Similarity of song patterns among humpback whales from Madagascar and Gabon indicates significant contact between South Atlantic and Southwest Indian Ocean populations

Y.RAZAFINDRAKOTO[1,2], S.CERCHIO[1,2,3], T.COLLINS[1,4], H. C.ROSENBAUM[1,2] AND S.NGOUESSONO[5]

[1]*Wildlife Conservation Society, Ocean Giants Program 2300 Southern Blvd., Bronx, NY 10460-1099, USA.*
[2]*Madagascar Country Program, Wildlife Conservation Society, B.P. 8500, Antananarivo, Madagascar*
[3]*Evolutionary Biology Program and Bioacoustics Research Program, Cornell Laboratory of Ornithology 159 Sapsucker Woods Rd. Ithaca, NY 14850, USA.*
[4]*Environment Society of Oman P.O. Box. 3955, P.C. 112, Ruwi Sultanate of Oman*
[5]*Agence National des Parcs Nationaux /Ministère de l'Economie Forestière BP 70 Parc National de Mayumba, Mayumba Gabon*

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ABSTRACT

Humpback whale song is unique for its hierarchical and complex structure, and the degree to which it is shared among individuals across extended oceanic ranges. Song similarity across regions indicates acoustic exchange between whale populations at some point in their migratory cycle. Photographic, genetic and acoustic surveys have been conducted to characterize humpback whale population wintering off Antongil Bay, Madagascar (Southwest Indian Ocean) and Iguela, Gabon (Eastern South Atlantic Ocean). Recordings of songs were made between 12 July and 10 September 2003 in Antongil Bay, and between 8 August and 30 September 2003 off Iguela. Songs from five singers each in Antongil Bay and Iguela (amounting to a total of 44 full and six incomplete song cycles) were used to assess song similarity between the two sites in this study. All of five major themes occurred in both regions, and a total of 13 of 16 phrases variants identified in the five themes was shared. The occurrence of song phrase types was virtually the same in both sites although they were not equally represented; the number of variants composing the 13 common phrases didn't show significant difference. Although the song composition was the same in Antongil Bay and Gabon, the sequence order of the theme was different. Our observations constitute the first evidence of song similarity between these two populations wintering in different ocean basins separated by the African continent during the primary singing season. Our findings suggest the occurrence of close acoustic exchange between the two populations.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) migrate annually between high latitude feeding grounds and low latitudes where breeding occurs. They are known to produce long and complex vocalizations, first described as "song" by Payne and Mcvay (1971). Humpback whale song is unique for its hierarchical structure, composed of a series of sounds occurring in a regular sequence and patterned in time (Payne and McVay 1971). Singing peaks during the winter months of the breeding season. There is also evidence of song production along migratory paths (Clapham and Matilla 1990, Cato 1991, Charif et al. 2001) and on the feeding grounds (Clapham 2000, Clark and Clapham 2004). The repeating cyclical sounds heard in the feeding grounds are structurally identical to the songs used in wintering areas (Mattila et al. 1987, McSweeney et al. 1989). Thus, song production occurs throughout the humpback whale migratory cycle.

Similarity of songs has been observed in different wintering areas within the same ocean basin, even though the breeding grounds may be separated by thousands of kilometers. In the North Pacific, whales that migrate to Mexico, Hawaii and Japan shared similar songs (Payne and Guinee 1983, Helweg et al. 1990, Cerchio et al. 2001) as well as those in Ryukyu and Bonin regions (Maeda et al. 2000). In the Southern Hemisphere, similarity was found in the whale songs from Tonga, New Caledonia, Eastern Australia and New Zealand in the South Pacific (Helweg et al. 1998, Eriksen 2003). Recent observations also revealed that whales migrating to Gabon and Brazil share the same songs within and between the breeding seasons (Darling and Sousa de Lima 2005). Song sharing across regions is believed to be cultural, resulting from acoustic exchange between populations during their migratory cycles. Payne and Guinee (1983) suggests three possible paths for this information exchange: (1) singers may have acoustic contact in the feeding grounds or along the migration paths, (2) singers may move between breeding areas within a single season, and (3) singers may alternate between different breeding grounds in different seasons.

Photographic, genetic and acoustic monitoring have been conducted to study humpback whale populations in Antongil Bay and Iguela, both historically known as whaling grounds (Braley 1848-1953, Starbuck 1878). These sites belong to two adjacent but different breeding "stocks" according to the seven major migratory streams that were defined in the Southern Hemisphere by the International Whaling Commission (IWC 2000, IWC 2004). These populations may share a common feeding ground in Antarctic Area III (10°- 40°E) which is believed to be the feeding grounds for whales wintering in the Southwestern Indian Ocean and off Western Africa in the Eastern South Atlantic (Mackintosh 1942). In this paper, we present evidence of song sharing between these populations which are considered isolated from each other while wintering in two different ocean basins.

METHODS

Study sites

Recordings of songs were conducted in Antongil Bay, Madagascar and at Iguela, Gabon located respectively in the Southwestern Indian and South Atlantic Oceans (Figure 1). Antongil (16°00'S, 49°55'E) is a large bay in northeastern Madagascar that covers an area of 2800 km^2. The bay is shallow with a mean depth of 41.4m (Ersts and Rosenbaum 2003). Songs were also recorded at Iguela (1°51'S, 9°20'E) situated in the central coast of Gabon. The survey area exceeds 1750 km^2 and extends 35 km from shore. The bathymetry of much of the Gabonese coast is uniform, and depths within the survey area never exceed 100 m (T.Collins, pers comm.). Observations of humpback whales engaged in characteristic wintering ground behaviors such as escorting and singing (Glockner 1983, Baker and Herman 1984) have been recorded at each survey site during each survey period.

Acoustical and visual surveys were conducted between 12 July and 10 September 2003 in Antongil Bay. Surveys were done using a 7-meter fiberglass boat powered with two 25hp engines which were used to track down individual singers using acoustic and behavioral checking. Singers were recognizable by their slow movements and were often observed fluking before diving. They also tended to breathe during readily recognizable song themes (Winn & Winn 1978; Helweg et al. 1990; Cerchio et al. 2001). Singers were difficult to localize in Gabonese waters and recordings were therefore made opportunistically, as singers were encountered. Recordings were made at Iguela between 8 August and 30 September 2003 from a nine meter rigid hull inflatable boat powered with an inboard 280hp diesel engine. When a singer was located, the boat approached to within 50m of the animal. Whales showed no obvious sign of awareness of a drifting and silent recording boat. Recordings were made using custom-built hydrophones attached to preamplifiers connected to Sony TCD-D100 digital audio tape (DAT) decks using a sampling rate of 44.1 kHz. System response was flat (+/- 3 dB) from approximately 50-17,000 Hz, although overall response was as low as 20Hz. Songs from solitary singers were preferentially sampled in order to

maximize recording quality. Songs were recorded for 45 minutes to one hour. Photo identification and genetic sampling of the singers were subsequently conducted at the end of the recording.

Songs were digitally recorded at 44.1 KHz and 16 bits, and DAT recordings were converted to digital wav files by D-D transfer on a personal computer using the program Avisoft-SASLab Pro (http://www.avisoft.de/). The files were subsequently downsampled to 16 kHz and continuous spectrograms were generated and printed out in Avisoft-SASLab Pro (using 512pt FFT, Hamming window) to assess qualitatively the diversity of phrases composing the themes. Spectograms illustrated in the results were made using 512 pt FFT within a Hamming window and 50% overlap with the sound analysis software Raven 1.1 developed by the Bioacoustic Research Program at Cornell Laboratory of Ornithology (http://www.birds.cornell.edu/brp/). The song structure criteria first described by Payne and McVay (1971) was used to qualitatively characterize songs. Each song consists of a sequence of different themes sung in a predictable order. Themes consist of different sets of repeated phrases that are formed by a distinct pattern of individual sounds called "units". The latter constitute the most fundamental elements of humpback song.

Song comparisons were made using the best quality recordings from solitary singers in Antongil Bay and Gabon; the chosen recordings were characterized by a signal-to-noise ratio (S/N) sufficiently high to clearly distinguish the phrases of the focal singer for the duration of the recording. The recordings used for both sites are presented in Table 1. The assignment of the theme labels was first carried out on Antongil Bay samples. The theme associated with breathing was composed of pulsive units with a "ratchet" like quality as documented at other sites globally (Winn and Winn 1978, Helweg et al. 1990, Cerchio et al. 2001). The phrases following the ratchet phrases were considered the first theme that labeled "Theme A" and all subsequent theme labels were assigned alphabetically thereafter in the song cycle. Variation in the number and spectral structure of units was used as the basis for classification of phrase variants within a given theme, which were labeled as the letter of the theme followed by a number to distinguish different variants. Songs from the two sites were visually compared to assess similarities; two phrase variants were considered to match if the general and spectral characteristics of sounds were in the same position. To illustrate the presence/absence of phrases in the song samples from the two sites, data was summarized in term of relative representation of each phrase variant in the region. The proportion of each phrase variant was calculated for each singer's sample, and relative representation in each region was calculated by averaging the proportions of each variant across singers. Individual means of variant repetitions per theme were averaged to generate a regional mean repetition per theme for each variant. Differences between the regional means of the common themes were tested using a Mann Whitney U test; the analysis was performed using Statview version 5.0. We used the average for each singer as sample in this statistical analysis to eliminate any bias towards long samples. The adjustment of the significance level using Bonferroni method was proceeded to avoid making type I error as multiple significance tests were conducted.

RESULTS

Song sample

Eleven singers were located in Antongil Bay and six song samples were recorded at Iguela during the 2003 breeding season. Five samples from Antongil Bay were chosen for inclusion in the analysis with a mean duration of 39 min 57 sec (SD=14min 53 sec; N=5). These recordings lasted for 3 hrs 19 min representing 25 full and five incomplete song cycles (Table 1). Five samples with a mean duration of 32 min 12 sec (SD=09 min 53 sec; N=5) from Iguela were also analyzed in this study; the recordings consisted of 17 full and one incomplete song cycles and had a duration of 2 hrs 41 min.

Song structure

The Madagascar and Gabon song recorded in 2003 consisted of five themes with 16 phrase variants. All five themes were recorded in both regions. The presence and relative contribution of phrase variants was virtually the same in both sites (Figure 2). Fifteen of the variants were found in Antongil Bay, 14 variants were found in the song from Iguela, and 13 phrase variants were shared between regions. The only striking difference was the absence of phrase variant D4 in Antongil Bay, which conversely was seen in all recordings from Gabon. Phrase variants A3 and A4 were absent in the recordings made in Iguela but these variants were only seen in one sample made at the beginning of the wintering season in Antongil Bay. The variant repetition per theme in the song of each region was shown in Table 2. The repetition of song variants were similarly represented in the song cycles in both sites; the phrase variants composing each common theme (A1, A2, B1, B2, B3, B4, C1, C2, D1, D2, D3, E1 and E2) did not differ significantly between the two sites.

Theme description

Theme A
Theme A had four variants (A1, A2, A3, and A4) that differed by the number of units and the spectral structure of the frequency modulated (FM) units (Figure 3). A1 and A2 variants presented similar spectral structure but differed in the number of units in the phrase. They had respectively two and three constant units. Variants A3 and A4 had similar structures with three identical units. However, the FM structure of their first unit varied greatly in term of spectral structure and duration.

Theme B
Theme B was a shifting theme (Payne and Payne 1985) formed by four variants (B1, B2, B3 and B4), thus the different types of units in the four variants progressively evolved with each phrase repetition from one variant to the next. The variant B1 consisted of two types of units, a linear contoured FM unit and rapid FM upsweep; this variant contained a total of six to seven units arranged in two distinct subphrases (Figure 4). The variant B2 was more simply formed by a linear contour FM unit and two FM upsweeps. The first FM unit of B3 tended to be shorter than in the previous variants, and the second unit was more modulated FM. B4 was formed with linear contour FM unit and short FM units.

Theme C
Theme C was represented by two variants (C1 and C2) that presented the same spectral structure, but differed by the number of units in the phrase. C1 and C2 had a constant frequency unit followed by a long FM upsweep, whereas in C2 the long FM upsweep was followed by a second constant unit (Figure 5).

Theme D
Four variants (D1, D2, D3 and D4) formed Theme D (Figure. 6). Variants D1 and D2 had similar patterns that were formed by a variable number of FM units with linear contour ranging from eight to ten. The two first units of D1 were deleted in D2 and the remaining units tended to be shorter. Variants D3 and D4 were structurally similar; a constant unit and three to four upswept FM units formed D3, whereas in D4 the four FM units were downswept.

Theme E
Theme E had two variants, E1 and E2 (Figure 7). Three broadband units of different duration formed E1. One broadband unit was followed by a repetition of single brief broadband unit. E2 was composed of three broadband units without the repeated single brief broadband unit. Theme E was most often associated with breathing, and the ratchet-like pulsive quality of the broadband units signaled to observers that the whale was about to come to the surface.

Theme sequence
Although Antongil Bay and Gabon shared the same themes, their order was arranged differently at both sites. The theme order in Antongil Bay was ABCDE with the exception of one sample (13 July 2003) which had the theme sequence of all recordings in Gabon, as ABCED. The difference between the theme sequences was the position of the theme associated with breathing, theme E. The placement of the variants in the theme A also had a small difference between the regions, the variant A1 was typically before A2 in Antongil Bay, whereas A1 typically followed A2 in Gabon recordings.

DISCUSSION

Song similarity has previously been documented between populations migrating within the same ocean basin despite breeding areas separated by thousands of kilometers (Winn et al. 1981, Payne and Guinee 1983, Helweg et al. 1998, Maeda et al. 2000, Cerchio et al. 2001). Our findings constitute the first evidence of song sharing between populations wintering in the South Atlantic and the Indian Ocean, separated by the continent of Africa during the primary singing season. Previously, song sharing and transmission has been documented between populations in different ocean basins in the Southern Hemisphere, between the eastern Indian Ocean and the South Pacific, separated by the continent of Australia (Noad et al. 2000). The mechanism of maintenance of similar song between widely separated assemblages is not fully understood (Payne and Guinee 1983, Noad et al. 2000, Cerchio et al. 2001). However, song sharing across regions is generally believed to be cultural and supposes acoustic contact of male humpback whales during some portion of their migratory cycle. Moreover, it reflects migratory relationships between populations within the regions.

The mobility of "wandering" males that carry the song between locations combined with the collective adoption of song novelty throughout the population is one hypothesis explaining the maintenance of song sharing across ocean basins (Payne and Guinee 1983, Noad et al. 2000, Cerchio et al. 2001; Darling & Sousa-Lima 2005). At question is whether male humpback whales can visit different breeding grounds within a season, or whether exchange and resultant song transmission occurs between seasons. Previous studies have shown individual whale movement between islands within a breeding assemblage in one season (such as among the Hawaiian Islands: Cerchio et al. 1998, Mate et al. 1998); however, these distances are very short in comparison to the present context. Humpback whales have the capacity to travel great distances over relatively short periods of time in the course of their yearly latitudinal migration (such as across the span of the Pacific Ocean: Darling & McSweeney 1985); however, this extent of movement has not been documented within a breeding season. In our study, the great distance separating Antongil Bay and Gabon, together with the southern hemisphere geography are clearly factors excluding acoustic contact as a result of whales migrating to both sites within a season. The whales would have to travel on a route that is at least 10,000 Km around Africa. Considering lowest and fastest speeds of travel of 62.5 km/day and 150 km/day respectively (Mate et al. 1998), if a whale maintained the same speed on a straight course, it would spend between 90 and 160 days traveling between the two sites. This period of time may represent the entire length of the breeding season for a given individual. Stone et al (1990) documented a distance record of migration by individually identified whales traveling over 8,000Km (one way) within five months; however this was also a latitudinal migratory movement. Therefore, we believe it would be high improbable for male humpback whales migrating to either Antongil Bay or Gabon to move between these separate breeding grounds, and thus rule out within season exchange as a mechanism maintaining song similarity.

Records of individual humpback whales switching breeding grounds from year to year have been recorded in many ocean basins (Chittleborough 1960, 1962, Darling and Jurasz 1983, Darling and McSweeney 1985, Baker et al. 1986, Perry et al. 1988, Darling and Cerchio 1993). The best evidence for song transmission resulting from whales switching breeding grounds in subsequent years was probably the observation made by Noad et al. (2000) between west and east Australia breeding grounds. To date there

are two documented cases of males switching breeding grounds between Antongil Bay and Gabon in subsequent years; a young male (Pomilla and Rosenbaum 2005) and an adult male (J. Loo & C. Pomilla pers. comm.) each identified by genetic recapture. These observations demonstrate that the males alternate breeding grounds between the West Indian Ocean and the east South Atlantic. Thus the hypothesis of acoustic contact due to the movements of whales between different breeding grounds in different seasons is one feasible explanation for similarity of the 2003 song between Antongil Bay and Gabon. It is intriguing that the theme sequence of all recordings from Gabon was seen in only one sample from Antongil Bay at the beginning of the season. This may represent the initial song of an individual that had in the previous year been in the South Atlantic; however, that particular variation in song rendition did not spread into the Antongil Bay population.

Previous studies have confirmed the presence of song production in high latitudes both prior to departure (autumn) and after return (spring) where males sing the same general song content as in the wintering areas (Matilla et al. 1987, McSweeney et al. 1989, Clark and Clapham 2004). Antongil Bay in the Southern Indian Ocean and Iguela off Western Africa are believed to share or have overlapping feeding areas in Antarctic Area III (10° - 40°E) (Mackintosh 1942). Therefore, song sharing between Antongil Bay and Gabon may be due to the acoustic contact of singers in the feeding areas. The song transmission between male humpbacks may also occur along a common migratory path that may diverge off the Cape of Good Hope. From the evidence presented here, it is not possible to distinguish between the previous two hypotheses, that of transmission due to switching breeding grounds in alternate years, and that of sharing of songs on common feeding areas or migratory paths. It is entirely possible, if not likely given what is known from other ocean basins, that it could be a combination of these mechanisms. Moreover, it is noteworthy that Darling and Sousa-Lima (2005) documented song sharing between Gabon and Brazil in 2001 and 2002. Together with our observations reported here for 2003, this suggests some degree of acoustic contact across a broad longitudinal range and three genetically distinct breeding populations (Pomilla et al. 2006, Rosenbaum et al. submitted) from the western South Atlantic to the western Indian Ocean.

Although singers migrating to Antongil Bay and Gabon shared the same song pattern, the samples recorded in both sites displayed small scale differences in the presence/absence of variants and the theme sequence in the song cycle. The evolution of the song recorded in Antongil Bay may suggest the role of geographical isolation during the breeding season to account for this difference. The sample of songs used in this paper is too small to track the temporal evolution of songs during 2003 in Antongil Bay and Iguela, as documented in the North Pacific in Hawaii and Mexico over a single season by Cerchio et al. (2001). However, the songs recorded in Antongil Bay appeared to change slightly throughout the season. It may be possible to distinguish between the several hypotheses discussed, using a longer term and more thorough sample over several years, tracking changes in song both within seasons and between seasons.

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Figure.1: The locations of the two breeding grounds of humpback whales where songs were recorded are indicated by the stars

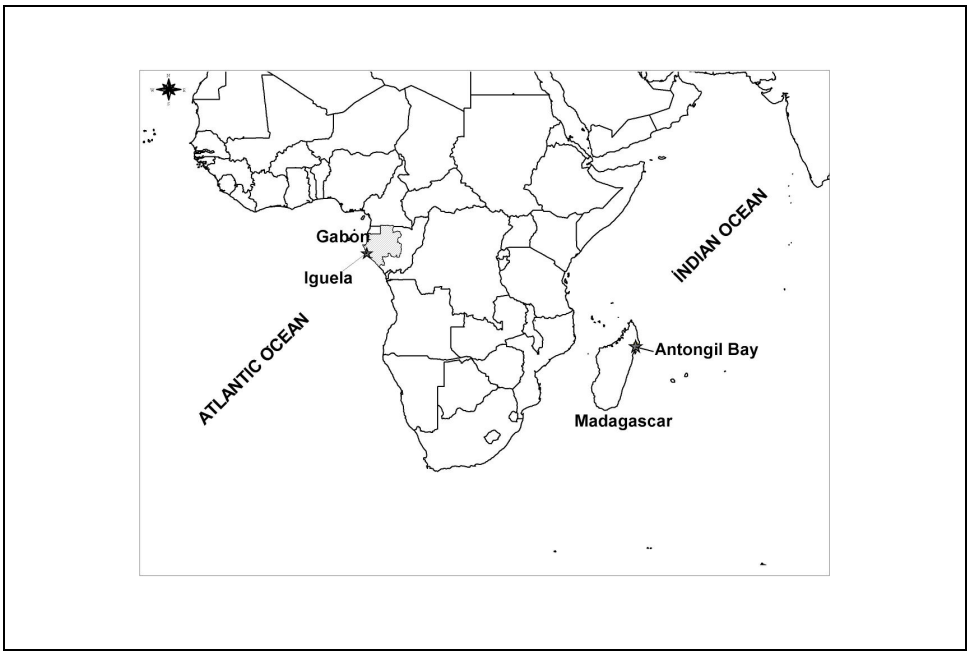

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Figure 2: Presence/absence of phrase variants and their respective proportion in songs recorded in Antongil Bay and Gabon

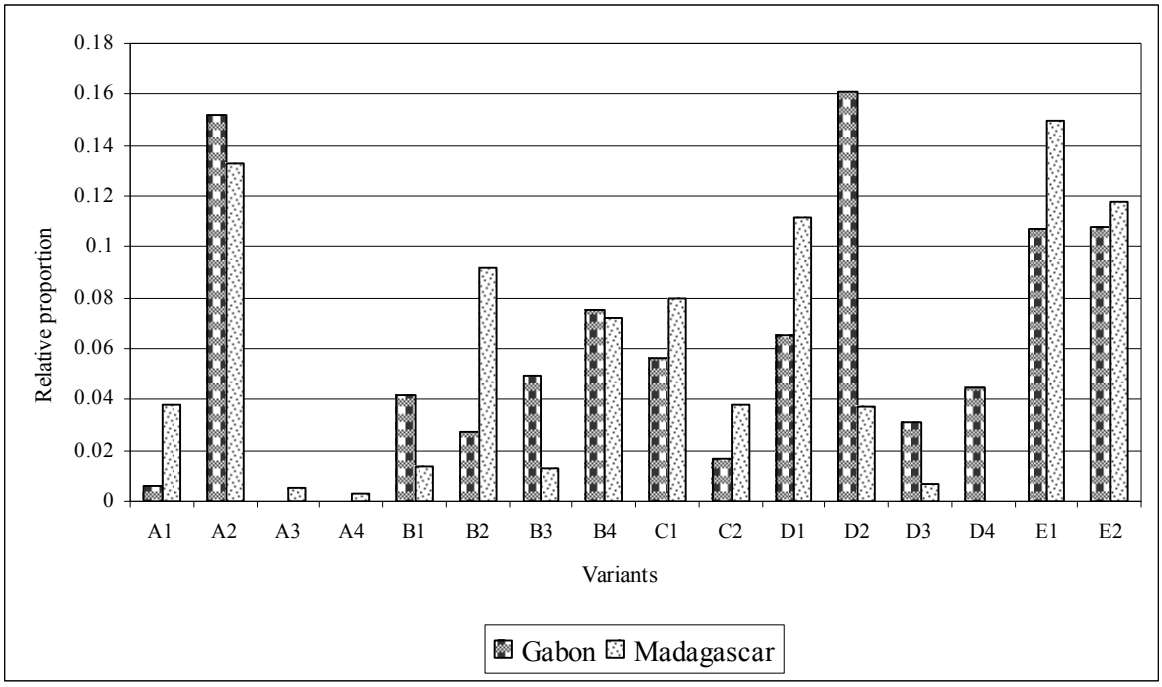

Figure 3. Antongil Bay and Iguela Theme A: Four variants constructed the phrase in Antongil Bay recordings whereas two formed the songs from Iguela
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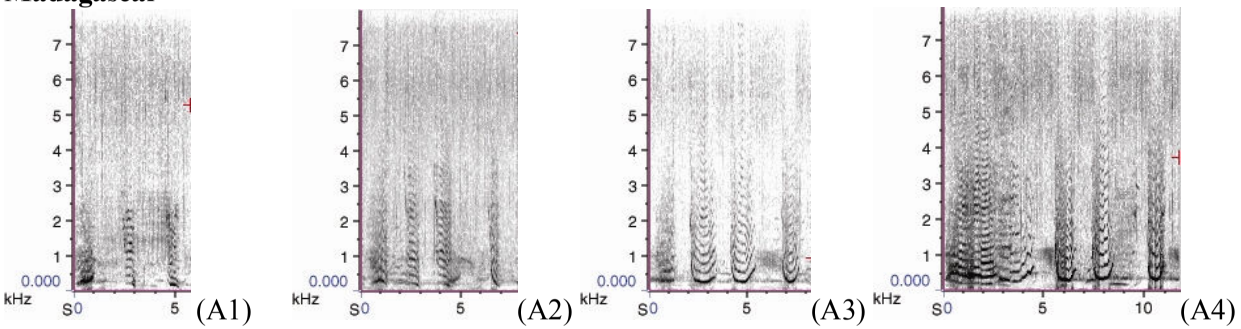
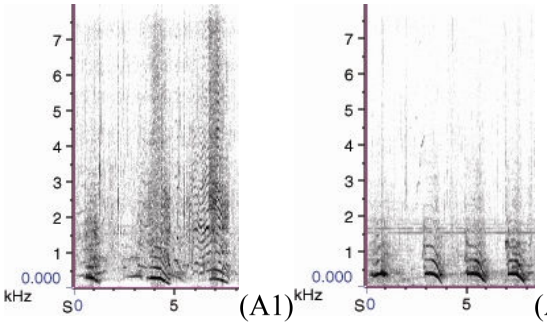
Madagascar



(A1) (A2) (A3) (A4)

Gabon



(A1) (A2)

Figure 4. Antongil Bay and Iguela Theme B was constructed by four variants

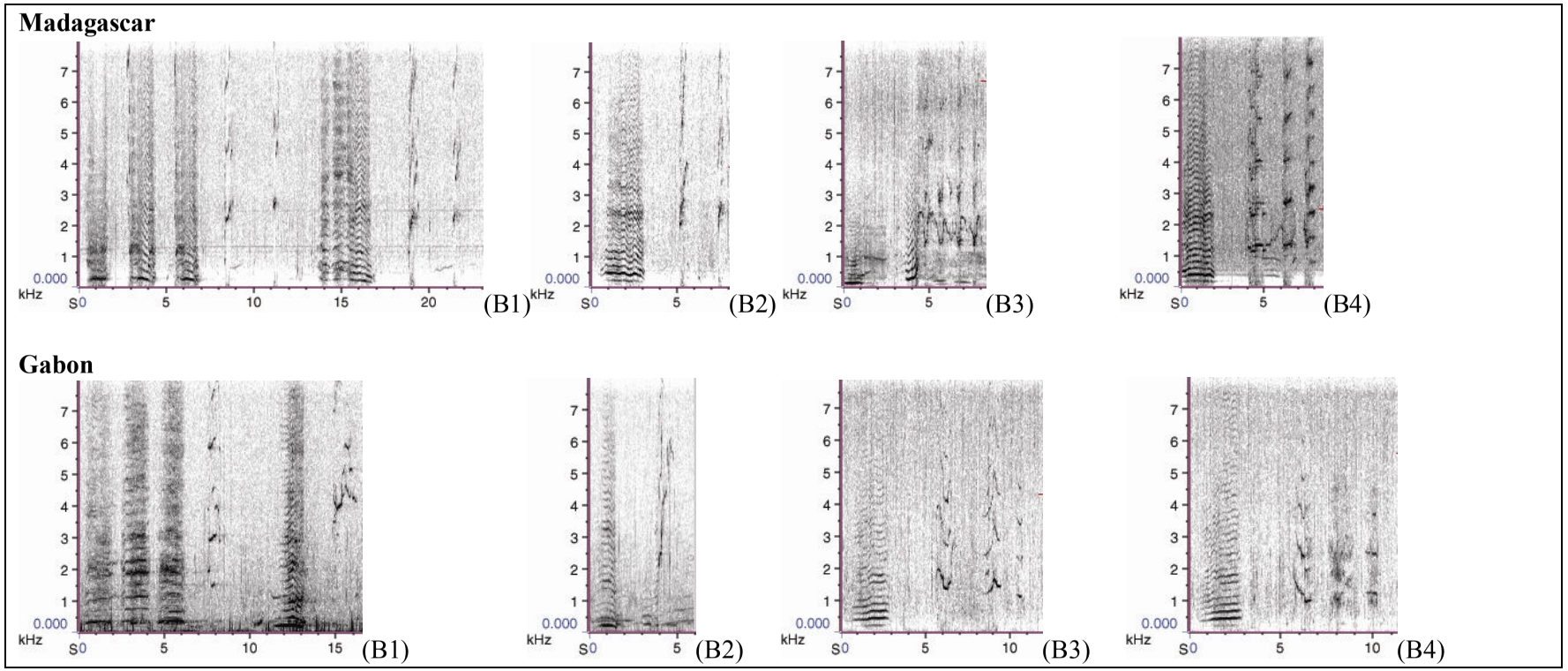


Figure 5. Antongil Bay and Iguela Theme C was constructed by two variants

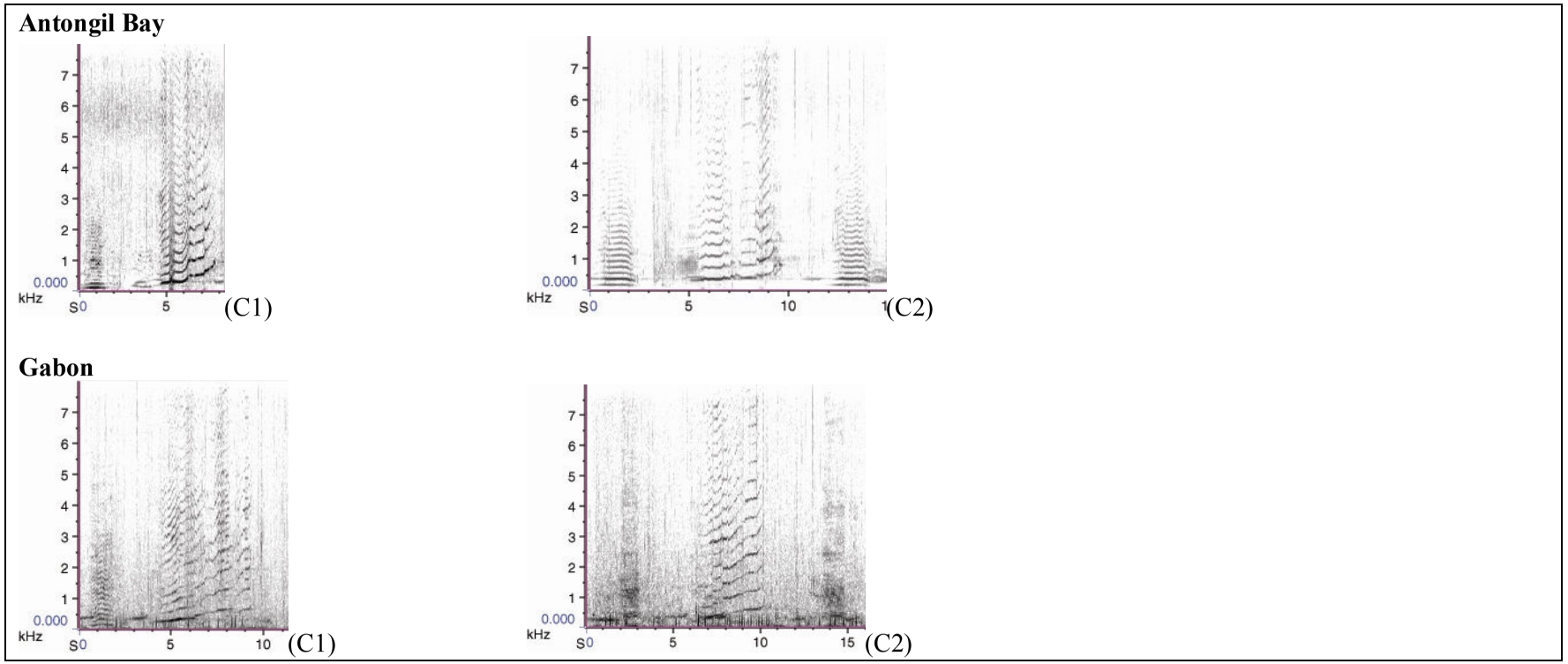


Figure 6. Antongil Bay and Iguela Theme D: Three variants constructed the phrase in Antongil Bay recordings whereas four formed the songs from Iguela.

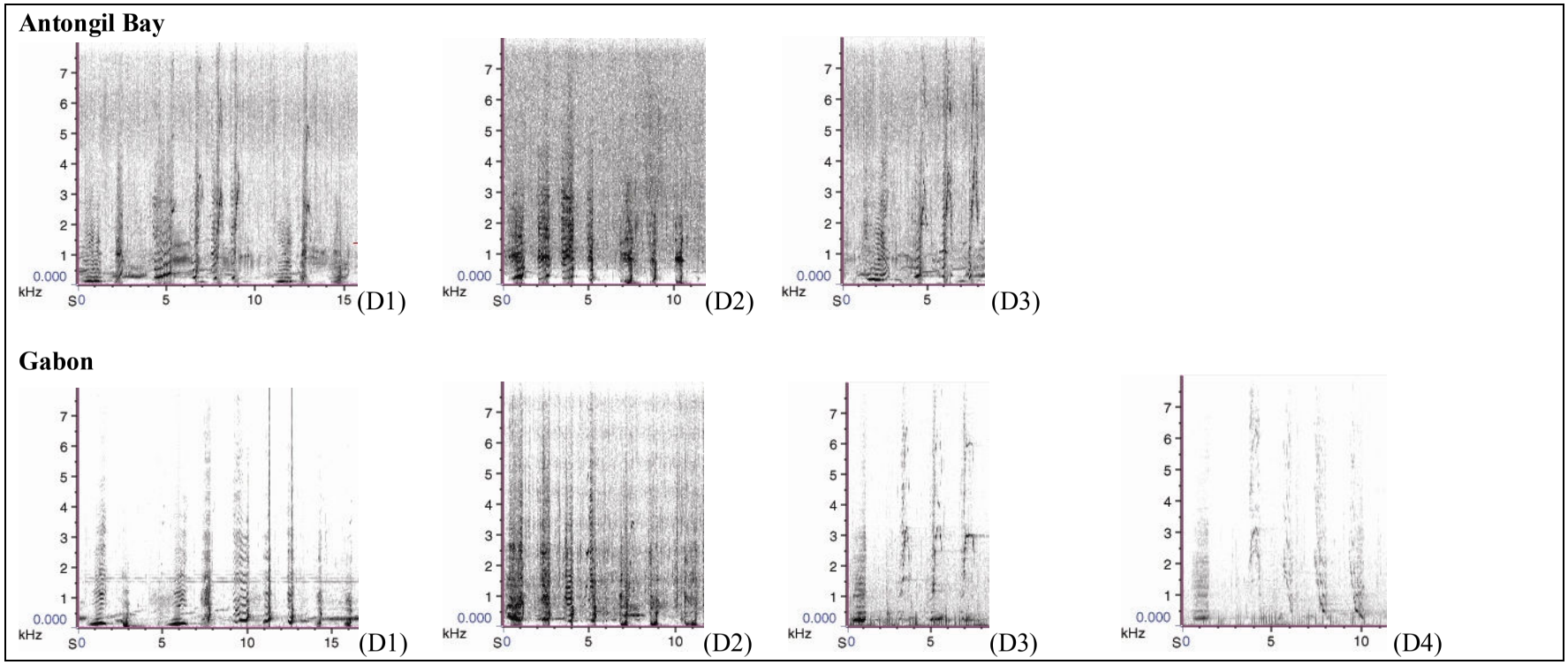


Figure 7. Antongil Bay and Iguela Theme E was constructed by two variants

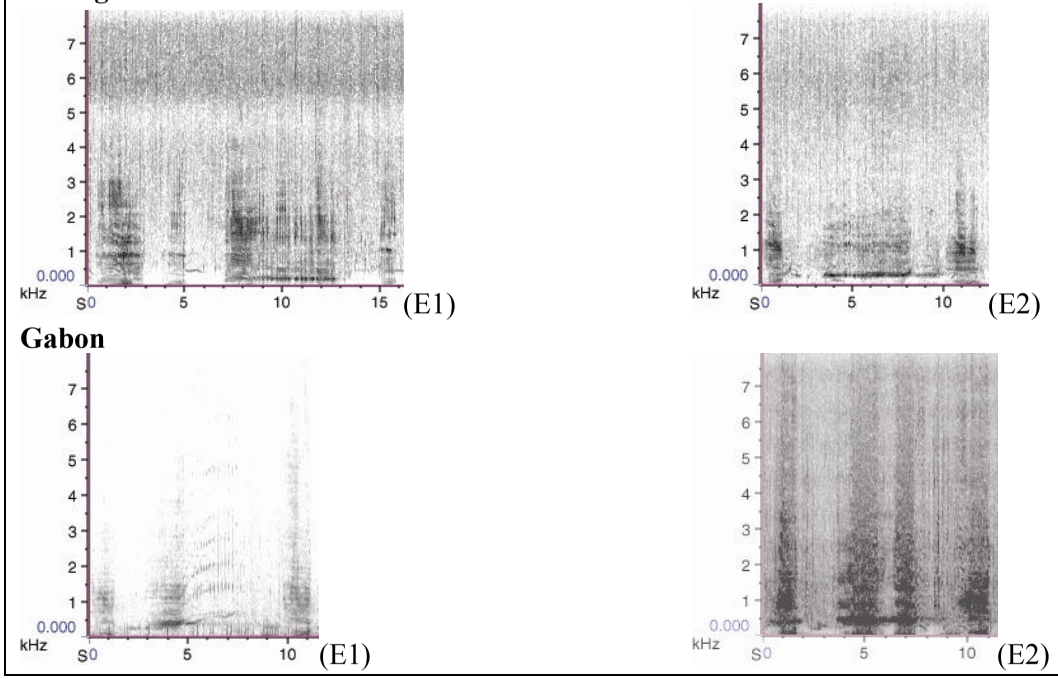


Table 1: High quality recordings used to assess the song similarity between Antongil Bay and Iguela. Recording made between 12 July and 10 September 2003 in Antongil Bay, Madagascar and 8 August and 30 September 2003 in Iguela, Gabon

Sites	Length of recording	# full song cycles	# incomplete cycles	# phrase variants	Total number of phrases
Antongil Bay, Madagascar	43 m 43 s	5	1	13	49
	63 m	5	1	12	63
	38 m 44 s	6	0	10	38
	29 m 40 s	6	2	12	44
	24 m 38 s	3	1	10	19
Total	199 m 45 s	25	5	57	213
Iguela, Gabon	24 m 59 s	5	1	10	40
	22 m 40 s	1	0	11	21
	28 m 43 s	5	0	12	43
	46 m 15s	4	0	12	32
	38 m 27 s	2	0	14	17
Total	161 m 2 s	17	1	59	153

Table 2: The regional means of each variant repetition per theme, its related standard deviation and the results of Mann Whitney U test.

Variants	**Antongil Bay**	**Iguela**	**P value**
A1	*1.22±1.50*	*0.15±0.22*	*0.1340*
A2	*4.01±1.94*	*5.12±1.50*	*0.5993*
A3	*0.60±1.34*	-	-
A4	*0.32±0.72*	-	-
B1	*0.40±0.43*	*1.43±0.45*	*0.0147*
B2	*2.48±2.19*	*1.05±0.87*	*0.3321*
B3	*0.87±1.64*	*1.59±1.15*	*0.3413*
B4	*2.13±1.26*	*2.91±1.77*	*0.4647*
C1	*2.19±1.13*	*2.08±1.22*	*0.9168*
C2	*1.02±0.98*	*0.6±0.38*	*0.7503*
D1	*3.24±1.09*	*7.45±5.68*	*0.2087*
D2	*4.01±1.94*	*5.19±1.69*	*0.0088*
D3	*1.16±0.76*	*1.4±1.04*	*0.3413*
D4	-	*2.17±0.75*	-
E1	*4.83±2.35*	*4.28±4.05*	*0.9158*
E2	*3.66±1.65*	*7.95±6.51*	*0.2506*