Comparison of humpback whale (*Megaptera novaeangliae*) songs in the southern Indian Ocean indicates limited exchange between populations wintering off Madagascar and Western Australia.

ANITA MURRAY[1,2], SALVATORE CERCHIO[1], ROBERT MCCAULEY[3], CURT S. JENNER[4], YVETTE RAZAFINDRAKOTO[5], DOUGLAS COUGHRAN[6], SHANNON MCKAY[7], AND HOWARD ROSENBAUM[1]

[1]*Wildlife Conservation Society, Ocean Giants Program, 2300 Southern Blvd., Bronx, New York 10460, USA.*
[2]*Ecology, Evolution, and Environmental Biology, Columbia University 10 Floor Schermerhorn Ext. 1200 Amsterdam Avenue, New York, New York, 10027, USA.*
[3]*Centre for Marine Science and Technology, Curtin University GPO Box U 1987, Perth, Western Australia, 6847, Australia.*
[4]*Centre for Whale Research, PO Box 1622 Fremantle, Western Australia, 6959, Australia.*
[5]*Wildlife Conservation Society Madagascar Country Program, B.P. 8500, Antananarivo, Madagascar.*
[6]*Senior Wildlife Office, Marine Wildlife Operations, Department of Environmental and Conservation, Nature Protection Branch, Western Australia, Australia.*
[7] *Deakin University Whale Ecology Group, School of Life and Environmental Science PO Box 423, Warrnambool, Victoria, 3280, Australia.*

ABSTRACT

The definition of stock structure, as designated by the International Whaling Commission, is a critical matter in the conservation of Southern Hemisphere humpback whales (*Megaptera novaeangliae*). The difficulty lies in defining stocks in such a way that demographically isolated subpopulations are protected from extirpation. One methodology used to determine stock structure in the Northern Hemisphere is song comparisons between one or more breeding assemblages. Song comparisons are an indirect test of whether or not seasonally isolated breeding populations are interacting during the migratory cycle, thereby creating potential for genetic exchange. Song comparisons in the Northern Hemisphere show that whales within an ocean basin sing similar songs across different breeding areas as a result of cultural transmission, whereas geographically isolated populations in different ocean basins sing songs with very different content. Aural and visual analysis of song was used to determine similarity in song content between breeding populations along the coasts of Madagascar and Western Australia. Fifteen individuals were recorded in Madagascar from July-August 2006. Three individuals plus ~2 hours of data logger recordings (resulting from a sampling scheme of recording 6:48 minutes every fifteen minutes over a total of four hours) was gathered in Western Australia from September-October 2006. Madagascar and Western Australia song shared only one theme out of eleven, whereas each population had four and six private themes, respectively. The co-occurrence of one theme indicates that these stocks overlap at some point during the migratory cycle. However, compared to other intra-ocean song comparisons, these populations differ substantially in the amount of overlapping song content. Previous analysis of Western Australia song showed that this population is capable of under going rapid song transformations within one year, which may have caused the unusually low amount of song similarity with Madagascar. Alternatively, the lack of song similarity, beyond that of one common theme between Madagascar and Western Australia, maybe the result of a greater or equal amount of interaction between inter-ocean breeding stocks than there is between whales within the southern Indian Ocean. Evidence for inter-oceanic migration can be found in both the Madagascar and Western Australian breeding stocks.

INTRODUCTION

A central question in the conservation of Southern Hemisphere humpback whales (*Megaptera novaeangliae*) is the definition of stock structure as designated by the International Whaling Commission (IWC). Effective management of humpback whale populations requires stock definitions that minimize

the possibility of local extirpation of demographically isolated feeding or breeding assemblages by limiting stock definitions to a decadal time scale and regional, ecosystem-based spatial scale (Clapham et al., 2008). The difficulty lies in defining these management units, leading many authors to argue for a multidisciplinary approach that integrates information from acoustic, genetic, photographic, and telemetric studies to define stocks as well as clarify stock relationships and movements (Dizon et al 1992; Clapham et al., 2008). One methodology used to discern the population structure of Northern Hemisphere humpback whales is song comparisons of breeding groups (Winn et al., 1981, Payne and Guinee, 1983, and Cerchio et al., 2001). Song comparisons are an indirect test of whether or not breeding assemblages that appear to be seasonally isolated are in fact geographically overlapping during the migratory cycle. Such an overlap creates the potential for genetic exchange between stocks. In this way, song comparisons can illuminate more recent exchanges or movements between two breeding groups than what may be revealed in genetic analysis, and this information is potentially useful to management agencies (Hatch and Clark, 2004; McDonald et al., 2006).

Within a breeding area all male humpback whales sing a similar song characteristic to that particular breeding season (Winn and Winn, 1978). Humpback whale song progressively changes during the breeding season (Payne et al., 1983; Payne and Guinee, 1983; Payne and Payne, 1985, Cerchio et al, 2001, Erikson et al., 2005). At the same time males are constantly updating their song so that at any one time during a breeding season an individual's song more closely resembles the song of whales around him than his own songs from previous years or months (Guinee et al., 1983). Such a synchronous change in the song of all males has been cited as strong evidence that whales are learning the changes from one another through vocal learning and cultural transmission (Payne and Guinee, 1983, Payne and Payne, 1985, Noad et al., 2000). Song similarity amongst male humpback whales is maintained through vocal learning and cultural transmission between individuals that are in acoustic contact while geographically overlapping. It is this characteristic of humpback whale song that allows researchers to use song comparisons to indicate whether or not two breeding groups are interacting at some point during the migratory cycle.

In the Northern Hemisphere, intra-oceanic song comparisons have shown that whales within the same ocean basin sing similar songs across different breeding areas and undergo synchronous changes in song within a breeding season and over several years (Winn et al., 1981, Payne and Guinee, 1983, Cerchio et al., 2001). In contrast, inter-oceanic song comparisons have found that breeding assemblages from different ocean basins and/or different hemispheres are geographically isolated populations that sing songs with the same general structure but very different content (Winn et al., 1981, Payne and Guinee, 1983).

In this study, humpback whale songs recorded in the coastal waters of Madagascar and Western Australia were analyzed to determine if whales within the southern Indian Ocean interacted during the migratory cycle. Based on Northern Hemisphere intra-oceanic song comparisons we would expect to find that these two breeding stocks sing similar songs within a breeding season. Similarities in song content (e.g., whales from different sites share at least some phrase types) would indicate that Madagascar and Western Australia breeding stocks are interacting. Alternatively, if these two breeding stocks do not interact, and are completely isolated from one another, then within the breeding season songs recorded at these two sites will share no phrase types and have completely different content.

METHODS

Humpback whale song was recorded in the southern Indian Ocean at five sites during the 2006 winter breeding season. Song was collected at two research sites in Madagascar: Antongil Bay and Anakao from July to September. In Western Australia song was collected from three research sites: Perth, Exmouth Gulf, and Pender Bay from September to October (Figure 1). At all recording sites except for Exmouth

Gulf, focal animal recordings were collected using digital equipment and a sampling rate of 44.1 kHz. In Madagascar individuals were confirmed using photo-identification of individually unique pigmentation patterns found on the underside of flukes, and/or the shape and unique scarring pattern of dorsal fins (Katona et al., 1979). In Western Australia individuals were not confirmed using photo-identification, but because the recordings were greater than 24 hours apart and from different locations it was assumed that each recording represented different individual whales.

Exmouth Gulf data was collected using a datalogger, that consisted of a hydrophone deployed, and left unattended, at 9m to 15m of water for a total deployment time of 4hrs with a sampling regime of recording for 6:48 minutes every 15 minutes using a sampling rate of 12kHz with a high frequency cutoff at 3kHz. Due to the method of song collection the number of actual individuals recorded by the Exmouth Gulf datalogger during the four-hour deployment period is unknown. There was no sufficient way to determine the number of individuals from the recordings; therefore the best course of action was to treat the recordings as one 'individual'. This was preferable to dividing the datalogger recordings into several 'individuals', which would likely create non-independent samples if consecutive recordings were actually from one individual.

Qualitative Analysis of Song. Humpback whale song structure is a complex arrangement of sounds that are repeated in a cyclical pattern and can be categorized into an ascending hierarchical series of units, subphrases, phrases, and themes (Payne and McVay, 1971; Furmhoff, 1983; Payne et al., 1983). To determine the qualitative song structure, printed spectrograms for recordings from Madagascar, Perth, and Pender Bay were made using Avisoft Saslab Bioacoustic software (www.avisoft.com), with an analysis band range of 0-8,000 Hz (sampled at 16kHz) and FFT size of 512 points. The phrase types and the sequence of themes were identified by visual inspection of the printed spectrograms, and by aural inspection using Raven 1.2.1 Bioacoustic Software (Cornel Laboratory of Ornithology, Bioacoustic Research Program), except for the Exmouth Gulf recordings which, because of the sampling scheme used to create these recordings, were not printed out and were only visually and aurally inspected using Raven 1.2.1. Once the phrase types and theme sequence were identified, theme transition probabilities and theme proportions for each individual were calculated. As well, a cursory examination of printed spectrograms from seven Antongil Bay, Madagascar 2005 recordings were used to visually compare Theme B from Madagascar 2005 song, Madagascar 2006 song, and Western Australia 2006 song.

Quantitative Analsysis of Song. Quantitative measurements of Madagascar and Western Australia 2006 song structure were made using Raven 1.2.1 Bioacoustic Software (Cornell Laboratory of Ornithology, Bioacoustic Research Program). Measured variables were grouped into five categories: theme duration, number of phrases per theme, phrase duration, number of units per subphrase 1, and number of units per subphrase 2. Averages per individual for each variable were used as samples in all statistical analysis, and two-tailed Mann-Whitney U-tests with Bonferroni adjusted significance levels were used to compare song from Western Australia and Madagascar.

RESULTS

In Madagascar a total of 15 individuals were recorded generating 16 recordings for a total of 14.38hrs of recordings, 58 song cycles, and 37 song fragments for analysis (Table 1). Fourteen individuals were recorded in Antongil Bay and one was recorded in Anakao. In Western Australia a total of four individuals, including the Exmouth Gulf datalogger recordings as one individual, were recorded during the 2006 Western Australia breeding season, generating 22 recordings, 5.88hrs of recordings, 3 song cycles, and 29 song fragments for analysis (Table 1). One individual was recorded in Pender bay, two were recorded in Perth, and the fourth 'individual' was recorded in Exmouth Gulf.

In Antongil Bay, Madagascar one individual was recorded twice, with a week between recordings (e.g. individual AB04) (Table 1). There was no observable difference in the singer's recordings so the recordings were combined. There were four recordings with no accompanying photographs, three in Antongil Bay and the Anakao recording. Because of its location, it is highly unlikely that the Anakao recording is an individual also recorded in Antongil Bay, and therefore the potential bias that can result from unknowingly recording an individual twice is most likely not an issue with regards to this recording. Three unidentified singers from Antongil Bay could potentially be re-sampled individuals. The probability of re-recording identified individuals was 0.09 (1 re-sampled individual out of eleven independent samples). Because the calculated probability of re-sampling individuals is low, and may be even lower due to differences in whale behavior, the unidentified singers were not viewed as a significant source of bias (Cerchio et al., 2001).

Madagascar 2006 Song. The Madagascar 2006 song consisted of five themes (A, B, C, D, and E), each with its associated phrase type (A, B, C, D, and E), three phrase type variants in Phrase B (B1, B2, B3), and three transitional phrases (BA, CD, and DC) (Figure 2 and Figure 4). There are three types of themes found in humpback whale song: static, shifting, and unpatterned (Payne and Payne 1985). Themes A, C, D, and E were static themes, meaning the phrase structure remained constant with each repetition. Theme B was a shifting theme, meaning the units underwent a transformation with each successive phrase repetition. Between two themes there may be a transitional phrase that combines subphrases from the theme that precedes the transitional phrase with a subphrase from the theme that follows the transitional phrase (Payne and McVay 1971; Payne and Payne, 1985). In the Madagascar 2006 song transitional Phrase BA is a combination of subphrases from phrase types found in Themes A and B, with the first subphrase taken from Phrase B1 and the second subphrase from Phrase A. The transitional Phrase CD consisted of the first subphrase from Phrase C, and the second subphrase from Phrase D. Transitional Phrase DC is the opposite combination, with the first subphrase coming from the Phrase D and the second subphrase from Phrase C.

The typical theme sequence for the Madagascar 2006 song was A-E-C-D-B, however there were some slight deviations from this sequence through the use of transitional phrases (Figure 5). Madagascar average theme durations ranged from 60 to 245 seconds and had between two to eleven repetitions of phrase types per theme. Phrase durations averaged between 18 to 25 seconds and had between three to seventeen units per phrase divided between two subphrases (Table 2). Not all the themes were equally represented in the Madagascar song. There were dominant themes that were sung for >20% of the song, and there were minor themes that were sung for <20% of the song. The dominant themes were Theme D, Theme B, and Theme A, and were sung sequentially, where as the minor themes were Themes E and C, which were also sung sequentially (Figure 6).

Western Australia 2006 Song. The Western Australia 2006 song consisted of seven themes (B, BF, F, G, H, I, and J), each with its associated phrase type (B, BF, F, G, H, I, and J), and five phrase type variants; three in Phrase B (B1, B2, B3) and two in Phrase G (G1, G2) (Figures 3-4). The themes were labeled to reflect any overlap with the Madagascar 2006 song. The theme found in both regions (Theme B) retained the name used in the Madagascar analysis. Themes unique to Western Australia were given names sequential to the last theme identified in the Madagascar song (Themes BF, F, G, H, I, and J). Themes B and G were shifting themes, and Themes F, BF, H, I, and J were static themes.

The typical theme sequence for the Western Australia 2006 song was B-G-H-I-J, however there were some slight deviations from this sequence with some individuals transitioning from Theme B to Theme BF or Theme F rather than Theme G (Figure 5). Western Australia average theme durations ranged from 37 to 257 seconds and had between two to eleven repetitions of phrase types per theme. Phrase durations averaged between 14 to 22 seconds and had between three to eleven units per phrase divide between two subphrases (Table 2). Not all themes were equally represented in the Western Australia song. There were

dominant themes that were sung for >20% of the song, and there were minor themes that are sung for <20% of the song. In the Western Australia song the dominant and minor themes alternated. The dominant themes were Theme B, Theme G, and J. The minor themes were Theme BF, Theme F, Theme H, and Theme I (Figure 6).

Theme BF is a combination of Western Australia Theme B and Theme F. Theme BF consisted of 2 or more repetitions of Phrase BF, therefore it was considered a combination theme rather than a transitional phrase. Transitional phrases are only sung once between the two themes whose subphrases are combined to make the transitional phrase.

Themes B, G, H, I, and J were found in all recordings. Theme F was found in Pender Bay and the Exmouth Gulf recordings, and Theme BF was found only in the Exmouth Gulf recordings. Treating the Exmouth Gulf datalogger recordings as one 'individual' recording, means that most likely data from possibly more than one singer was pooled; thereby increasing the possibility that song characteristics due to several individuals is attributed to one singer. This becomes an issue when song characteristics, such as Theme BF, are only found in Exmouth Gulf. There is no way to resolve whether or not Theme BF is due to one individual, and is therefore an individual song characteristic, or whether it is due to several individuals and is therefore a population characteristic. For the themes recorded in two or more research sites (Themes B, F, G, H, I, and J) combining the Exmouth Gulf datalogger recordings does not pose such a problem because it is clear that these themes are a population characteristic as they are found in other Western Australia regions beyond Exmouth Gulf.

Theme B. Theme B was the only theme found in both Western Australia and Madagascar during the 2006 breeding season. Theme B from the Madagascar 2006 song and Theme B from the Western Australia 2006 song are considered the same theme, because they are both shifting themes with phrases that undergo a similar transformation in units, although with small-scale exceptions to their overall similarity (Figure 4). The two themes had similar acoustical characteristics placed in the same positions in the three phrase type variants that comprise Theme B.

In Madagascar, Theme B was a shifting theme comprised of three phrase type variants: Phrases B1, B2, and B3 that reflect three stages of unit transformation within Theme B. In subphrase one a single broadband unit is typically repeated 3 times in Phrase B1 before gradually merging to form one broadband unit in Phrase B2, which is then transformed into a narrowband unit in Phrase B3. In subphrase two there are typically two high frequency ascending units in Phrase B1, that progressively curve over during Phrase B2 to become a series of 4 units in Phrase B3.

Theme B was also a shifting theme in Western Australia comprised of three phrase type variants: Phrases B1, B2, and B3 that reflect three stages of unit transformation within Theme B. In subphrase one a single ascending unit was typically repeated 6 times in Phrase B1 before gradually merging to form one narrowband unit in Phrase B2 and Phrase B3. In subphrase two there are typically two high frequency ascending units in Phrase B1 that progressively curve over during Phrase B2 to become a series of 4 ascending then descending units.

The theme transition probabilities for the common Theme B differed between the two regions. In Madagascar song Theme B had only one possible transition to Theme A, but in the Western Australia song Theme B had three transition possibilities, to BF, to F, and to G (Figure 5). The relative representation of Theme B was slightly greater in Madagascar than Western Australia, but this was not a statistically significant difference (Figure 6) ($U=15.00$, Expected value=24.00, Variance (U)=67.50, $p=0.323$).

Quantitative differences in Theme B from Madagascar and Western Australia were only detected at the phrase and subphrase level. The duration for Phrases B1 and B2 were significantly longer in the Madagascar 2006 song than in the Western Australia 2006 song (Figure 7) (Phrase B1: U=52.00, Expected value=26.00, Variance (U)=77.90, $p< 0.0001$, and Phrase B2: U=52.00, Expected value=26.00, Variance (U)=78.00, $p< 0.0001$). There was no significant difference in Phrase B3 durations between the two regions. There were significant differences in the number of units per subphrase between Theme B phrase type variants from Madagascar and Western Australia (Figure 8). Phrase B1 had a significantly greater average number of units per subphrase one in Western Australia 2006 song than in the Madagascar 2006 song (U=0.00, Expected value=26.00, Variance (U)=77.81, $p<0.001$). The reverse was true for subphrase two of Phrase B1; the average number of units per subphrase two was significantly greater in the Madagascar 2006 song than the Western Australia 2006 song (U=49.50, Expected value=26.00, Variance (U)=76.95, $p<0.003$). For Phrase B2 the two regions only differed in the number of units per subphrase two, with Madagascar phrases containing a significantly greater average number of units per subphrase two than Western Australia phrases (U=51.50, Expected value=26.00, Variance (U)=77.90, $p<0.001$). There were no significant differences between the two regions in the number of units per subphrases for Phrase B3.

The relationship between Theme B from Madagascar and Western Australia was further complicated when a cursory comparison of spectrograms from seven recordings of Madagascar 2005 song were visually compared to 2006 song from both regions (Figure 4). All three songs (i.e. the Madagascar 2005 song, the Western Australia 2006 song, and the Madagascar 2006 song) had the same two units in the second subphrase of Phrase B1, and the same unit in the first subphrase of Phrases B2 and B3. The Madagascar song of 2005 had units in the second subphrase (for Phrases B2, and B3) that were of greater similarity to the units found in Western Australia 2006 song than those found in Madagascar 2006 song, based upon visual inspection. Finally, the first subphrase of Phase B1 from the Madagascar 2005 song had a single unit whereas the Western Australia 2006 song and the Madagascar 2006 song had a series of units that eventually merged into one unit over the duration of Theme B. This transformation of a series of units into one unit is lacking in the Madagascar 2005 song.

DISCUSSION

Based on the results of previous intra-ocean song comparisons one would expect to find a complete overlap in song content between Madagascar and Western Australia 2006 songs (i.e. song from both regions have all the same themes). Contrary to the expected, what this study found was that the two regions had only one theme in common. For the 2006 breeding season, Western Australia and Madagascar songs differed in the number of themes (and therefore phrases) and in thematic order. Western Australia song had a greater number of themes and phrase types than Madagascar song. Between Madagascar and Western Australia there were a total of eleven themes, and ten of these themes were unique to either region; Madagascar had four: A, E, C, and D and Western Australia had six: BF, F, G, H, I, and J. There was no overlap in content or structure for the phrase types found in these unique themes. According to the conclusions drawn from previous song comparison studies the song differences in Madagascar and Western Australia breeding stocks would imply that these two stocks have limited interaction and are predominantly isolated from one another throughout the migratory cycle. However, these two stocks did share at least one theme in common, indicating some connectivity. Despite a low level of song similarity, the existence of Theme B in both regions indicates that these two stocks are in acoustic contact with one another at some point in the migratory cycle.

Although Theme B was found in song from both regions, the relative representation of this theme was different in the Madagascar and Western Australia 2006 songs. Theme B was a dominant theme in both regions, but it was sung for a greater proportion in the Madagascar song than the Western Australia song (however this was not statistically significant). There was also a difference in transition probabilities for

Theme B between the two regions; Western Australia Theme B could transition to one of three other themes, where as, Theme B in the Madagascar song consistently transitioned to only one theme.

Theme B from the Madagascar 2006 song and Theme B from the Western Australia 2006 song are considered the same theme, because the two themes were shifting themes with phrases that went through a similar transformation in units. The themes had similar acoustical characteristics with units placed in the same positions in the three phrase type variants that comprise Theme B. However, there were some small-scale distinctions in Theme B between the regions. In the first subphrase, Madagascar began with a series of broadband units, where as Western Australia began with repetitions of an ascending unit, but in both regions these repeated units eventually merged into one narrowband unit. In the second subphrase both regions began with two ascending units that underwent a similar transformation. However, this transformation led to a divergence between the two regions in the type of unit found in subphrase two of Phrases B2 and B3. Quantitative differences in Theme B existed at the phrase and subphrase level between the two regions. Madagascar Phrases B1and B2 had longer phrase durations than Western Australia, and between the two regions there was a significant difference in the number of units used in subphrases one and/or two for Phrases B1 and B2.

Reviewing the Madagascar 2005 song revealed qualitative similarities in Theme B that extends over two years as well as some differences. All three songs (i.e. the Madagascar 2005 song, the Western Australia 2006 song, and the Madagascar 2006 song) had the same two units in the second subphrase of Phrase B1, and the same unit in the first subphrase of Phrases B2 and B3. The Madagascar 2005 song and the Western Australia 2006 song have similar units in the second subphrase for Phrases B2 and B3, which differ from the second subphrase units found in Phrases B2 and B3 from the Madagascar 2006 song. Finally, the first subphrase of Phrase B1 in the Madagascar 2005 song lacked the transformation of a series of units into one unit that was found in the Madagascar 2006 and Western Australia 2006 song.

The presence of Theme B in both the Madagascar and the Western Australia 2006 song, along with the similarity in unit transformation found within Theme B from both regions, can be taken as evidence of cultural exchange between these two breeding stocks. This type of cultural exchange can only occur when individuals from Madagascar and Western Australia are in acoustic contact and are therefore geographically overlapping. Additionally, from the evidence reviewed above, it appears that the Theme B found in Western Australia 2006 song was an intermediate version of the Theme B found in Madagascar 2005 and 2006 song. This maybe why small-scale distinctions in Theme B existed between the regions within the 2006 winter breeding season. The similarities in theme structure and the unit similarities found in Theme B from Madagascar 2005 and Western Australia 2006 songs, suggest that there was some level of interaction amongst the two breeding stocks between 2005 and 2006.

At what point along the migratory cycle do these two stocks interact cannot be answered by this song comparison, due to the limited temporal sampling. Whether this overlap occurs during the feeding season, on migration routes, or during the breeding season is unclear from these results. However, a genetic analysis of whales in Feeding Areas III and IV suggest that whales from Madagascar and Western Australia breeding stocks may be mixing on the feeding grounds (Loo et al, 2007). While the majority of singing occurs on breeding grounds, singing does occur during migration and on summer feeding grounds (Mattila et al., 1987; McSweeney et al., 1989; Clapham & Mattila, 1990; Cato, 1991; Clark and Clapham, 2004). Some number of whales from Madagascar and Western Australia maybe in acoustic contact during the feedings season and this maybe where cultural exchange in song content occurs. Alternatively, the similarity of Western Australia Theme B in 2006 with Madagascar Theme B in 2005, suggests that there may have been a longitudinal movement of some number of individuals from Madagascar to Western Australia between the 2005 and 2006 breeding seasons (breeding ground switching). A more detailed analysis of song from the two regions with larger samples and covering multiple years could reveal the likely path of exchange.

Interpretations and Implications of Limited Exchange. The songs from Madagascar and Western Australia 2006 breeding season had an unusually low level of overlap in song content than would be expected based on the results of previous intra-ocean song comparisons (Table 3). A majority of the song comparisons conducted to date have been in the Northern Hemisphere, and thus it is generally expected that breeding stocks within an ocean basin will almost completely overlap in song content. Based on the results of this study it appears that the generalities gathered from Northern Hemisphere song comparisons are not necessarily applicable to southern Indian Ocean breeding stocks. This deviation from other intra-ocean song comparisons is possibly due to an unusually rapid rate of temporal change in Western Australian song, or a greater amount of interactions between breeding stocks in *different* ocean basins in the Southern Hemisphere, which is not possible in the Northern Hemisphere.

Within the North Pacific all comparisons have shown that Mexico and Hawaii completely overlap in terms of theme and thematic order, and the songs in these two regions change in a similar manner (Winn et al., 1981; Payne and Guinee, 1983; Cerchio et al., 2001). Within the North or South Atlantic geographically separated breeding sites shared all the same themes sung in the same order, and the song changed overtime in a similar ways (Winn et al., 1981; Darling and Sousa-Lima, 2005). Finally, in the South Pacific there was some overlap in themes between breeding sites, but it was not as great as the overlap seen in the North Pacific and the North/South Atlantic (Gill et al., 1995; Helweg et al., 1998). Yet, all of these studies found a greater amount of overlap in song content than this study.

Why does the Indian Ocean differ from these other areas? Dawbin and Eyre (1991) tracked changes in theme composition within the Western Australian song over a span of 5 years, the 1986 and 1987 songs had only one theme in common, and the 1987 and 1988 songs had no overlapping themes. However, between 1988 and 1990 the songs had a complete overlap for all four themes. Thus, it appears that during some years the Western Australian song may undergo a year of rapid temporal change in song, and in other years exhibit a more progressive temporal change in song. These differential rates in song transformation maybe why a comparison between Madagascar and Western Australia only yielded one common theme. Only one breeding season was reviewed in this study, and the 2006 season could have been a year of rapid temporal changes in Western Australia song minimizing the overlap in song content between the two regions. A multiyear song comparison may find that there are years in which the two regions (Madagascar and Western Australia) share very little in terms of song content, compared to years when there is a greater overlap in song content between the two regions.

Alternatively, the lack of song similarity beyond Theme B between Madagascar and Western Australia, maybe the result of a greater or equal amount of interaction between inter-ocean breeding stocks than there is between whales within the southern Indian Ocean. Evidence for inter-oceanic migration can be found in both the Madagascar and Western Australian breeding stocks. Chittleborough (1965) found evidence for migration from the Pacific Ocean to the Indian Ocean when two whales, originally marked off the coast of Eastern Australia, were harvested off the coast of Western Australia. Noad et al. (2000) observation of a complete replacement of Eastern Australian song with Western Australian song in a span of two years also suggests an inter-oceanic migration of adult males from the Indian Ocean to the Pacific Ocean. An individual biopsied in Feeding Area III (believed to be the feeding area for Madagascar breeding stock) had a haplotype that was not detected in breeding groups from Gabon and Madagascar, but it was present in whales from the South Pacific breeding group (Rosenbaum et al., 2006; Loo et al., 2007; Olavarria et al, 2007). Pomilla and Rosenbaum (2005) using microsatellite genotyping of breeding sites in Madagascar and Gabon, discovered evidence of an inter-oceanic migration, of one male humpback whale, from the Indian Ocean to the Atlantic Ocean. More recently, Loo and Pomilla (*pers. comm.*) have found evidence of another adult male migration between these breeding areas. As well, a song comparison of breeding sites in Madagascar and Gabon, has found that in 2003 both regions shared

the same themes indicating that these two inter-oceanic breeding stocks are in acoustic contact at some point in the migratory cycle (Razafindrakoto et al, 2009).

Unlike the Northern Hemisphere there are no geographical barriers prohibiting inter-oceanic interaction of whales from different breeding stocks in the Southern Hemisphere. Whales from breeding sites on the coasts of Africa (i.e. Madagascar and Gabon) or whales from the Australian coasts (i.e. Eastern and Western Australia) maybe interacting with one another to a greater extent than whales from breeding sites within the Indian Ocean. However, further studies are necessary to confirm this supposition. Alternatively, it maybe that Southern Hemisphere breeding stocks are interacting with both inter- and intra-oceanic stocks to varying degrees, potentially creating years when inter-oceanic song comparisons would find a greater overlap in song content than intra-oceanic comparison, and vice versa.

In conclusion, it appears that whales from Madagascar and Western Australia geographically overlapped at some point between 2005 and 2006. The level of interaction between Madagascar and Western Australia, at least from this study, appears to be less than other ocean basins. Future studies will certainly clarify whether whales in the Indian Ocean are really more isolated from one another than what has been found for whales of other intra-ocean song comparisons, or whether this is just an artifact of a single year comparison. This study is the first indication that these two stocks have acoustic contact with one another, and is therefore an important contribution to our cumulative knowledge regarding the relationship between Southern Hemisphere breeding stocks. This study represents one step of many in understanding the interactions of whales within the southern Indian Ocean. However, what is becoming increasingly clear is that the relationship of whales in the Southern Hemisphere is most likely different from that of the Northern Hemisphere in terms of the interaction between intra- versus inter-ocean breeding stocks.

ACKNOWLEDGEMENTS

We are grateful to the Wildlife Conservation Society in New York, Wildlife Conservation Society Madagascar Country Program, Madagascar Masoala National Park, and the American Museum of Natural History for the institutional support provided in both the field and laboratory. We are also grateful to the Madagascar field crew, in particular Matt Leslie, Norbert Andrianarivelo, and the Malagasy mariners: Maro Jose, Raoul Jaozandry, Yves, Philbert, and Sandra Veloharisoe for their support during the Madagascar 2006 field season.

LITERATURE CITED

Cato, D. (1991) Songs of Humpback whales: the Australian perspective. *Memoirs of the Queensland Museum*, **30**(2):277-290.

Cerchio, S.; Jacobson, J. and Norris, T. (2001) Temporal and Geographical variation in songs of humpback whales, Megaptera novaeangliae: synchronous change in Hawaiian and Mexican breeding assemblages. *Animal Behaviour*, **62**:313-329.

Chittleborough, R.G. (1965) Dynamics of two populations of the humpback whale, Megaptera novaeangliae. *Australian Journal of Marine and Freshwater Research*, **16**(1):33 – 128.

Clapham, P. J.; Aguilar, A. and Hatch, L.T. (2008) Determining spatial and temporal scales for management: lessons from whaling. *Marine Mammal Science,* **24**:183-201.

Clapham, P.J. and Mattila, D.K. (1990) Humpback whale songs as indicators of migration routes. *Marine Mammal Science*, **6**:155-160.

Clark, C. W. and Clapham, P. J. (2004) Acoustic monitoring on a humpback whale (*Megaptera novaeangliae*) feeding ground shows continual singing into late spring. *Proc. of the Roy. Soc.: Biological Series,* **271**:1051–1057.

Darling, J. and Sousa-Lima, R. (2005) Songs indicate interaction between humpback whale (*Megaptera novaeangliae*) populations in western and eastern South Atlantic Ocean. *Marine Mammal Science,*

21:557-566.
Dawbin, W. H. and Eyre, E.J. (1991) Humpback whale songs along the coast of western Australia and some comparison with east coast songs. *Memoirs of the Queensland Museum*, **30**(2):255-257.
Dizon, A.E.,; Lockyer, C.; Perrin, W.F.; Douglas, P.D. and Sisson, J. (1992) Rethinking the stock concept: A phylogeographic approach. *Conservation Biology*, **6**(1):24-36.
Erikson, N.; Miller, L.; Tougaard, J. and Helweg, D. (2005) Cultural change in the songs of humpback whales (*Megaptera novaeangliae*) from Tonga. *Behaviour*, **142**:305-328.
Furmhoff, P. (1983) Aberrant songs of humpback whales (*Megaptera novaeangliae*): clues to the structure of humpback songs. In: *Communication and Behavior of Whales* edited by Payne, R. Boulder, CO: Westview Press. pp. 81-129.
Gill, P.C.; Eyre, E. J.; Garrigue, C.; and Dawbin, W. H. (1995) Observations of humpback whales (*Megaptera novaeangliae*) on a cruise to New Caledonia and the Chesterfield reefs. *Memoirs of the Queensland Museum*. **38(2)**:505-511.
Guinee, L. N.; K. Chu and E. M. Dorsey (1983) Changes over time in the songs of known individual humpback whales (*Megaptera novaeangliae*). In: *Communication and behavior of whales* edited by Payne, R. Boulder, CO: Westview Press. pp 59-80.
Hatch L.T. and Clark C.W. (2004) Acoustic differentiation between fin whales in both the North Atlantic and North Pacific Oceans, and integration with genetic estimates of divergence. *Report SC/56/SD6 presented to the IWC Scientific Committee.*
Helweg, D.; Cato, D.; Jenkins, P.; Garrigue, C. and McCauley, R. (1998) Geographic Variation in South Pacific Humpback Whale Songs. *Behaviour*, **135**:1-27.
Katona, S.; Baxter, B.; Brazier, O.; Kraus, S.; Perkins, J. and Whitehead, H (1979) Identification of humpback whales by fluke photography. In: *Behavior of marine animals*, *Vol 3* edited by Winn, H.E. and Olla, B.L. Plenum Press, New York, p 33-44
Loo, J.; Pomilla, C; Olavarria, C; Aguayo, A.; Thiele, D.; Baker, S.; Ensor, P. and Rosenbaum, H (2007) Genetic structure of feeding aggregations of humpback whales in the Southern Ocean. *Report SC/59/SH24 presented to the IWC Scientific Committee.*
Mattila, D.; Guinee, L. and Mayo, C. (1987) Humpback whale songs on a North Atlantic feeding ground. *Journal of Mammalogy*, **684**:880-883.
McSweeney, D.J.; Chu, K.C.; Dolphin, W.F. and Guinee, L.N. (1989) North Pacific humpback whale songs: a comparison of southeast Alaskan feeding ground songs with Hawaiian wintering ground songs. *Marine Mammal Science,* **5**:139-148.
McDonald, M. A.; Mesnick, S. L. and Hildebrand, J.A. (2006) Biogeographic characterization of blue whale song worldwide: using song to identify populations. *Journal of Cetacean Research and Management*. **8**:55-65.
Noad, M.; Cato, D.; Bryden, M.; Jenner, M. and Jenner, C. (2001) Cultural revolution in whale songs. *Nature,* **408**:537.
Olavarria, C.; Baker, C.S.; Garrigure, C.; Poole, M.; Hauser, N.; Caballero, S.; Florez-Gonzalez, L.; Brasseur, M.; Bannister, J.; Capella, J.; Clapham. P.; Dodemont, R.; Donoghue, M.; Jenner, C.; Jenner, M-N.; Moro, D.; Oremus, M.; Paton, D.; Rosenbaum, H. and Russell, K. (2007) Population structure of humpback whales throughout the South Pacific and the origins of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series*. **330**:257-268.
Payne and Guinee (1983) Humpback whale songs as an indicator of stocks. In: *Communication and Behavior of Whales* edited by Payne, R. Boulder, CO: Westview Press. pp. 333-358.
Payne and McVay (1971) Songs of Humpback Whales. *Science*, **173**:585-597.
Payne, K. and Payne, R. (1985) Large Scale Changes over 19 Years in Songs of Humpback Whales in Bermuda. *Z.Tierpsychology,* **68**:89-114.
Payne, K.; Tyack, P. and Payne, R. (1983) Progressive changes in the songs of humpbacks: a detailed analysis of two seasons in Hawaii. In: *Communication and Behavior of Whales* edited by Payne, R. Boulder, CO: Westview Press. pp. 9-57.
Pomilla, C. and Rosenbaum, H. (2005) Against the current: an inter-oceanic whale migration event.

Biology Letters, **1**:476–479.
Rayner, G. W. (1940) Whale marking: progress and results to December 1939. *Discovery Reports*. **19**:245-284.
Razafindrakoto, Y., Cerchio, S., Collins, T., Rosenbaum, H., Ngouessono, S. (2009) Similarity of humpback whale song from Madagascar and Gabon indicates significant contact between South Atlantic and southwest Indian Ocean populations. *Report SC/61/SH8 presented to the IWC Scientific Committee.*
Rosenbaum, H.C.; Pomilla, C.; Olavarría, C.; Baker, C.S.; Leslie, M.C.; Mendez, M.; Caballero, S.; Brassuer, M.; Bannister, J; Best, P.B.; Bonatto, S.; Collins, T.; Engel M.H.; Ersts, P.J.; Findlay, K.P.; Flórez-González, L.; Garrigue, C.; Hauser, N.; Jenner, C.; Meyer, M.; Minton, G.; Poole, M.; Razafindrakoto, Y. (2006). A first and preliminary analysis of mtDNA sequences from humpback whales for breeding stocks A-G and X. *Report SC/A06/HW59 presented to the IWC Scientific Committee.*
Winn, H.; Thompson, T.; Cummings, C.; Hain, J.; Hudnall, H.; Hays and Steiner, W. (1981) Song of Humpback whale population comparison. *Beh. Ecol. and Sociobiology*. **8**:41-46.
Winn and Winn (1978) The song of the humpback whale Megaptera novaeangliae in the West Indies. *Marine Biology*, **47**(2):97-114.

LOCATION	INDIVIDUAL	DATE	DURATION	SONG CYCLES	SONG FRAGMENTS
Antongil Bay	AB01	20-Jul-2006	1:31:00	16	3
Antongil Bay	AB02	21-Jul-2006	0:43:21	6	2
Antongil Bay	AB03	24-Jul-2006	1:06:00	5	4
Antongil Bay	AB04a	26-Jul-2006	1:05:00	3	2
Antongil Bay	AB04b	2-Aug-2006	2:08:00	5	4
Antongil Bay	AB05	23-Aug-2006	1:27:48	6	2
Antongil Bay	AB06	24-Aug-2010	0:25:13	2	2
Antongil Bay	AB07	26-Aug-2006	0:53:07	1	2
Antongil Bay	AB08	26-Aug-2006	0:47:57	2	2
Antongil Bay	AB09	27-Aug-2006	1:12:07	4	2
Antongil Bay	AB10	29-Aug-2006	0:42:24	2	2
Antongil Bay	AB11	29-Aug-2006	0:28:42	2	2
Antongil Bay	AB12	29-Aug-2006	0:12:28	1	2
Antongil Bay	AB13	1-Sep-2006	0:29:04	1	2
Antongil Bay	AB14	4-Sep-2006	0:25:09	1	2
Anakao	AN01	17-Sep-2006	0:46:00	1	2
Madagascar Totals		**13 Days**	**14:23:20**	**58**	**37**
Pender Bay	PB01	9-Sep-2006	0:55:00	2	2
Perth	PE01	17-Sep-2006	0:14:00	0	1
Perth	PE02	25-Sep-2006	0:28:00	1	1
Exmouth Bay	EXDatalogger	17-Oct-2006	2:16:20	0	25
Western Australia Totals		**4 Days**	**3:53:20**	**3**	**29**

Table 1. Madagascar and Western Australia Song Recordings: In Madagascar a total of fifteen individuals was recorded during the 2006 breeding season. Individual 4 was recorded twice; the two recordings are denoted as 4a and 4b. Fourteen individuals were recorded in Antongil Bay and one was recorded in Anakao. In Western Australia a total of four individuals, including the Exmouth Gulf datalogger recordings as one individual, were recorded during the 2006 breeding season. One individual was recorded in Pender bay, two were recorded in Perth, and the fourth 'individual' was recorded in Exmouth Gulf.

Location	Theme	Theme Duration (sec) (±S.D.)	Number of Phrases/Theme (±S.D.)	Phrase	Phrase Duration (sec) (±S.D.)	Subphrase 1: number of units (±S.D.)	Subphrase 2: number of units (±S.D.)
Madagascar	**A**	119.32 (±79.58)	4.89 (±3.20)	**A**	22.07 (±1.72)	4.41 (±1.60)	3
Madagascar				**BA**	20.19 (±2.11)	3.76 (±1.66)	3
Madagascar	**B**	215.94 (±94.40)	10.59 (±4.59)	**B1**	18.69 (±1.85)	3.09 (± 1.70)	2
Madagascar				**B2**	18.55 (±1.67)	1	2
Madagascar				**B3**	17.51 (±1.32)	1	4.37 (± 0.54)
Madagascar	**C**	60.39 (±29.53)	2.34 (±1.02)	**C**	23.14 (±2.47)	11.83 (± 2.49)	5.01 (± 0.56)
Madagascar				**CD**	23.32 (±2.45)	10.08 (± 2.54)	4
Madagascar				**DC**	22.31 (±1.40)	6.10 (± 1.00)	5.00 (± 0.47)
Madagascar	**D**	244.59 (±208.67)	9.38 (±7.72)	**D**	23.76 (±2.45)	4.28 (±1.16)	4.00 (± 0.17)
Madagascar	**E**	61.41 (±38.67)	2.34 (±1.52)	**E**	24.66 (±3.92)	2.92 (±0.47)	10.09 (±2.95)
Western Australia	**B**	137.74 (±55.18)	7.00 (±2.70)	**B1**	14.40 (±1.66)	6.72 (±1.95)	2
Western Australia				**B2**	15.14 (±1.23)	1	2
Western Australia				**B3**	15.64 (±1.87)	1	4.39 (±1.55)
Western Australia	**BF**	36.87 (±17.85)	2.2 (±0.97)	**BF**	16.18 (±1.40)	3.39 (±0.73)	3.09 (±1.23)
Western Australia	**F**	65.11 (±23.41)	3.67 (±1.49)	**F**	15.47 (±1.40)	3.02 (±0.15)	5.35 (±1.87)
Western Australia	**G**	182.17 (±62.59)	9.67 (±3.43)	**G1**	13.90 (±2.29)	1	3.33 (±0.95)
Western Australia				**G2**	16.54 (±1.11)	1	4.99 (±0.55)
Western Australia	**H**	179.55 (±83.41)	6.71 (±2.39)	**H**	19.76 (±1.21)	3	4.32 (±0.56)
Western Australia	**I**	147.06 (±74.17)	5.44 (±2.07)	**I**	22.28 (±1.69)	2.53 (±0.75)	7.77 (±0.60)
Western Australia	**J**	257.01 (±80.30)	10.83 (±4.38)	**J**	18.07 (±1.92)	2.95 (±0.21)	3.32 (±1.20)

Table 2. The averages and standard deviations (±S.D.) for measured variables from the Madagascar 2006 (top) and the Western Australia 2006 (bottom) themes and phrases.

Intra-Ocean Basin	Breeding Sites	Song Similarities	Authors
North Pacific	Mexico vs Hawaii	Shared all 4 themes & sychronous song transformation	Winn et al., 1981
North Pacific	Mexico vs Hawaii	Shared all 5 themes & sychronous song transformation	Payne & Guinee, 1983
North Pacific	Mexico vs Hawaii	Shared all 5 themes & sychronous song transformation	Cerchio et al., 2001
North Atlantic	West Indies vs Cape Verde	Shared all 6 themes & sychronous song transformation	Winn et al., 1981
South Atlantic	Gabon vs Brazil	Shared all 6 themes & sychronous song transformation	Darling & Sousa-Lima, 2005
South Pacific	New Calidonia vs East Australia	Shared all 3 themes	Gill et al., 1995
South Pacific	New Calidonia (NC) vs East Australia (EA) vs Tonga	Shared 7out of 9 themes across all sites, 8 out of 9 themes for EA vs NC, 7 out of 9 themes for Tonga vs NC, and 6 out of 9 themes for EA vs Tonga	Helweg et al., 1998
Sothern Indian Ocean	Madagascar vs Western Australia	Shared 1 out of 11 themes	Murray et al.

Table 3. Summary of results from Intra-Ocean song comparisons conducted in the North and South Pacific, the North and South Atlantic, and the Southern Indian Ocean. The similarity in song content and transformation is described in the Song Similarities column. Song comparisons of the North Pacific and North/South Atlantic have complete overlap in song content, thematic order, and synchronous changes in song, the South Pacific comparisons have some overlap in song content and thematic order, and this southern Indian Ocean comparison has only a slight overlap in song content. Of all the intra-ocean song comparisons conducted to date this study found the least amount of overlap in song content.

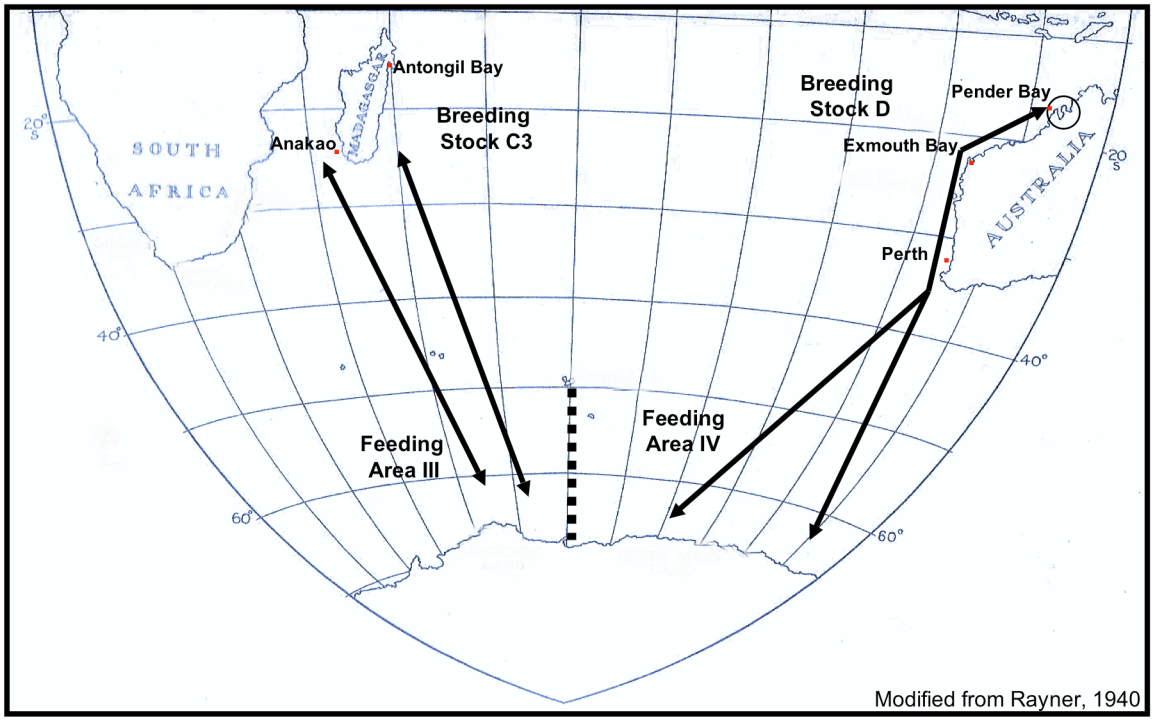


Figure 1. The Feeding Areas, migration route, breeding stock designations, and research sites for Madagascar and Western Australia; migration routes are represented by black arrows and research sites are labeled and designated with red dots. Madagascar whales migrate from Feeding Area III to the coast of Madagascar and are designated as breeding stock C3 by the International Whaling Commission (IWC). Madagascar song was recorded in Antongil Bay and Anakao. Western Australia whales migrate from Feeding Area IV to the coast of Western Australia and are designated as breeding stock D by the IWC. Western Australia song was recorded in Perth, Exmouth Gulf, and Pender Bay.

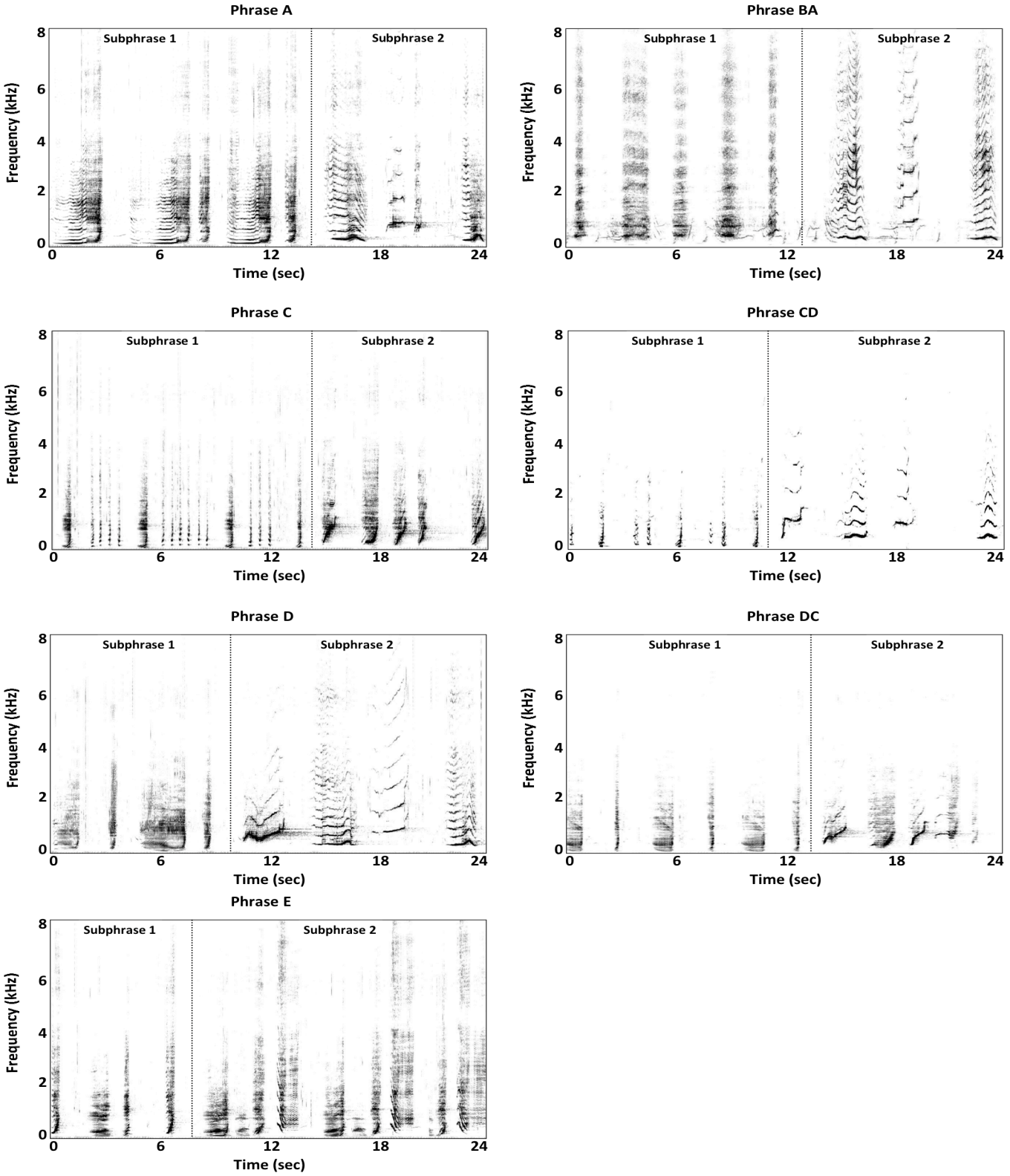


Figure 2. Spectrogram of phrase types from the Madagascar 2006 song. Subphrases for each phrase are separated by dashed line, the y-axis is frequency in kHz and the x-axis is time in seconds, the sound intensity is represented by the lightness or darkness of the grey scale. Spectrograms were made using Raven 1.2.1 with an FFT of 512 and an overlap of 90%.

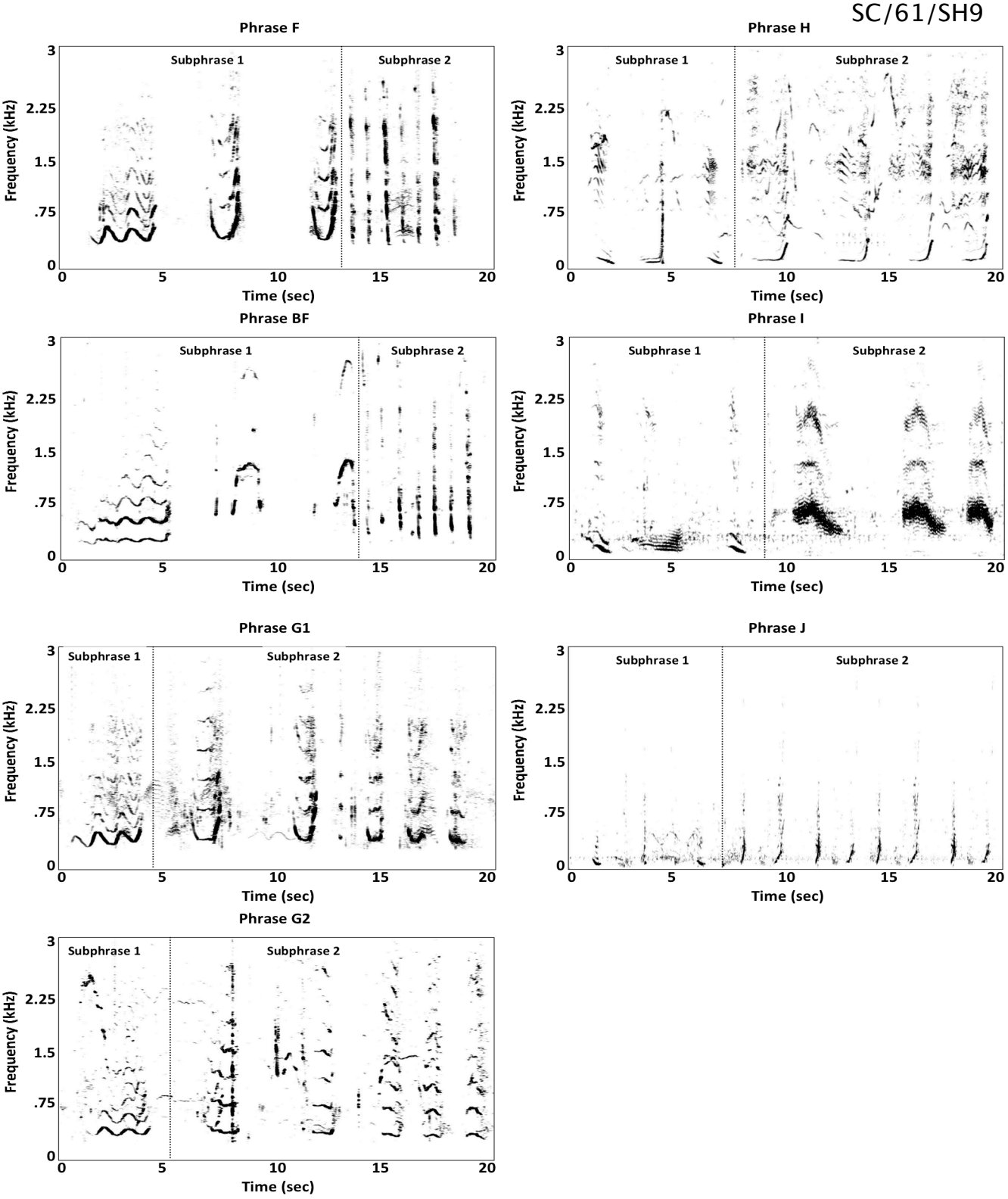


Figure 3. Spectrograms of phrase types and phrase type variants from the Western Australia 2006 song. Subphrases for each phrase are divided by black dash line, the y-axis is frequency in kHz and the x-axis is time in seconds, the sound intensity is represented by the dark or lightness of the grey scale. Spectrograms were made using Raven 1.2.1 with an FFT of 512 and an overlap of 90%.

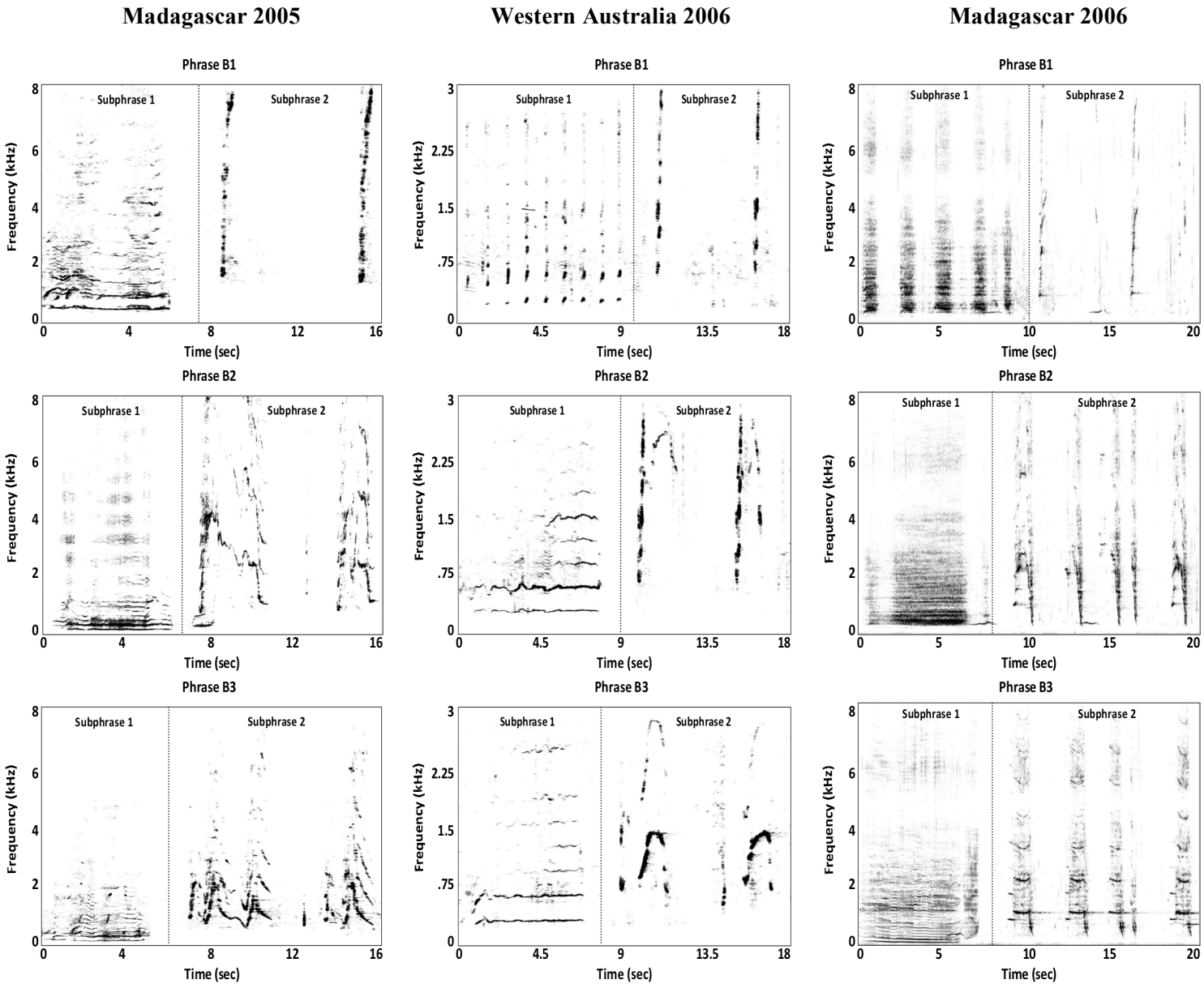
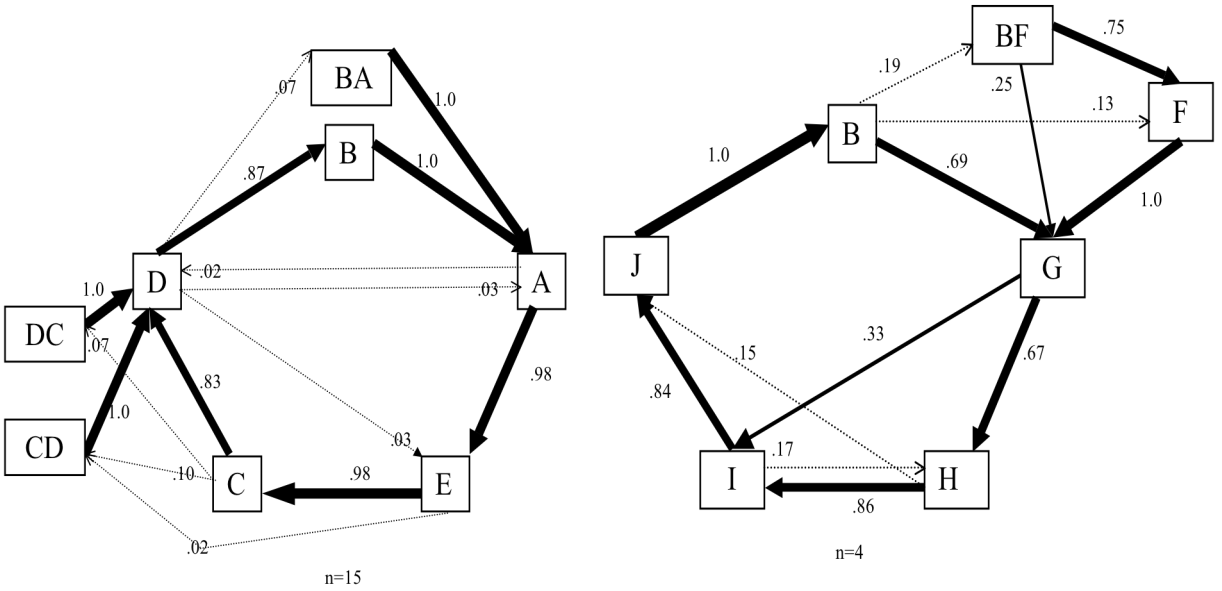


Figure 4. Spectrograms of the three phrase type variants found in Theme B from Madagascar 2005 (left), Western Australia 2006 (middle), and Madagascar 2006 (right). The subphrases are divided by black dashed lines for each phrase, the y-axis is frequency in kHz and the x-axis is time in seconds, the sound intensity is represented by the dark or lightness of the grey scale. Spectrograms were made using Raven 1.2.1 with an FFT of 512 and an overlap of 90%. Western Australia Theme B appears to be an intermediate form of Theme B found in Madagascar 2005 and 2006 song.



Madagascar 2006 Song

Western Australia 2006 Song

Figure 5. The theme transition probabilities for the Madagascar 2006 (right) and Western Australia (left) songs; Western Australia had more themes and therefore more phrase types than Madagascar. There were no transitional phrases in the Western Australia song. Madagascar had four unique themes: A, E, C, and D. Western Australia had seven unique themes: BF, F, G, H, I, and J. The two regions had one theme in common, Theme B.

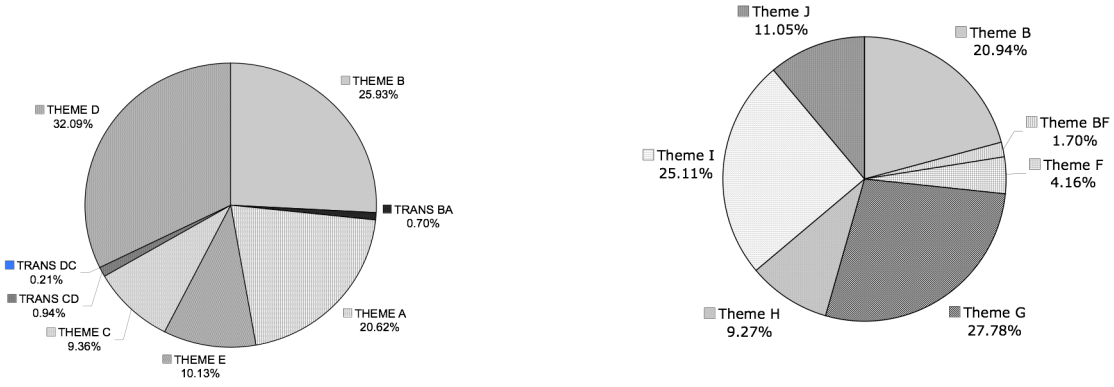


Figure 6. The theme representations for Madagascar 2006 (right) and Western Australia 2006 (left); Madagascar dominate Themes D, B, &A were sung sequentially, and minor Themes E&C were sung sequentially. Western Australia dominant Themes B, G, &I and minor Themes BF, F, H, &J alternated. The theme proportions for shared Theme B was slightly greater in Madagascar them Western Australia, but this was not a statistically significant difference.

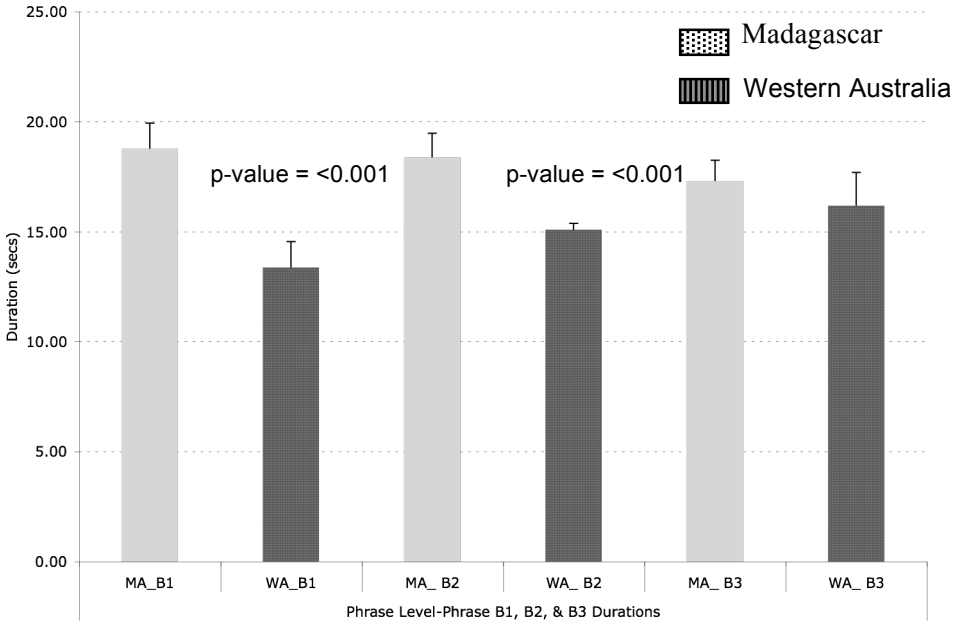


Figure 7. The phrase duration in seconds for the three phrase type variants found in Theme B from Madagascar 2006 and Western Australia 2006. MA stands for Madagascar (gray) and WA stands for Western Australia (black). The Madagascar Phrases B1 and B2 had significantly longer durations than the Western Australia Phrases B1 and B2.

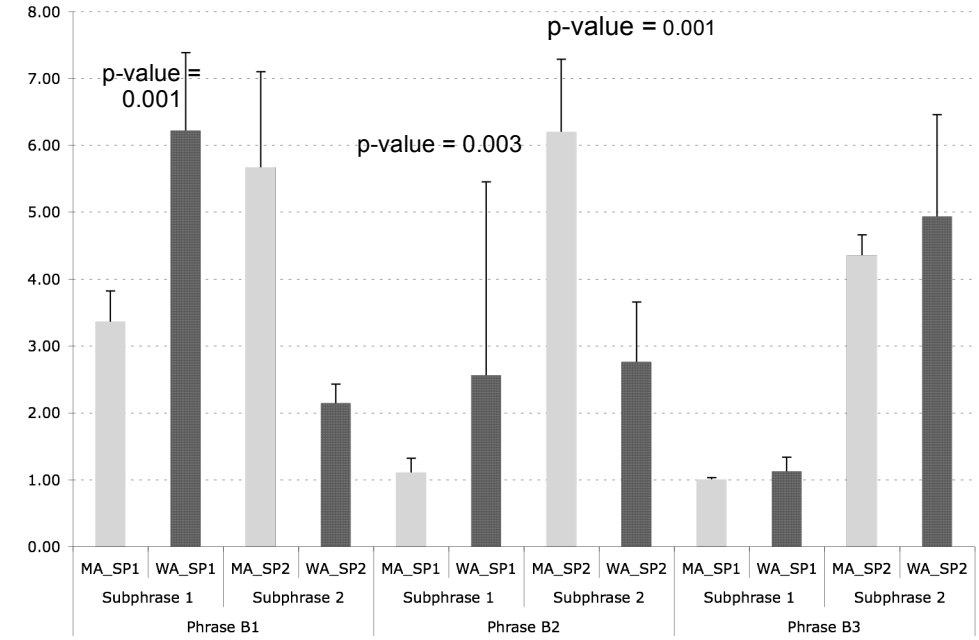


Figure 8. The number of units per subphrases in Phrases B1, B2, and B3 for Madagascar 2006 and Western Australia 2006 songs; MA stand for Madagascar (gray) and WA stand for Western Australia (black). Madagascar Phrase B1 and B2 had significantly different numbers of units in subphrase one and/or two than Western Australia Phrases B1 and B2.