relatively short duration (usually a maximum of three weeks in the boreal spring or autumn) of boat-based surveys, these opportunistic recordings were limited in their recording length, in the number of samples collected each season, and in the temporal period during which recordings were collected. Consequently, for these seasons there exist only a few useable samples occurring either in early season or late season. Despite yielding far fewer samples of humpback whale song compared to years with available archival recorder deployments, some boat-based recordings were made in close proximity to singing whales, and as such were useful for describing the qualitative structure of songs and occurrence of phrase-types during these seasons. Additionally, utilising these data revealed the consistent presence of singers throughout the decade and offered a basis for analysis of progressive temporal shifts in song characteristics.

A song sample was defined as a single song session, believed to be recorded from a single individual. Different song samples were not necessarily independent, as it is possible that the same individual was recorded multiple times within a year or across years, and this holds for both the boat-based and archival recordings. During the 2009/2010 season a few poor-quality boat-based recordings were collected, but these did not yield complete songs (representing all phrases for the year) or clear examples of any phrases suitable for spectrographic representation. Therefore, the 2009/2010 season is not included in most analyses, but rather only two phrases are included in the quantitative assessment of phrase durations. There were no samples collected during the 2018/2019 season, representing a one-year gap in the decade sequence. Sample size for the remaining years with only boat-based recordings ranged from 2 to 7 samples/year (Table 1). The duration of recordings in these years ranged from 62.5 min to 202.9 min, and mean duration of samples ranged from 31.2 min to 50.7 min (Table 1). When including the archival recorders, a total of 98 samples were reviewed, for 5,254 min of recording. In the following descriptions and figures a winter season (which straddles a pair of consecutive years) will be

referred to by the second year in the pair, (e.g., 2015/2016 → 2016) even if examined samples came entirely from the early season (e.g., November 2015).

Table 1. Summary of song samples used for qualitative assessment of song structure and phrase content of humpback whale songs recorded off Oman between the 2010/2011 and 2019/2020 breeding seasons.

Season	Sample Type	Samples	Min Date	Max Date	Mean Sample Dur. (min)	Total Rec (min)
2011	Boat-based Archival	7	3/18/2011	3/29/2011	31.8	222.8
2012	Archival	32	12/6/2011	5/1/2012	86.3	2761.2
2013	Archival	33	12/5/2012	5/23/2013	46.9	1546.1
2014	Boat-based	7	2/16/2014	2/28/2014	29.0	202.9
2015	Boat-based	6	2/26/2015	3/14/2015	25.0	150.1
2016	Boat-based	2	11/22/2015	11/23/2015	38.8	77.5
2017	Boat-based	2	3/28/2017	3/29/2017	50.7	101.5
2018	Boat-based	2	12/13/2017	3/9/2018	31.2	62.5
2019	No Samples	0	-	-	-	-
2020	Boat-based Archival	7	11/15/2019	5/14/2020	18.5	129.3
Total		**98**	**3/18/2011**	**5/14/2020**	**39.8**	**5253.9**

Sample – India

Three sets of recordings of humpback whale song recorded in the southeast Arabian Sea off the west coast of India during 2011 and 2017 were contributed for comparison to the Oman sample:

(1) Fragments of humpback whale song recorded by an autonomous ambient noise recorder situated off the southwestern coast of India near Cochin, Kerala were provided by G. Latha and M.M. Mahanty (Mahanty et al. 2015). These data consisted of ten 30-second samples recorded during January (n=3), February (n=6) and March (n=1) of 2011.

(2) Short samples of high signal-to-noise ratio (SNR) song recorded near Grande Island off the central western coast of India near Goa, using an autonomous archival recorder, were provided by S. Madhusudhana. The original sample was recorded during nine days in March 2017, during which song was recorded in 1-minute clips on a 15-min duty cycle on six days, as reported in (Madhusudhana et al. 2018); only exemplars of the eight phrase types defined in Madhusudhana et al. (2018) were provided for comparison, as opposed to the original 1-minute files with song.

(3) Lastly, two short samples of song (1m7s and 57s duration) recorded off the central western coast of India near Goa in March 2017 were provided by D. Sutaria and A. Patil. These recordings were extracted from video footage shot underwater during a scuba dive, associated with the dive operator DiveGoa (Patil and Sutaria, unpublished data).

Qualitative Assessment of Song Structure / Phrase Classification

Initial phrase classifications determined in Cerchio et al. (2018) from 2011, 2012 and 2013 song samples were used as a basis on which to classify and numerically label different phrase-types across the 10 years, according to general guidelines presented in Cholewiak et al. (2013). In all cases, the transition from one phrase-type to another was unambiguous based upon markedly distinct arrangements of different units. Distinct phase-types were initially numbered based upon their order of presentation in the song, which remained invariant for all song sessions across the 10 years. In cases where there was minor variation, comprising a change in unit-type within the same general phrase-type, and that variation was consistent across a sequence of several phrases, a phrase variant was alphabetically labelled (e.g., Phrase 1a and 1b), as described in Darling et al. (2019). Linking of same phrase lineages across seasons was based both on similarity of phrase-type structure and presentation order in the song. When two different variants were present during the same season, they were given different alphabetic labels; however, in cases where phrases changed across years but were not accompanied by concurrently occurring different variants, the phrase variant label from the previous season was maintained. These across-year changes were considered progressive cultural evolution within the same lineage, not the introduction of a new phrase variant that created a new lineage through lineage splitting. The absence of samples from 2019 presented some challenges to the analysis and interpretation of temporal change across the decade. This is in part due to the apparent presence of substantial change either prior to or during the 2020 season, as will be described. Therefore we address the period from 2011 to 2018 separately from the 2020 season.

The samples from India were examined after all phrase types and lineages were defined for the 10-year period off Oman. Phrases were diagnosed in the India recordings based on both the signals present in the India recordings (which was limited in all cases by recording duration, quality and/or SNR), and comparison to exemplar phrases from Oman in the years of the India recordings (2011 and 2017) as well as adjacent years. In this manner the similarity of phrases between the two regions was qualitatively assessed, more specifically to identify the presence of phrase types in India that were previously defined in Oman from any year, or alternatively define potentially novel phrases in the India sample that were not in the Oman sample.

Quantitative Assessment of Phrase Representation and Duration

To provide a quantitative measure of song content and change across years, proportional phrase representation and phrase durations were measured. Proportional representation of each phrase type within the song was measured by counting the number of each phrase in the entire sample for a year, and representing this as a proportion of the total number of phrases (i.e., the sum of all phrase counts for the entire year). Ideally this would have been done for each individual singer or session separately, and then averaged across all individuals for a year; however, our samples for many sessions were too small to assure representative sampling of each individual singer, and thus summing across all samples likely provided a better assessment of proportional representation for each phrase in the population. Phrase duration was measured on spectrographs for each phrase from the start of the phrase to the start of the next. Mean duration was then calculated across all phrases in each year for each phrase type, combining variants of the same phrase-type to reduce complexity. These quantitative measures were only conducted on the Oman sample, as the India sample was not large enough to provide meaningful results.

Results

Song changes from 2011 through 2018 off Oman

Seven different phrase-types were classified during the 2011 to 2018 seasons off Oman (Figure 1, Appendix 1). Two phrase-types were classified into 3 variants each (Phrase 1a, 1b, and 1c; Phrase 6a, 6b, and 6c), three were classified into 2 variants each (Phrase 2a and 2b; Phrase 3a and 3b; Phrase 5a and 5b) and two had no variants (Phrase 4; Phrase 7), resulting in 14 different phrase lineages. Eight phrase lineages were documented to go extinct at some point during the 8 years (Phrases 1b, 2a, 2b, 3a, 4, 5a, 5b, and 6a), as indicated by disappearance from the song in a given year and not being present thereafter in subsequent years; three entire phrase-types with all variants went extinct (Phrase 2 by 2018; Phrase 4 by 2012; Phrase 5 by 2015). In six cases there was an apparent split in a lineage resulting in a new variant, sung concurrently in the season with its "parent" phrase, and maintained in subsequent years as a separate new lineage (Phrase 1b from 1a in 2012; Phrase 1c from 1a in 2015; Phrase 2b from 2a in 2013; Phrase 3b from 3a in 2014; Phrase 6b from 6a in 2012; Phrase 6c from 6b in 2018). In only one case was a novel phrase introduced that had no unambiguous similarity or connection to an existing phrase-type that would infer a lineage split (Phrase 7 in 2017). Changes in the song attributed to lineage extinction, lineage splitting, and introduction of novel phrase-type were evenly spread throughout the 8-year period, with never more than 2 extinction or splitting events in a single year, and no year or series of years indicating dramatic change (Table 2).

In most phrase lineages and pairs of consecutive years, the progressive change observed across the 8-year period was very gradual, with a few exceptions of more substantial change based on a subjective consideration of relative differences across years. Phrase-type 1 illustrates a good example of both gradual change and substantial change between pairs of years, as well as lineage extinction and splitting (presented in Figure 1; see Appendix 1 for similar illustrations of change of all other phrase types). In the small sample from 2011, only one variant was present (Phrase 1a). In 2012, there were two distinct variants, Phrases 1a and 1b, which always were sung with several repetitions of 1a before switching to several phrases of 1b; thus, representing an apparent lineage splitting event between 2011 and 2012. A second apparent lineage split occurred in 2015, with the appearance of Phrase 1c. A lineage extinction event was observed during 2013, when Phrase 1b was present in early season, but not late season, and was absent by 2014 and thereafter. Across-year change in Phrase 1a was gradual from 2011 to 2014, a four-year span during which the phrase was virtually the same with only minor shifts in the frequency band and shapes of some units. Slightly more change was observed between 2014 and 2015 with the addition of a unit and slightly more shift in unit shapes, but still gradual compared to typical changes in other populations. Between 2015 and 2016 there was relatively more substantial change, in the number, frequency band, and shape of units. A similar degree of substantial change was observed between 2016 and 2017, and then there was a return to relatively gradual and minor change between 2017 and 2018. For all other phrase-types, change between 2011 and 2018 tended to be more gradual and minor (Appendix 1). It is important to recognize that in other populations of humpback whales, progressive change in phrase-types across years tends to be more dramatic. As an example, three years of progressive change off Kaua'i, Hawai'i (Figure 2), may be considered qualitatively similar to the 8 years of accumulated change observed in Phrase 1a off Oman (Figure 1).

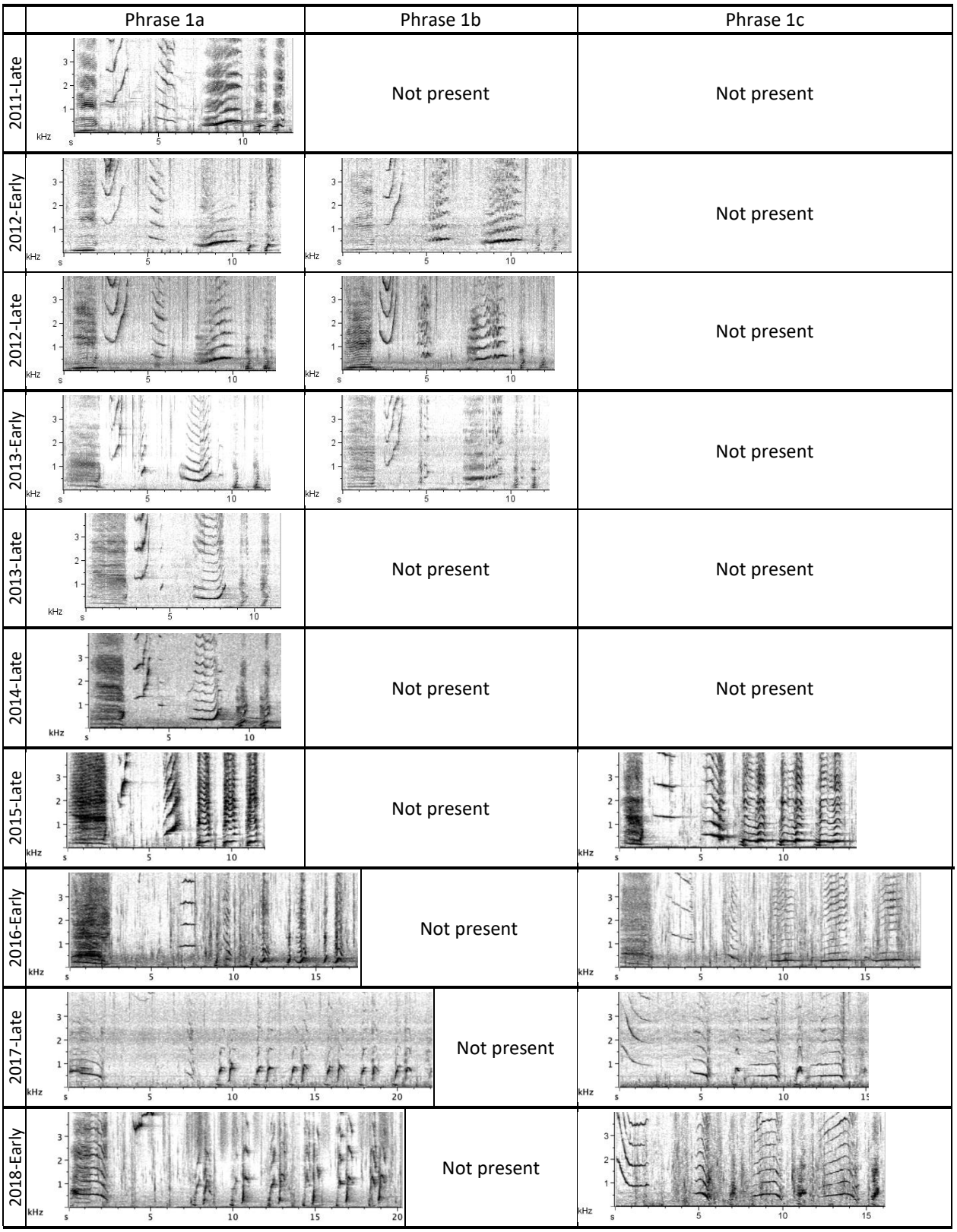


Figure 1. Progression of changes in Phrase-type 1 from 2011 to 2018, illustrating examples of phrase lineage splitting (appearance of 1b in 2012, and 1c in 2015), lineage extinction (Phrase 1b by 2013), and progressive change across years (Phrase 1a from 2011 to 2018).

Table 2. Summary of changes in 2011 - 2020 song content attributed to extinction and splitting of phrase lineages, introduction of novel lineages, and a subjective determination of relative progressive change within a lineage. Displayed are the number of events since the previous year, and the lineages in which it occurred.

Year	Lineage Extinction	Lineage Split	Novel Lineage Introduction	Substantial Change within lineage	Total Change Events
2012	2 (Phrases 4, 5a)	2 (Phrases 1b, 6b)	0	0	4
2013	1 (Phrase 6a)	1 (Phrase 2b)	0	0	2
2014	2 (Phrases 1b, 2a)	1 (Phrase 3b)	0	1 (Phrase 6b)	3
2015	1 (Phrase 5b)	1 (Phrases 1c)	0	0	2
2016	0	0	0	1 (Phrase 1a)	1
2017	2 (Phrases 2b, 3a)	0	1 (Phrase 7)	2 (Phrases 1a, 1c)	5
2018	0	1 (Phrase 6c)	0	0	1
2019	?	?	?	?	?
2020	1 (Phrase 3b)	5 (Phrases 1d, 1e, 1f, 6d, 7b)	0	3 (Phrase Lineages 1, 6, 7)	9

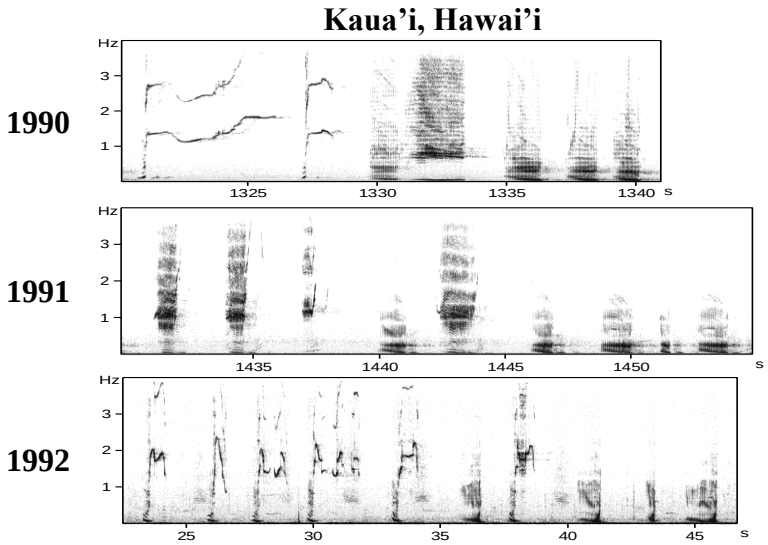


Figure 2. Qualitative example of typical progressive change in phrase structure of humpback whale song from other populations, as evident across three years in Hawai'i. The Hawaiian phrases were recorded off Kaua'i (Cerchio et al. 2001 and unpublished data; Phrase 3B), and verification of the three exemplar phrases for each year being from the same lineage (i.e., homologous) come from many intermediate versions of the phrase across the three-year period.

Song Changes in 2020

On first assessment of phrase content in 2020, there appeared to be a dramatic shift that could be interpreted as a diffusion event from another population (Figure 3). By late 2020, songs were entirely composed of five short phrase variants that are distinctly different from all phrases present in 2018. However, this assessment is complicated by the absence of any samples from 2019, and a relatively small sample in early 2020. On closer inspection and comparison of 2018 and early 2020 phrases, it is apparent that no novel phrase type lineages were introduced in 2020; conversely, the five different phrase variants that emerged are clearly derived from four parent phrase variants found in 2018 song (Phrases 1a, 1c, 7, and 6b). In all cases, a complex phrase made up of two subphrases was simplified by the dropping of one of the subphrases. To clearly understand this process requires the description of a more general framework for this particular type of change. A common phrase structure in humpback whale song globally is the combination a simple subphrase composed of a single motif (which we will label "A"), followed by a second subphrase that is composed of a motif (which we will label "B") that is repeated some number of times:

"A B B B"

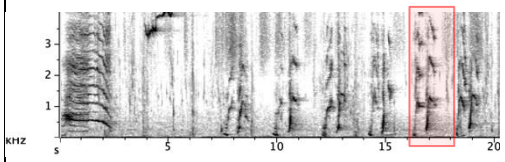
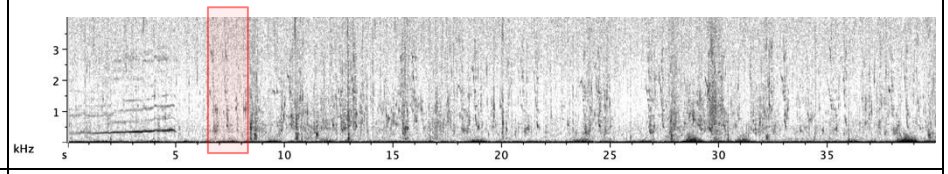
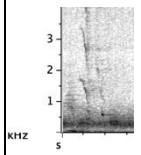
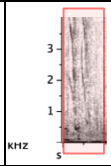
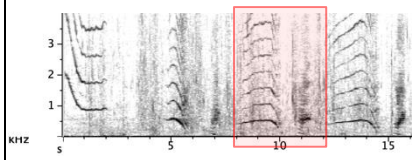
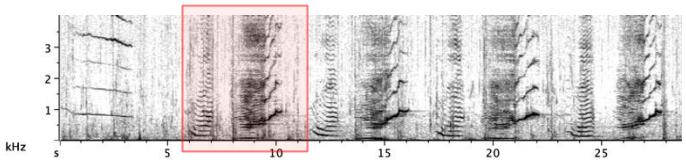
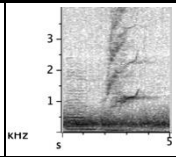
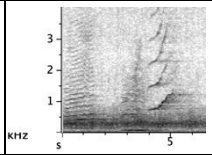
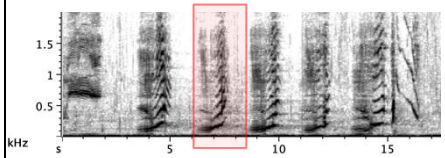
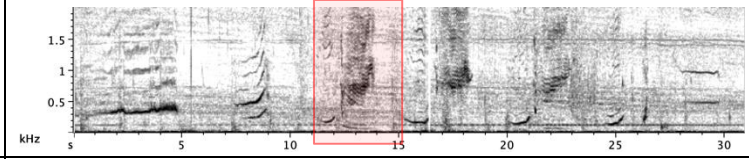
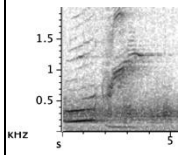
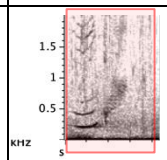
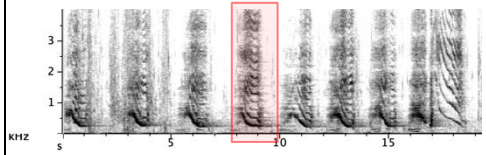
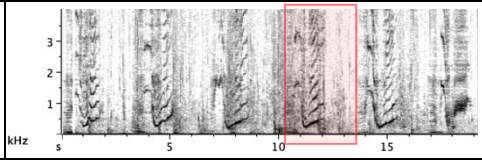
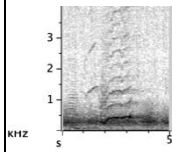
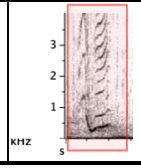
In the process that we observed, the phrase lengthened from one year to the next due to increases in the number of repetitions of B, and eventually the simple subphrase (A) was dropped so that the motif of the repetitive subphrase (B) became the entire phrase:

Year 1		**Year 2**		**Year 3**
"A B B B" - "A B B B"	→	"A B B B B B" - "A B B B B B"	→	"B" "B" "B" "B" "B"

This process is evident in the change between 2018 and 2020 in all phrase types that occurred in the song in 2020 (Figure 3), and has been observed in other populations (Payne & Payne 1985, Cerchio et al. 2001).

In early 2020, the three simple variants that were first observed were sung concurrently with their 2018 complex parent phrase (Phrase 1d from 1a; Phrase 7b from 7; Phrase 6d from 6b), and all three simple variants were maintained in the late 2020 season song. Phrase 1c was observed in early 2020 without a simplified variant; however, by late 2020, two variants appeared from 1c (Phrases 1e and 1f). This shift in composition was not entirely unpredictable; both phrase duration and complexity had been increasing over the decade (see below), and it appears this season was subject to a trend in simplification of those earlier, complex parent phrase variants. The shift to a short and simple phrase variant was consistent within each phrase lineage observed in 2020 and, therefore, indicates a song-change process phenomenon, rather than a cultural diffusion event (Figure 3). In addition to the described process that was observed within Oman samples, a separately conducted review of songs from the SWIO during 2019 and 2020 revealed no obvious similarities or shared phrases with the 2020 Oman song.

Figure 3 (next page). Progression of changes in complexity and duration in 2018 complex phrase variants that shifted to simple phrase variants in 2020. Red boxes show best representatives of sub-phrase lineage, starting with parent phrase variants in 2018 and marked in early 2020 phrase variants. Phrase variants labelled with italics indicate that variant's first observation. Note: Phrase 7a in 2020 is consistent with the phrase from 2018, and since an alternate variant was identified in the same year, the phrase in 2018 was modified as "7(a)" to maintain phrase lineage labelling. Spectrogram parameters: 2018: sample rate of 44.1kHz, FFT of 4096 pt; 2020: sample rate of 96kHz, FFT of 8192 pt, or sample rate of 44.1kHz, FFT of 4096 pt, or sample rate of 24kHz, FFT of 1024 pt; all spectrograms: 50% overlap, Hann window.

2018 Parent Phrase Variant		2020 - Early		2020 - Late	
1a		1a		1d	
		1d			
1c		1c		*1e*	
				1f	
6b		6b		6d	
		6d			
7(a)		7a		7b	
		7b			

Phrase Composition and Durations

Diversity of the major phrase-types appeared to gradually decrease over the decade, beginning with six observed phrase-types in 2011, then five phrase-types from 2012 to 2014, then four phrase-types from 2015 to 2018, and finally three phrase-types in the 2020 season (Figure 4). However, this is somewhat compensated by lineage splitting and consequent presence of different variants of the phrase-types, which amounted to 6 to 7 phrase-type variants for most of the period from 2011-2018, and an increase to 9 in 2020 (Figure 4). Despite any apparent changes in diversity, longevity of phrase-types ranged from 4 to 10 years, indicating substantial stability. Phrase-type 1 was present in every season, and was a dominant phrase is several years. Notably, the 2017 season marked the song with the least usage of any phrase-type 1. This could be explained by the small sample size from the season (n = 2) and consequent potential that these samples are not fully representative of the population trends; however, the same was true for both adjacent seasons (2016 and 2018). Given that phrase-type 1 represented 1/3 of each year's song composition from 2011 through 2015, it was markedly reduced between 2016 and 2018 when it represented less than 1/4 of the song each season. Phrase-type 6 was also observed in every season, and a steady increase in its proportional use in the song was observed from 2011 through 2017. Phrase-type 6 proportional representation then followed a decrease in the consecutive two seasons of the decade. Earlier seasons appear to have the most balanced song composition in terms of proportional phrase-type usage. While composition did shift from year to year, the majority of these shifts were by no means dramatic. Although, song observed in 2017 and 2020 are notable exceptions: phrases 6b and 3b dominated 2017 song composition and phrase-type 1 dominated 2020 song composition, both dissimilar to what was observed in the preceding seasons (Figure 4).

Considering phrase length, two phrase-types appeared to hold a fairly consistent duration when present in a season (Figure 5). Phrase-type 2 (between ~4 sec and ~6 sec) and phrase-type 5 (between ~10 sec and ~14 sec) maintained a relatively stable phrase length over 6 and 5 years, respectively; both of which were subjects of extinction events after 2016 and 2014, respectively. Phrase-types 1, 6, and 7 displayed similar trends in duration, involving a gradual increase across seasons, followed by a dramatic decrease in length. Each peaked in duration during 2018 at ~20 sec long, and then concurrent with the shift from complex to simple phrases in 2020, their phrase duration decreased during 2020 to less than 10 sec (Figure 5). Similarly, after several seasons of observed increase in phrase complexity, late 2020 phrases distinctly simplified in number of and repetitions of units within sub-phrases. For example, Phrase 1a in 2018 was about 20sec long and composed of ~14 units. In early 2020, Phrase 1a was consistent in following the decade's year-over-year trend of an increase in duration and complexity (up to >30sec and >30 units long), but Phrase 1d (~2sec and 2 units long) emerged as a simplified phrase variant from a modified sub-phrase in its 1a parent phrase variant.

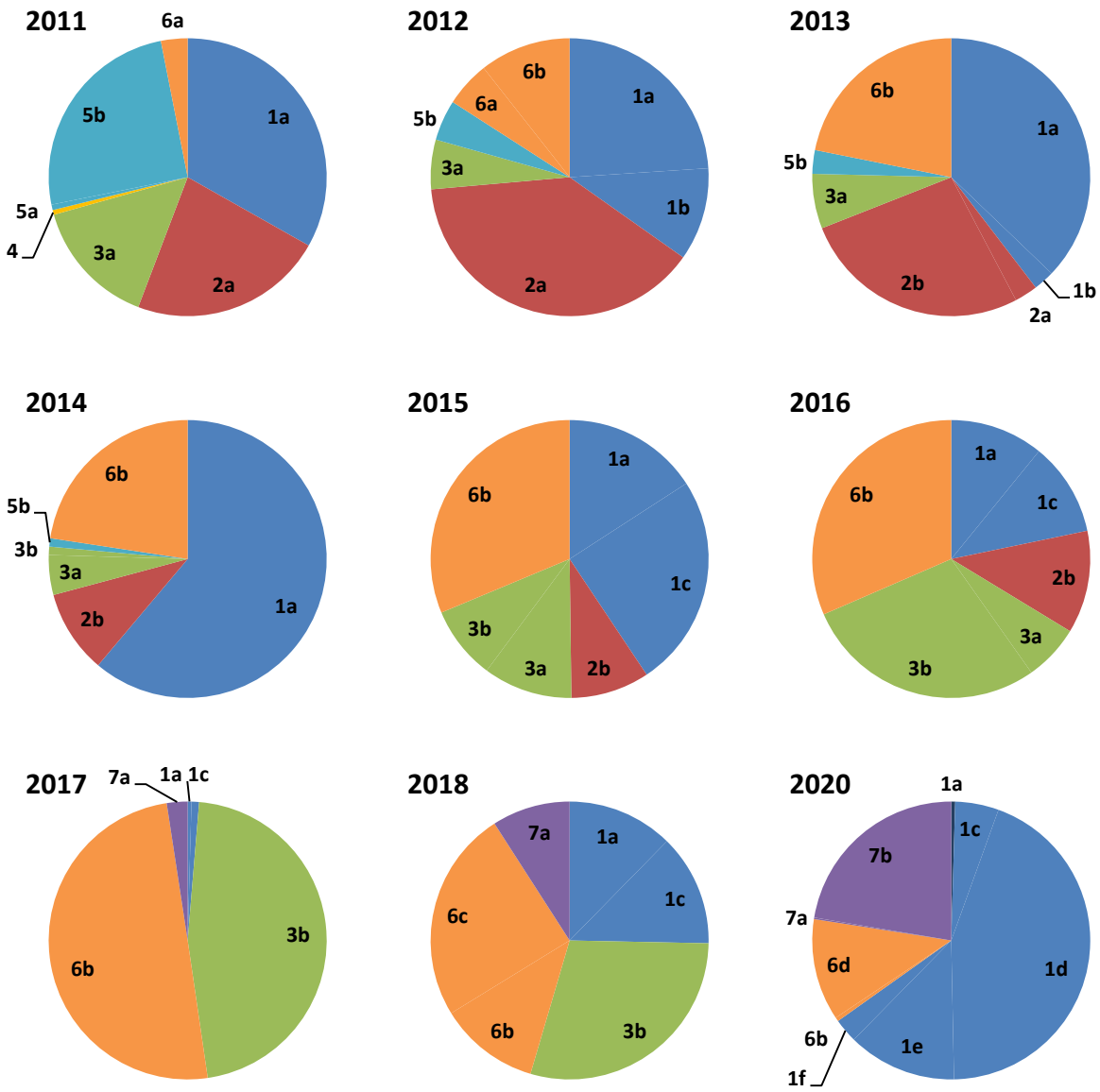


Figure 4. Pie charts illustrating proportional representation of phrase-types in the song for each year over the period 2011 to 2020 (with no data in 2019). Different phrase variants within each phrase-type are shown with the same color, with each phrase variant lineage labelled.

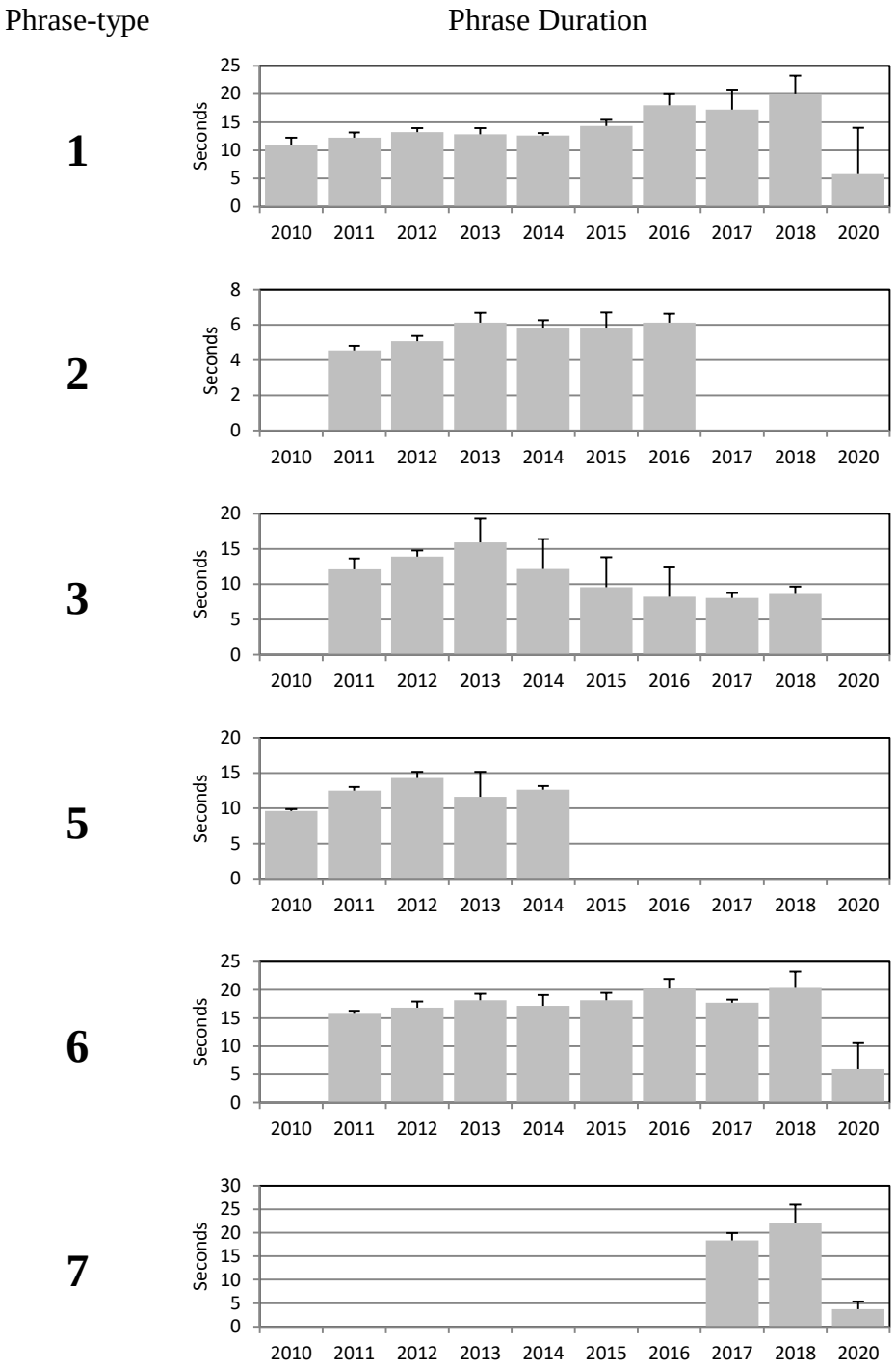
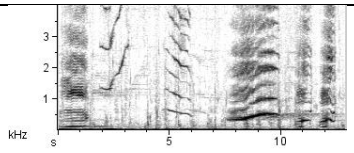
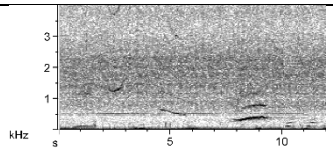
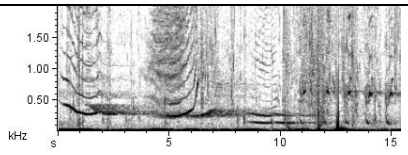
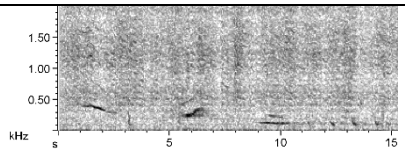


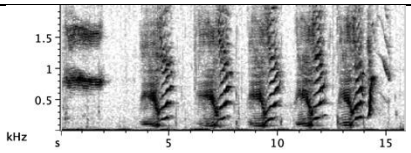
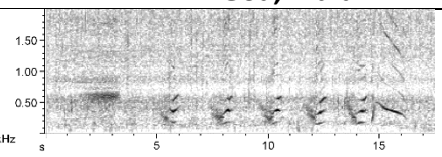
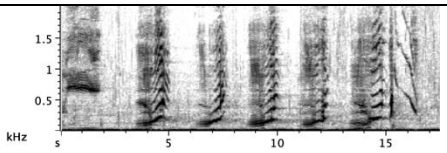
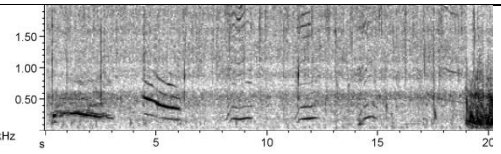
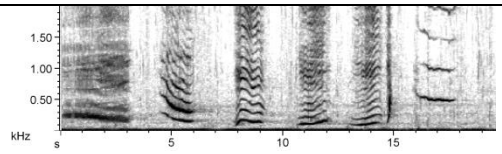
Figure 5. Mean duration of phrases (with standard deviation), averaged by year for 2010 to 2020, and displayed for each phrase-type with variants within phrase-types lumped. Blank years indicate no observation of that phrase-type was recorded, and therefore represent seasons when those lineages was either pre-introduction or post-extinction, or no samples provided examples of that phrase-type (certainly true for the small sample of 2010, when only 2 phrase-types were identified).

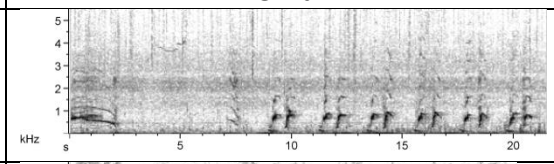
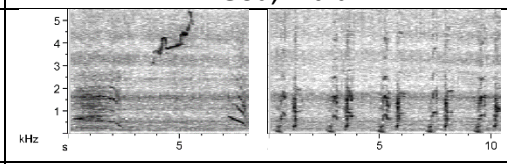
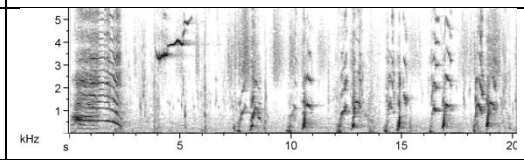
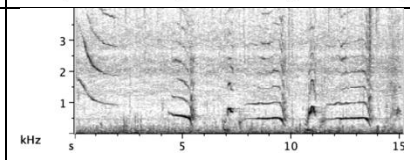
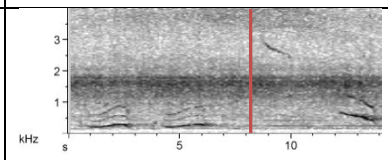
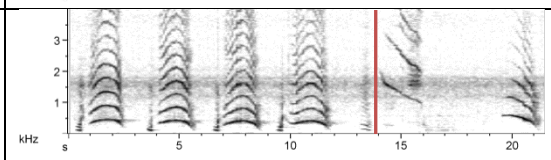
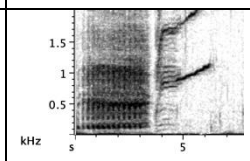
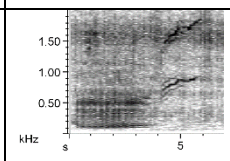
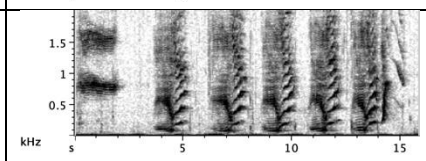
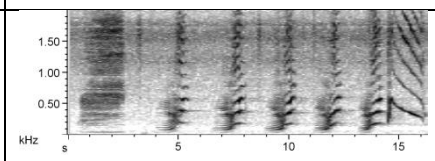
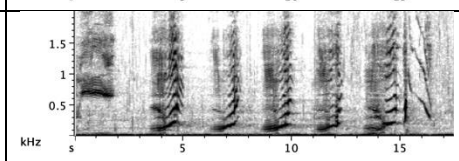
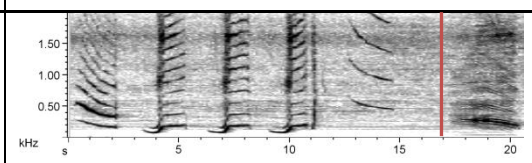
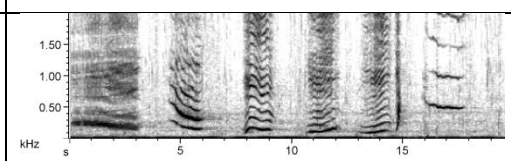
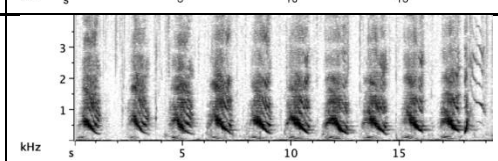
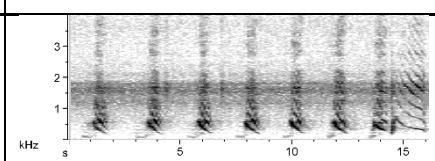
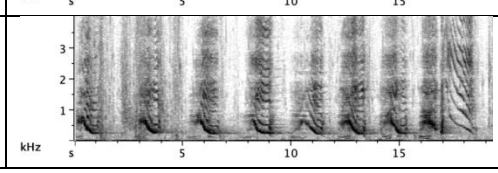
Comparison of Oman and India Phrases

In all samples from India, all defined phrases could be considered examples of phrase-types previously defined from the Oman sample (Figure 6). There were no apparent novel phrases recorded off India during the two years in which the samples were collected. In 2011, despite the very short duration and low SNR of the samples recorded off Kerala (Mahanty et al. 2015), two phrases could be defined that matched phrase-types 1a and 6a from Oman for the same year (Figure 6A). The two separate samples from March 2017 independently recorded off Goa had overlap in phrase content and both consisted of phrases defined in Oman during 2017 and 2018. It is conceivable that these Goa recordings were not independent and represent the same singer(s), as is also the case in the Oman samples; however, this is unavoidable in a small population, and whether from the same or different individual(s), the overlap in phrase content reinforce the similarities between the regions. The short sample recorded by Patil and Sutaria (unpublished data) contained two different phrases, phrase-types 6b and 6c (Figure 6B). The phrase exemplar clips provided by Madhusudhana et al. (2018) were examples of their definitions of nine phrase-types, labelled Theme I through Theme IX, which they defined from a series of 1-min samples recorded every 15 minutes and required reinterpretation in context of the phrase definitions we created for Oman. Since there is some subjectivity to phrase definitions, and their classifications were limited by the short duty-cycled samples and lack of entire songs, it is not unexpected that in some cases the same phrase may be divided differently, starting with a different unit, or lumped or split in different ways. We concluded that the nine themes presented in Madhusudhana et al. (2018) represented six different phrase-types from Oman song (Figure 6C): phrase-type 1a (Theme III and IX combined, and Theme VII as a slight variation on the second subphrase), phrase-type 1c (Theme II and Theme VIII, each starting at a different unit in the phrase, and respectively have two and four repetitions of the same unit in subphrase 2), phrase-type 3b (Theme IV), phrase-type 6b (Theme V), phrase-type 6c (Theme I, starting at a different unit in the phrase), and phrase-type 7 (Theme VI). An important observation when considering the Goa March 2017 samples, is the greater apparent similarity between many of the phrases with their counterparts in Oman song recorded in the next early 2018 season (November 2017) as compared to the concurrent late 2017 season (March 2017). For phrase-types 1a, 6b and 7, there is qualitatively greater similarity across seasons (with Oman early 2018), whereas for phrase-type 6c, the phrase was never recorded in the two samples from Oman in late 2017, but first seen in the early 2018 season (Figure 6C).

Figure 6 (next 2 pages). Comparison of phrases recorded in India with counterparts found in Oman song for: (A) Kerala, India, recorded by the National Institute of Ocean Technology, January to March 2011 (Mahanty et al. 2015); (B) Goa, India, extracted from underwater video collected by DiveGoa, March 2017 (Patil and Sutaria, unpublished data); and (C) Goa, India, recorded by the National Institute of Oceanography, March 2017 (Madhusudhana et al. 2018). In cases where the phase exemplar provided by Madhusudhana et al. (2018) starts with a different unit in the phrase, a red line represents where the Oman phrase definition commences (phrase-types 1c and 6c, in panel C), and thus the subphrases within the phrase are essentially reversed.

(A)		Oman	Kerala, India
1a	2011-Late		
6a	2011-Late		

(B)		Oman	Goa, India
6b	2017-Late		
	2018-Early		
6c	2017-Late	Not present	
	2018-Early		

(C)		Oman	Goa, India
1a	2017-Late		
	2018-Early		
1c	2017-Late		
			
3b	2017-Late		
6b	2017-Late		
	2018-Early		
6c	2017-Late	Not present	
	2018-Early		
7	2017-Late		
	2018-Early		

Discussion

Songs recorded from Arabian Sea humpback whales off Oman between 2011 and 2013 were previously found to be distinct from songs recorded in the Southwest Indian Ocean (SWIO), with no phrase-types shared between singers from the two distant regions (Cerchio et al. 2018). During that three-year period, Oman singers also displayed very little progressive change that is typical of all previously studied humpback whale populations. Importantly, the presence of SWIO song was documented off Oman during the Boreal summer of 2012, indicating that multiple SWIO males were present in the Arabian Sea during an at least 25-day period in the Austral winter breeding season; the presence of these singers presented the opportunity for exchange of song material from the SWIO, however there was a lack of diffusion of SWIO song into the Arabian Sea population's song during that three-year period. Without comparative recording effort during other Boreal summers off southern Oman, it is not possible to say whether this was a regular phenomenon during our decade study period, or a rare event that occurred in 2012.

The results of this qualitative analysis of an additional seven years of data, extending the monitoring period to ten years, 2011-2020, reinforced the findings of the initial three-year study. During the first eight years, the Oman song maintained a relatively slow and gradual change with only a few exceptions of substantive change within existing phrase lineages between consecutive years, and only one apparent introduction of a new phrase type. In the final two years of the monitored period, there was a dramatic shift in all phrases resulting in a very different song by the end of 2020; however, all of these changes were interpreted to result from rearrangement of phrase elements or motifs within the previously existing phrase lineages. There was no indication of large-scale introductions of new phrase-types, or replacement of old phrases with completely novel ones. In all but one instance, new phrases were described as variants of previous phrases, resulting from the splitting of existing lineages and formation of new variant lineages from an existing phrase-type. Therefore, there was no indication of the large-scale cultural diffusion events observed in Southern Hemisphere populations, in which the entire song is replaced by the song of immigrant whales when populations with different songs come into contact (Noad et al. 2000, Garland et al. 2011).

There was one example of an apparently novel phrase type being introduced during 2017 (Phrase 7, Appendix 1), that could not be confidently attributed to a lineage splitting event. It is conceivable that this did in fact split from Phrase 6a, as it shared some similarity and also immediately preceded Phrase 6a in the song; however, the similarities were not strong enough to unambiguously draw that conclusion, and the samples were too small (only 2 from 2016 and 2 from 2017) to track changes through the years. It is worth noting that between 2011 and 2018, the greatest number of changes documented for any year occurred in 2017 (Table 2), so it is possible that some stimulus was instigating more extensive change. It should also be noted, however, that the samples for the pair of consecutive years were recorded in the early 2016 season (November 2015) and late 2017 season (Mar 2017), so the differences between the samples essentially represent two seasons worth of accumulated changes.

Probably the most intriguing finding of this decade-long study is the dramatic change that occurred at the end of the period during 2020. These changes appeared to be entirely due to long-term processes in the gradual evolution in humpback whale song. Several studies in other ocean basins have found that progressive changes in song phrases result in a lengthening of phrase duration over time (Payne et al. 1983, Cerchio et al. 2001, Kowarski 2020). Phrase duration

cannot increase indefinitely, and therefore processes must exist by which humpback whale singers reduce length and complexity, or re-introduce simple short phrases. Both the extinction of long phrases, and the cleaving off of elements or motifs within long complex phrases to create new simple phrases, have been observed previously in the North Atlantic and North Pacific Oceans (Payne & Payne 1985, Cerchio et al. 2001). If our interpretation is accurate, it is this later process that occurred during 2020, and interestingly it was observed in all existing phrase lineages simultaneously. We are not aware of this specific phenomenon being previously documented elsewhere. Therefore, it appears that the isolation of the Arabian Sea population may present an opportunity to study the fine scale details of singing behaviour and the processes of gradual and progressive evolution within songs of humpback whales, without the confounding influence of new material introduced from other populations. The cultural diffusion that occurs across stocks in the large ocean basins of the Southern Hemisphere and North Pacific appears to obscure these processes due the apparent propensity for individuals in those populations to adopt the novel material that is introduced to them from migrant whales.

Similarities between song samples recorded off Oman and in the eastern Arabian Sea off the west coast of India are unambiguous, reinforcing the interaction between singers off Oman and India that was also reported in preliminary form in Cerchio et al. (2018). Connectivity between the western and eastern Arabian Sea has also been recently indicated by the documented movement of a satellite tagged whale (Willson et al. 2018), and an opportunistic photographic recapture of a highly distinctive male whale that was first observed in the Gulf of Masirah in Oman in October 2011, and again off the coast of India in December 2019 (Arabian Sea Whale Network, website: https://arabianseawhalenetwork.org/2020/01/16/new-evidence-for-movement-of-arabian-sea-humpback-whales-between-oman-and-india/). An intriguing aspect of the song similarity documented in our study, is an apparent greater similarity between the versions of phrases recorded off India in March 2017 with those recorded off Oman at the start of the following season in November 2017, than there was between the India phrase versions and those recorded concurrently off Oman in March 2017. This suggests that some of the changes observed off Oman during the 2018 season may have originated in the eastern Arabian Sea the previous year, and were transmitted by movements of animals to Oman. The observation is entirely qualitative, as the small samples involved (even for the Oman songs for which there were only 2 song sessions in each season) do not allow a quantitative evaluation of similarity. Therefore, any interpretations should be considered preliminary. Allowing this caveat, this trend could suggest some structure between potential subpopulations in the Arabian Sea, with a seasonal lag in the progress of a song change between Oman and India implying the movement of whales between seasons, as opposed to during seasons. It is noteworthy that the only whale satellite tagged off Oman that crossed the Arabian Sea was a female, traveling from Oman to India and back in the course of a 103-day period; conversely, all of 9 males tagged during the same effort remained off the Arabian Peninsula for the entire duration of the tags (Willson et al. 2018, Willson 2021). Since song is a male-mediated behaviour, this raises the possibility that, for at least males, mixing across the Arabian Sea may not be random, resulting in some population structure. Extending this supposition to consider impacts on demographic parameter estimation, such structure could in turn introduce heterogeneity of capture probability into abundance estimation models that use data from only Oman (i.e., introducing a negative bias in abundance estimates). As such, the findings of this study should serve as greater incentive to conduct vessel-based surveys and genetic sampling of live and beach-cast humpback whales in the areas off the coast of India where whales have been recorded, as photographic comparisons and genetic analysis

will provide further, and perhaps more definitive means of understanding the scope and scale of potential interactions and/or sub-structure between ASHW on the eastern and western sides of the Arabian Sea. Photographic recaptures will provide direct evidence and character of exchange and allow an estimation of exchange rate that is currently occurring, whereas genetic comparisons will provide an assessment of the long-term historic levels of exchange. In the meantime, in the absence of genetic samples or recapture data on individuals off India, detailed comparisons of songs could provide more clues to the level of connectivity between the regions, and the nature of exchange; for example, random and fluid as a single well-mixed population, versus partial mixing with cross seasonal exchange between semi-segregated subpopulations, as occurs in other ocean basins. New recording efforts conducted simultaneously off Oman and the west coast of India during 2021 to 2023 and beyond potentially represent the first collection of detailed song samples on both sides of the Arabian Sea during multiple concurrent years. Detailed comparison of these song samples in future analytical efforts will inform our understanding of connectivity of whales between these regions, as well as the long-term processes that guide change in humpback whale song.

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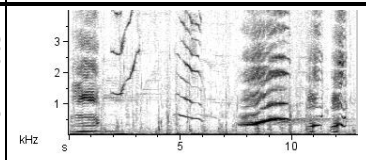
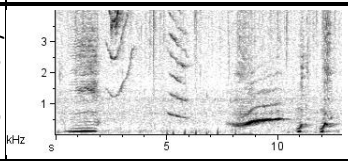
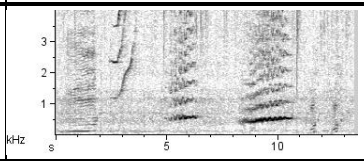
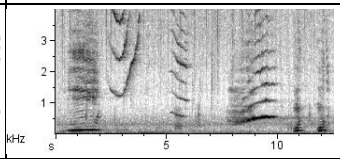
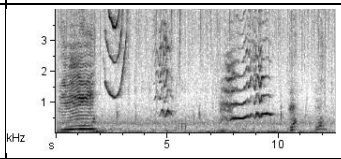
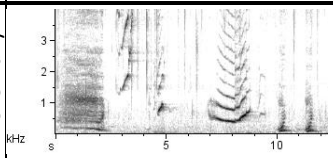
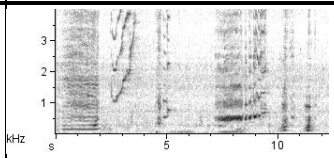
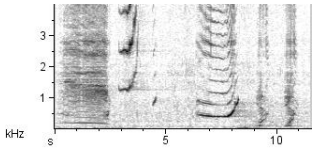
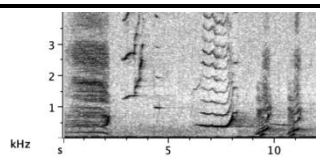
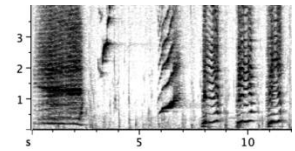
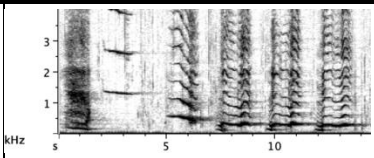
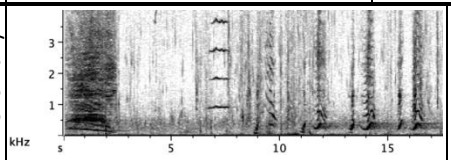
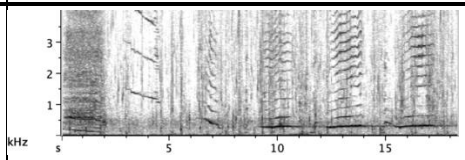
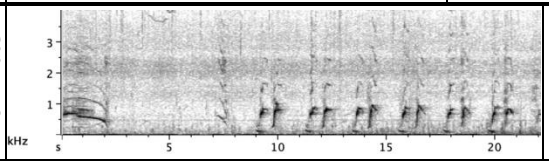
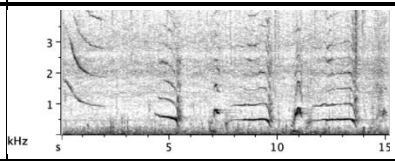
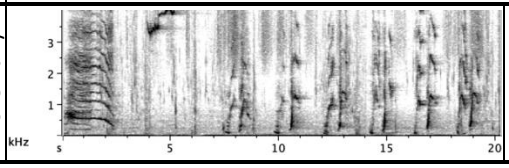
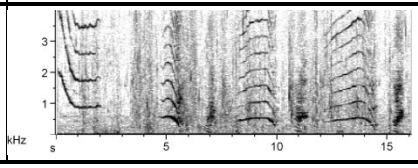
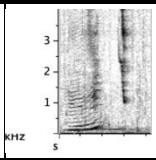
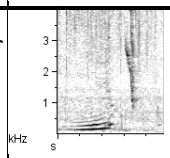
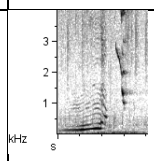
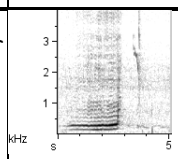
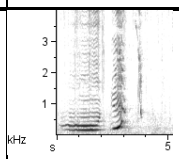
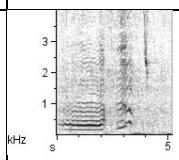
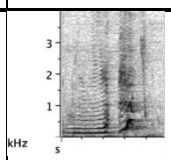
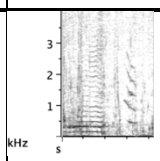
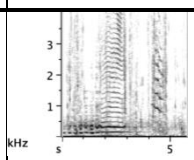
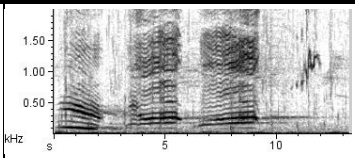
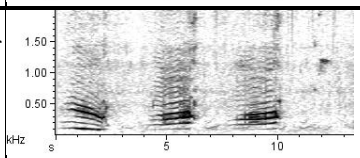
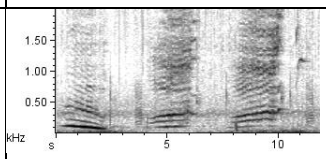
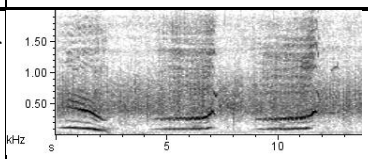
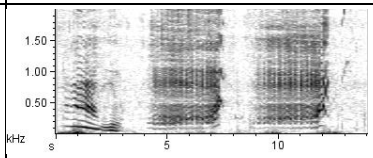
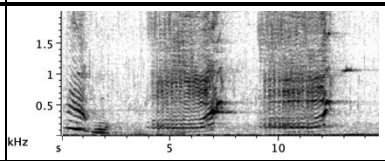
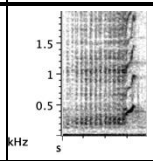
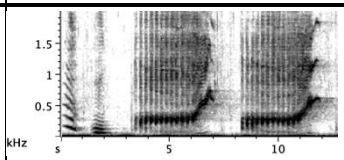
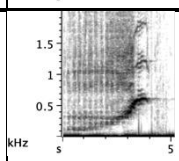
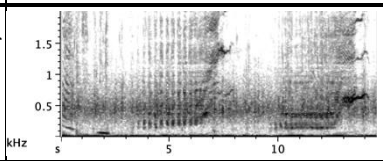
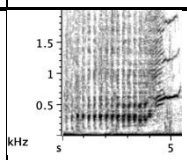
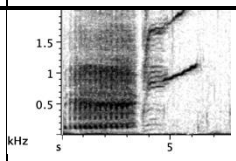
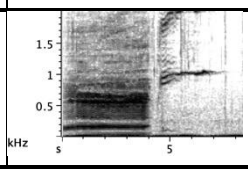
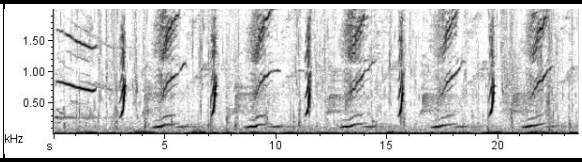
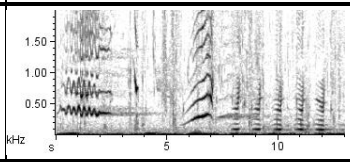
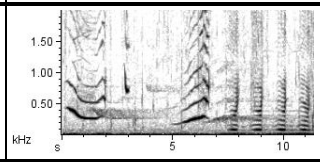
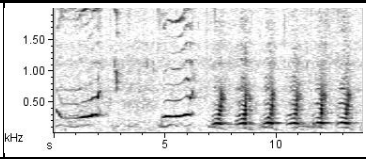
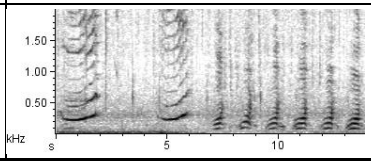
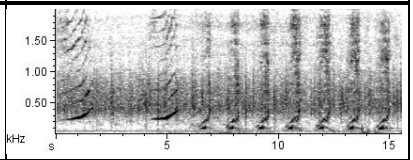
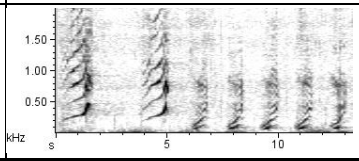
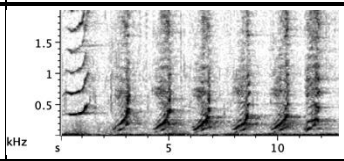
APPENDIX 1 – Exemplar phrases for all phrase lineages and years observed to be sung by humpback whales off Oman between 2011 and 2018. See Figure 3 for 2018 to 2020 changes.

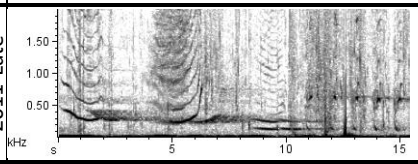
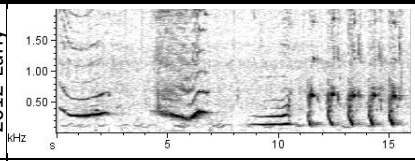
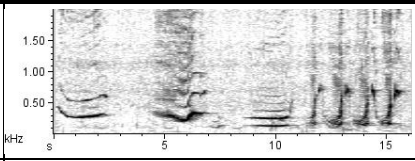
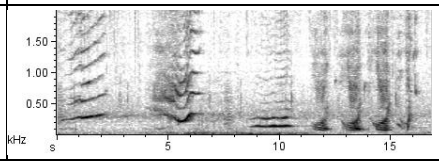
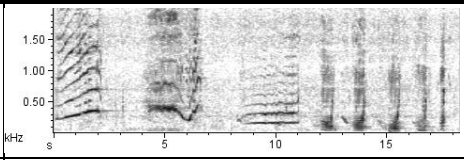
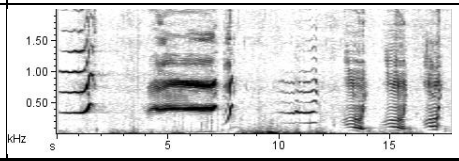
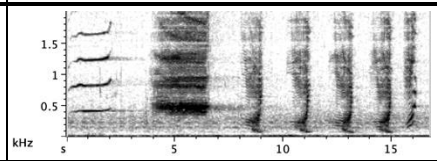
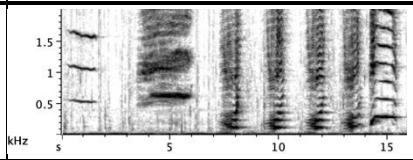
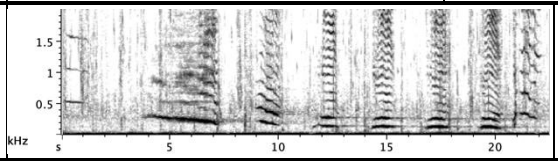
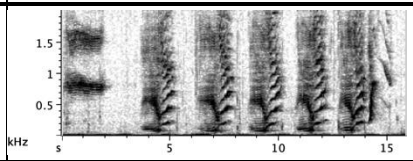
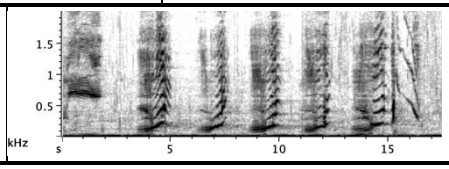
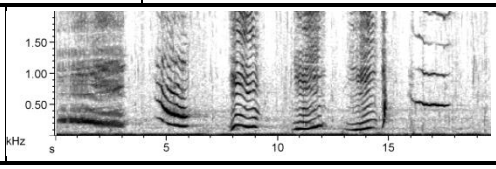
	Phrase 1a	Phrase 1b	Phrase 1c
2011-Late		Not present	Not present
2012-Early			Not present
2012-Late			Not present
2013-Early			Not present
2013-Late		Not present	Not present
2014-Late		Not present	Not present
2015-Late		Not present	
2016-Early		Not present	
2017-Late		Not present	
2018-Early		Not present	

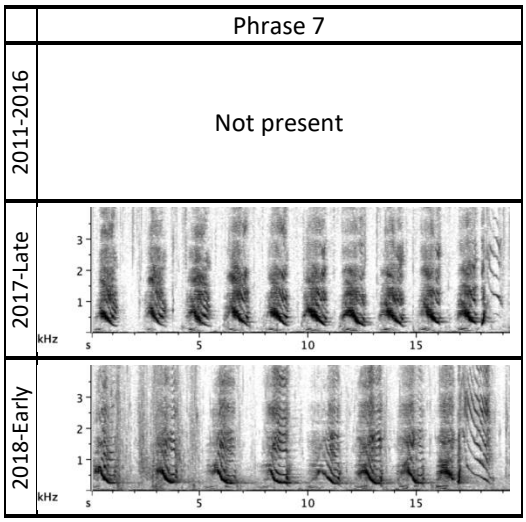
	Phrase 2a	Phrase 2b
2011-Late		Not present
2012-Early		Not present
2012-Late		Not present
2013-Early		
2013-Late	Not present	
2014-Late	Not present	
2015-Late	Not present	
2016-Early	Not present	
2017-2018	Not present	Not present

	Phrase 3a	Phrase 3b
2011-Late		Not present
2012-Early		Not present
2012-Late		Not present
2013-Early		Not present
2013-Late		Not present
2014-Late		
2015-Late		
2016-Early		
2017-Late	Not present	
2018-Early	Not present	

	Phrase 4
2011-Late	
2012-2018	Not present

	Phrase 5a	Phrase 5b
2011-Late		
2012-Early	Not present	
2012-Late	Not present	
2013-Early	Not present	
2013-Late	Not present	
2014-Late	Not present	
2015-2018	Not present	Not present

	Phrase 6a	Phrase 6b	Phrase 6c
2011-Late		Not present	Not present
2012-Early			Not present
2012-Late	Not present		Not present
2013-Early	Not present		Not present
2013-Late	Not present		Not present
2014-Late	Not present		Not present
2015-Late	Not present		Not present
2016-Early	Not present		Not present
2017-Late	Not present		Not present
2018-Early	Not present		



Spectrogram parameters: 2011, 2014 to 2018: sample rate of 44.1 or 48kHz, FFT of 4096 pt, 50% overlap, Hann window. 2012 and 2014: sample rate of 22kHz, FFT of 1024 pt, 50% overlap, Hann window.