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Information theory analysis of Australian humpback whale song

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Songs produced by migrating whales were recorded off the coast of Queensland, Australia, over six consecutive weeks in 2003. Forty-eight independent song sessions were analyzed using information theory techniques. The average length of the songs estimated by correlation analysis was approximately 100 units, with song sessions lasting from 300 to over 3100 units. Song entropy, a measure of structural constraints, was estimated using three different methodologies: (1) the independently identically distributed model, (2) a first-order Markov model, and (3) the nonparametric sliding window match length (SWML) method, as described by Suzuki *et al.* [(2006). "Information entropy of humpback whale song," *J. Acoust. Soc. Am.* **119**, 1849–1866]. The analysis finds that the song sequences of migrating Australian whales are consistent with the hierarchical structure proposed by Payne and McVay [(1971). "Songs of humpback whales," *Science* **173**, 587–597], and recently supported mathematically by Suzuki *et al.* (2006) for singers on the Hawaiian breeding grounds. Both the SWML entropy estimates and the song lengths for the Australian singers in 2003 were lower than that reported by Suzuki *et al.* (2006) for Hawaiian whales in 1976–1978; however, song redundancy did not differ between these two populations separated spatially and temporally. The average total information in the sequence of units in Australian song was approximately 35 bits/song. Aberrant songs (8%) yielded entropies similar to the typical songs. © 2008 Acoustical Society of America. [DOI: 10.1121/1.2967863]

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I. INTRODUCTION

Male humpback whales (*Megaptera novaeangliae*) sing complex songs that are believed to be an important element of the humpback mating system (Winn and Winn, 1978; Tyack, 1981; Darling and Bérubé, 2001). Songs are sung predominantly on the winter breeding grounds and during migration to and from the breeding grounds, but may sometimes be heard on high-latitude feeding grounds (Clapham and Mattila, 1990; Cato, 1991; Clark and Clapham, 2004). Analyses of song from humpbacks of the Northern and Southern Hemispheres reveal a hierarchical structure of repeating themes in a largely stereotyped order (Payne and McVay, 1971; Guinee and Payne, 1988; Cato, 1991; Suzuki *et al.*, 2006). Themes consist of repeated phrases, which are composed of discrete sound elements called units. Unit durations can range from less than 1 s to longer than 5 s with an average of approximately 1 s. Spac-

ing between the units is typically on the order of 2–5 s. Sometimes there are minor variations in frequency and timing between phrases and units within the same theme. The whales may repeat the song several times in the course of a song session, usually surfacing to breathe or "blow" in between consecutive songs. Song duration has been reported to range from 6 to 35 mins, whereas song sessions can last for up to 22 h (Payne and McVay, 1971; Winn and Winn, 1978).

The song structure of the Northern Hemisphere humpbacks has been studied more extensively than that of their Southern relatives. This is attributed to the difference in the geographic distribution of whales on breeding grounds between the two hemispheres (Cato, 1991). Whales on the Northern Hemisphere breeding grounds are relatively concentrated within close proximity to shore, whereas they are more dispersed during offshore migrations. The opposite is true in many parts of the Southern Hemisphere. Whales are more widely distributed on broad continental shelf breeding grounds (e.g., in Australia or Africa) or around scattered island groups (e.g., in Oceania), and known concentrations of

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whales in Australia, in particular, are more easily observed on the migration route that closely follows the coastline in some places (Dawbin, 1966; Simmons and Marsh, 1986; Cato, 1991; Cato *et al.*, 2001; Noad and Cato, 2007; Noad *et al.*, 2004).

Males within the same breeding stock or population typically sing the same song; however, the songs are not sung synchronously. Males from different stocks and different oceans sing different songs (Payne, 1978; Winn and Winn, 1978) although songs used by populations within the same ocean basin are often similar (Payne and Guinee, 1983; Helweg *et al.*, 1990, 1998). Song exchange between the hemispheres has not been observed due to geographic separation and out of phase migration patterns (Cato, 1991). Information theory provides a mechanism to investigate and relate the sequence of song units from different humpback stocks where individual song units, phrases, and themes can be drastically different.

For the purposes of this study, song structure specifically refers to the sequence of units. It does not capture any information on the timing differences or subtle variations between occurrences of the same units. While we do not dispute the possibility that information may be contained in other song parameters such as differences in the duration of the same units, timing between units, frequency differences, etc., humpback song has evolved in an acoustically complex environment where signals are subjected to frequency dependent reverberation and attenuation. The limited results available analyzing the timing and frequency characteristics of song units indicate that there is relatively little variation in these features, making it unlikely that these features contain substantial information (Macknight *et al.*, 2001; Au *et al.*, 2005). Songs are only viable for conveying information about individuality or fitness if they exhibit reliably perceivable interindividual differences (Tyack, 1981; Macknight *et al.*, 2001). Signals traveling long distances underwater are likely to experience both distortions in timing and relative energies at different frequencies due to heterogeneities along the transmission path making these parameters unattractive for discriminating between individuals over long distances (Michalopoulos, 1997). Consequently, the sequence of units is the feature of the song most robust to transmission through the underwater acoustic channel as singer position, listener position, and oceanographic conditions vary. This does not negate the potential for other avenues of information transfer through humpback song. It merely acknowledges the sequence of units as the most robust channel for conveying information.

The information theory techniques in this study focus on the estimation of the *information entropy*, or simply entropy in the sequel (Shannon, 1948; Sec. 2.1 of Cover and Thomas, 1991). Intuitively, the entropy of a source is a measure of how much uncertainty the output sequence of the source contains. For the case when the source is a humpback whale singing a sequence of units, the entropy measures how unpredictable the next unit in the song is. The structure of humpback song implies constraints on the order of the units produced. Because these constraints make the next unit in the song predictable, songs that are highly structured have a

reduced entropy. In contrast, songs composed of the same units but with less structure are more uncertain and less predictable, resulting in higher entropies for the sequence of units. The definition of mutual information (see Cover and Thomas, 1991, Theorem 2.4.1) implies that the entropy of a source establishes an upper bound on the amount of information conveyed by the source's output. A detailed analysis of humpback song using entropy estimates and correlation techniques showed that for whales singing on the Hawaiian breeding grounds, songs had strong structural constraints indicative of a hierarchical structure and conveyed a maximum amount of information of less than 1 bit/s (Suzuki *et al.*, 2006).

This study uses the same information theory techniques as Suzuki *et al.* (2006) in the analysis of song sequences produced by migrating Australian humpbacks. Entropy estimates were calculated using an independent identically distributed (iid) model, first-order Markov model, and nonparametric sliding window match length (SWML) method. In addition, both long-term and short-term correlations were computed for each song session. The objectives of the study were (1) to determine an upper bound on the amount of information potentially conveyed in the unit sequence of Australian whale song, (2) to determine if there is quantitative evidence that the songs are consistent with a hierarchical structure, and (3) to compare the entropy in the sequence of units produced by migrating Australian males to the sequence of units produced by males on the breeding grounds of Hawaii.

II. METHODS

Acoustic recordings of migrating humpback whales were made for six consecutive weeks off the coast of eastern Australia at Peregrine Beach as part of the Humpback Whale Acoustic Research Collaboration (HARC) (Noad *et al.*, 2004; Thode *et al.*, 2006; Dunlop *et al.*, 2007). A distributed horizontal array of five moored hydrophone buoys provided 228 h of humpback song recordings from September to October 2003. The buoys were configured in a T-shape with buoys 1–3 oriented parallel to shore at a distance of 1.5 km. The buoys were spaced approximately 700 m apart. Buoys 4 and 5 were positioned in a straight line perpendicular to the shore running offshore to the east of buoy 2 and were separated by approximately 600 m. A VHF radio transmitter in each buoy transmitted the signal from a High Tech MIN96 hydrophone with a built-in +40 dB preamplifier to a Royal Australian Navy type 8101 four-channel sonobuoy receiver or a Winradio receiver. In the absence of a song at a reasonable signal-to-noise ratio (SNR), acoustic sampling occurred for 2 min every 15 mins. When whale song was detected at a SNR that allowed the sequence of units be clearly discernible, continuous recording commenced via a National Instruments E-series data acquisition card and was stored to a computer hard drive. All channels were recorded simultaneously by ISHMAEL software (D. Mellinger, NOAA) at 22 kHz. ISHMAEL also performed localizations of singing whales using standard hyperbolic techniques (Noad *et al.*, 2004).

A human classifier manually sequenced the units in each song session using COOL EDIT PRO software that provided simultaneous playback of the acoustic signal and visual spectrogram. Song units were assigned letters as symbols (A, B, C, ...), and a dictionary of units specific to the eastern Australia humpback whale song in 2003 was created so that consistency was maintained over the course of the analysis. Biases associated with human classifiers were not strong enough to warrant the use of automated classifiers, as the work by Suzuki *et al.* (2006) showed that song structure analyzed by entropy estimation was robust to the choice of classifier. There was an approximate 5% disagreement between human classifiers in Suzuki *et al.* (2006), which indicated that classification was not always clear. Based on the low percentage of disagreement between human observers in the previous study, in addition to the substantial time and effort of employing multiple human classifiers, only one human classifier was utilized in this study. Units that stood out from the typical sequence of a phase or theme were double-checked for any error in classification or transcription.

Song sessions meeting the following criteria were considered for analysis: (1) uninterrupted, (2) a minimum of 300 consecutive units (approximately 20 min), and (3) independent with no overlap of other songs. If multiple song sessions were identified on the same day, acoustic localization and visual observations via theodolite were used to determine if multiple song sessions could be attributed to the same singer. In many instances song sessions from the same singer were interrupted or masked at times by passing ships. If multiple song sessions were identified as potentially coming from the same singer, only the longest song session of this singer was used in the analysis. A total of 48 song sessions ranging in length from 300 to over 3100 units were included in the analysis. This corresponded to song session durations of approximately 20 min–3.5 h.

The first phase of the analysis involved quantifying basic song session characteristics. Song alphabet size, statistical stationarity, and period were determined. A statistically stationary source has the same probability distribution at any point in time. Note that the statistical stationarity of the song should not be confused with the singing whale's physical movement, or lack thereof. This study focuses on the stationarity of singers in the statistical sense, not the physical sense, so references to stationarity in the remainder of the paper are understood to be in the statistical sense. The size of each song alphabet ($|A|$), or number of different discrete sound units, was tallied. Alphabet size limited the maximum entropy (H_{\max}) to $\log_2|A|$, which was attainable only if each classified unit was independently and uniformly distributed. The time invariance of the probability distribution of a stationary source implies that the autocorrelation function of a stationary source also does not vary with time. To check for stationarity, short-time (or partial) discrete autocorrelations were performed on the unit sequences at different points in the song session (Suzuki *et al.*, 2006) to determine if each song source (a singing humpback whale) was stationary.

The autocorrelations also provide a perspective on the ability of Markov sources to model humpback whale song. The probability distribution of a stationary source is the same

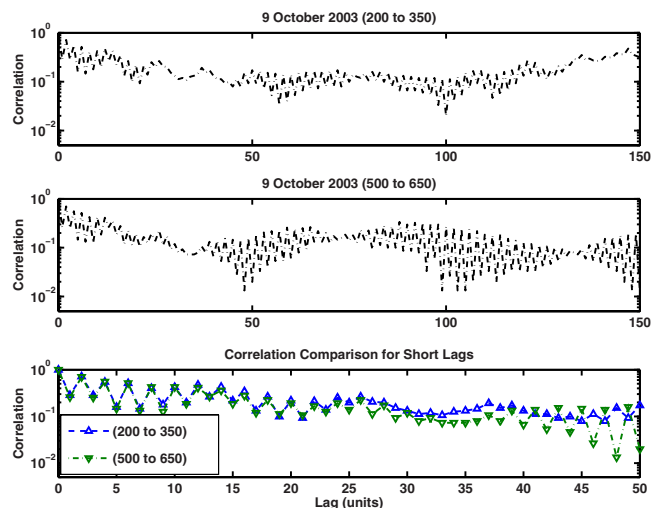


FIG. 1. (Color online) Two short-time autocorrelation estimates from song session 36. The top two panels plot the correlations for units in the ranges [200, 350] and [500, 650], respectively. Note that the correlation functions diverge substantially for lags greater than 100 units, indicating that the song is nonstationary. The third panel shows both correlations on the same axes for small lags. The values generally agree closely to each other with lags smaller than 30, indicating that the song may be considered locally stationary for lags less than 30 units.

at any point in time; consequently, the autocorrelation of a stationary source is the same at any point in the song. Any irreducible Markov model is a stationary source (Feller, 1960). The correlation function estimated from a finite realization of a song may fluctuate somewhat about the true correlation, but if the correlation function varies substantially at different points in the song, the source is not stationary and thus cannot be a Markov model. Partial song autocorrelation estimates were calculated using two nonoverlapping 151-unit song sections (Fig. 1). There was an order of magnitude divergence between the correlation functions for each song section, which indicated a nonstationary source. This lack of stationarity precludes a Markov source for the sequence of units in the song and implies that the song includes constraints beyond those embodied by a first-order or higher-order Markov model. However, comparison of the correlations showed that the songs could be considered locally stationary for lags less than 30 units. Local stationarity is a prerequisite for entropy estimation using the SWML estimator. A window length of 30 units was used as the maximum window size for the SWML estimator in the second phase of analysis. Entire song session autocorrelation estimates, or global autocorrelations, were computed to determine the periodicity of each song (Fig. 2).

In the second phase of analysis, three different entropy estimators were applied to each song session: (1) the iid model (H_{iid}), (2) the first-order Markov model (H_M), and (3) the SWML estimator (H_{SW}). The mathematical theory underlying each method and a comparison of the methods are in Suzuki *et al.* (2006). The iid model is based on the assumption that each song unit is statistically independent and identically distributed. There is no memory requirement associated with this model. In a first-order Markov model, the current unit depends on the previous song unit but not on any earlier units. This model presumes a structure that has a

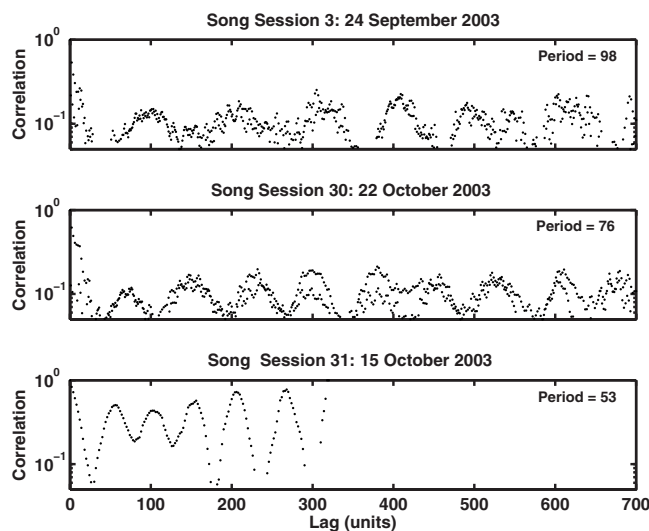


FIG. 2. Global autocorrelation estimates for three song sessions. Song session 3 had a song period of 98 units. Song session 30 had a song period of 76 units and song session 31 had a song period of 53 units.

memory of one unit. Most of our recordings lacked the length necessary to obtain accurate entropy estimates for higher-order Markov models (see Sec. I.B.5 of Suzuki *et al.*, 2006). Consequently, we limited our Markov model entropy estimation to first order and used the stationarity analysis discussed in the previous paragraph to rule out higher-order Markov models. The SWML entropy estimator relates the average length of a matching string of units within a fixed window to the entropy of the sequence (Wyner and Ziv, 1989). Based on the short-time correlation analysis, the range of window lengths used in this analysis was 10–40 units. The SWML estimator does not use a model and has the least restrictive assumptions, making it more applicable to a wider class of sources. The window size generating the minimum SWML entropy estimate for each song session is presented in parentheses after each value of H_{SW} in Table I. As noted in Sec. I.B.7 of Suzuki *et al.* (2006), the window size producing the minimum entropy estimate for the SWML estimator is a balance between a statistical bias if the window is too short and a violation of the local stationarity assumption if the window is too long.

We also used the SWML entropy estimate to estimate the redundancy (ρ) for each song session [Eq. (6) in Suzuki *et al.*, 2006]. Shannon (1948) defined redundancy to quantify the percentage that a message's length would be reduced when going from a coding using a naive representation, which requires H_{\max} bits/symbol to the optimal coder, which compresses the sequence to the source entropy H bits/symbol (Theorem 2 in Suzuki *et al.*, 2006). For example, a plain ASCII file uses 8 bits for each character, but a compression program can often compress an ASCII file to be much smaller. The difference in the lengths of these files, normalized by the original length of the ASCII file, is the redundancy ρ . Because the SWML estimator has a positive bias, the resulting estimates of redundancy actually underestimate the redundancy and may be considered a lower bound on ρ .

The entropy estimates were used to make two hypothesis tests for each song. The first test compared H_{iid} with H_M .

If H_M is significantly smaller than H_{iid} this indicates that the song source has sequential structure or memory, and knowing the current unit reduces uncertainty about the next unit. The second test compared H_M with H_{SW} for each song session. If H_{SW} is significantly smaller, this indicates the song source contains a structure whose memory extends beyond just one unit, as assumed by the first-order Markov model.

III. RESULTS

Table I summarizes the entropy data for all 48 song sessions analyzed. For each song session, the table presents the three entropy estimates H_{iid} , H_M , and H_{SW} measured in bits, as well as the song redundancy (ρ) for each song session. Song session duration is in units, the alphabet size is $|A|$, and the maximum possible entropy $H_{\max} = \log|A|$. Table II reports the maximum total information that could be conveyed by the sequence of units in each song. The estimated period (length) of the song was obtained from the global autocorrelation function. The final column in Table II represents the maximum information that could be conveyed by the sequence of units in the song and is the product of the song period and H_{SW} reported in bits. The average of the maximum information that could be conveyed per song at the unit level equaled 34.5 bits/song.

Global autocorrelations showed oscillations relating to the periodicity, or song length, during each song session (Fig. 2). The average song length was $97 (\pm 39)$ units. 4 of the 48 song sessions analyzed were considered to be composed of “aberrant” songs based on unit characteristics. In this study we defined aberrant songs as those substantially different from the typical song of the region at the unit level. This differs from the definition of aberrant song used by Frumhoff (1983), which discriminated at the level of song themes. Three of the songs we labeled as aberrant (song sessions 1, 16, and 45) used fewer than six of the units seen in the typical song. Song session 10 was considered aberrant because over 75% of the song units were not consistent with the units from the other songs recorded in the population and may have originated from another population, e.g., from the western Australian population. The songs of east and west coast males are typically very different due to differences in song units, but a small number of “foreign” singers have been previously cited as initiating a song exchange between the two populations (Noad *et al.*, 2000).

The results of the statistical analysis of the entropy estimates generated by the iid and Markov models are shown in Fig. 3. The confidence intervals were obtained by generating 1000 bootstrap sequences using an iid source whose distribution matched the observed distribution of symbols in the song (see Suzuki *et al.*, 2006 for details). The bound on the one-tailed 0.95 confidence interval associated with each circle reflects the 50th lowest of the first-order Markov model entropy estimates from the series of 1000 estimates obtained from the bootstrap sequences generated by the iid model. The confidence intervals do not overlap with any of the Markov entropy estimates for the actual songs leading to a rejection of the null hypothesis $H_{iid} \leq H_M$ for every song

TABLE I. Song session entropy estimates. $|A|$ is the song alphabet size. H_{\max} is the limit of maximum entropy based on alphabet size. Window size for the SWML estimator is (n) . The * denotes aberrant song sessions.

Song session	Date	Length (units)	A (units)	$\log_2 A $ H_{\max}	iid H_{iid}	Markov H_M	SWML $H_{\text{SW}}(n)$	Redundancy ρ
1*	9/24/2003	506	4	2.00	1.57	0.64	0.38(10)	0.81
2	9/24/2003	392	11	3.46	2.80	1.21	0.62(10)	0.82
3	9/24/2003	854	12	3.58	2.95	1.12	0.57(15)	0.84
4	9/26/2003	972	12	3.58	2.03	1.08	0.65(10)	0.82
5	9/26/2003	1355	13	3.70	2.78	1.19	0.51(14)	0.86
6	9/26/2003	976	14	3.81	2.90	1.07	0.41(13)	0.89
7	9/28/2003	797	8	3.00	2.49	0.79	0.28(12)	0.91
8	9/30/2003	869	17	4.09	2.70	0.83	0.15(16)	0.96
9	9/30/2003	885	13	3.70	2.82	1.06	0.45(14)	0.88
10*	10/1/2003	434	10	3.32	2.47	1.18	0.50(14)	0.85
11	10/1/2003	1624	10	3.32	2.41	0.98	0.29(13)	0.91
12	10/1/2003	332	10	3.32	2.62	1.08	0.53(15)	0.84
13	10/1/2003	640	12	3.58	2.92	1.03	0.37(14)	0.90
14	10/4/2003	447	7	2.81	1.87	0.88	0.30(10)	0.89
15	10/4/2003	707	11	3.46	2.75	1.10	0.47(10)	0.86
16*	10/29/2003	286	3	1.58	1.48	0.48	0.21(10)	0.87
17	10/29/2003	594	9	3.17	2.44	0.94	0.29(13)	0.91
18	10/29/2003	547	6	2.58	2.23	0.93	0.28(10)	0.89
19	10/29/2003	798	13	3.70	2.72	1.13	0.34(13)	0.91
20	10/29/2003	3166	13	3.70	2.80	1.19	0.43(12)	0.88
21	10/28/2003	527	10	3.32	2.40	0.84	0.34(14)	0.90
22	10/7/2003	377	9	3.17	2.37	0.98	0.29(13)	0.91
23	10/7/2003	835	12	3.58	2.98	1.15	0.69(14)	0.81
24	10/27/2003	610	7	2.81	1.91	0.79	0.19(10)	0.93
25	10/30/2003	501	8	3.00	2.24	0.94	0.22(10)	0.93
26	10/10/2003	1400	9	3.17	2.24	0.81	0.23(13)	0.93
27	10/10/2003	954	9	3.17	2.64	1.05	0.35(10)	0.89
28	10/13/2003	352	12	3.58	2.82	0.98	0.44(15)	0.88
29	10/19/2003	649	11	3.46	2.62	0.88	0.35(13)	0.90
30	10/22/2003	1912	12	3.58	3.04	1.14	0.59(10)	0.84
31	10/15/2003	322	6	2.58	1.97	0.91	0.39(10)	0.85
32	10/15/2003	583	11	3.46	2.85	1.09	0.60(10)	0.82
33	10/14/2003	2311	12	3.58	2.59	0.98	0.36(14)	0.90
34	10/8/2003	646	12	3.58	2.61	1.01	0.28(10)	0.92
35	10/8/2003	2543	16	4.00	2.97	1.12	0.51(13)	0.87
36	10/9/2003	844	12	3.58	3.03	1.09	0.49(13)	0.86
37	10/9/2003	507	12	3.58	2.78	1.00	0.36(13)	0.90
38	10/9/2003	1026	12	3.58	2.56	0.91	0.30(13)	0.92
39	10/11/2003	628	11	3.46	2.43	0.92	0.28(14)	0.92
40	10/11/2003	333	11	3.46	2.90	1.21	0.47(10)	0.86
41	10/26/2003	685	6	2.58	1.76	0.65	0.20(10)	0.92
42	10/12/2003	1192	13	3.70	2.88	1.04	0.36(13)	0.9
43	10/20/2003	1112	11	3.46	2.63	0.93	0.45(14)	0.87
44	10/24/2003	446	13	3.70	3.06	1.13	0.51(10)	0.86
45*	10/24/2003	696	5	2.32	1.95	0.62	0.20(13)	0.91
46	10/21/2003	346	8	3.00	2.11	0.73	0.26(10)	0.91
47	10/23/2003	613	8	3.00	2.30	0.92	0.32(15)	0.89
48	10/23/2003	528	8	3.00	2.05	0.68	0.31(14)	0.90

session. This suggests that the iid model does not adequately represent the structure of the recorded humpback song.

Comparison of the entropy estimates generated by the Markov model for the actual song sequence (H_M) and SWML estimates (H_{SW}) is shown in Fig. 4. The 95% confidence interval on H_{SW} was calculated under the null hypothesis that the song was generated by a first-order Markov source. This confidence interval was obtained by generating

1000 bootstrap sequences using a first-order Markov source whose transition probabilities match the observed symbol transitions in the song (see Suzuki *et al.*, 2006 for details). The bound on the one-tailed 0.95 confidence interval associated with each square reflects the 50th lowest of the SWML entropy estimates from the series of 1000 estimates obtained from the bootstrap sequences generated by the Markov model. The confidence intervals overlap with only one of the

TABLE II. Total information in the unit sequence of song sessions. Bits is a measure of song information content calculated from the product of the song period and H_{SW} . The * denotes aberrant song sessions.

Song session	SWML H_{SW}	Period	Bits
1*	0.38	41	15.7
2	0.62	56	34.8
3	0.57	98	55.6
4	0.65	77	50.5
5	0.51	115	58.7
6	0.41	112	45.9
7	0.28	179	49.9
8	0.15	282	43.5
9	0.45	75	33.8
10*	0.50	120	60.4
11	0.29	119	34.9
12	0.53	62	32.7
13	0.37	90	33.3
14	0.30	72	21.6
15	0.47	79	37.1
16*	0.21	69	14.5
17	0.29	74	21.5
18	0.28	75	21.0
19	0.34	110	37.4
20	0.43	88	37.8
21	0.34	81	27.5
22	0.29	90	26.1
23	0.69	75	51.8
24	0.19	91	17.3
25	0.22	144	31.7
26	0.23	117	26.9
27	0.35	122	42.7
28	0.44	91	40.0
29	0.35	83	29.1
30	0.59	76	44.8
31	0.39	53	20.7
32	0.60	53	31.8
33	0.36	125	45.0
34	0.28	89	24.9
35	0.51	112	57.1
36	0.49	80	39.2
37	0.36	111	40.0
38	0.30	73	21.9
39	0.28	184	51.5
40	0.47	83	39.0
41	0.20	73	14.6
42	0.36	121	43.6
43	0.45	82	36.9
44	0.51	77	39.3
45*	0.20	110	22.0
46	0.26	100	26.0
47	0.32	79	25.3
48	0.31	73	22.6

SWML entropy estimates leading to a rejection of the null hypothesis $H_M \leq H_{SW}$ for almost every song session. This suggests that a first-order Markov model does not accurately model the structure of the recorded humpback song. This is consistent with our conclusion based on the short-term correlations that the song is not stationary and therefore cannot be modeled by a Markov model.

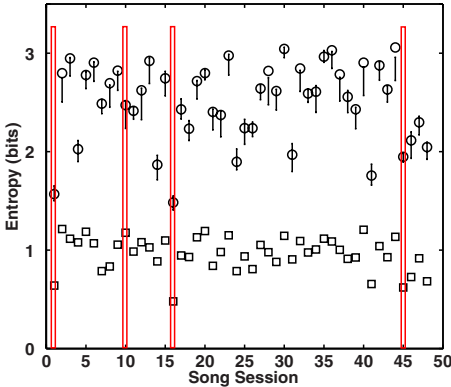


FIG. 3. (Color online) H_{id} values (circles) and H_M values (squares) for all song sessions in Table I. The one-tailed 95% confidence intervals extending from each circle indicate the lower limit on H_M under the null hypothesis that the song was generated by an iid source. The confidence intervals do not overlap with any of the H_M values leading to a rejection of the null hypothesis $H_{id} \leq H_M$ for every song. The vertical bars indicate aberrant song sessions.

Aberrant song sessions are indicated in Figs. 3 and 4 by bar markers. On average, the iid and Markov model entropy estimates of aberrant song sessions had entropy estimates less than most of the nonaberrant song sessions. However, the statistical comparison of the entropy estimates for the aberrant song sessions was consistent with that of the nonaberrant song sessions. This implies that the structure of the aberrant song sessions are not adequately modeled by either the iid or first-order Markov models, even though these sessions use a smaller set of units. Song session 10 showed no overall difference in entropy value or statistical significance compared to nonaberrant song sessions.

Figure 5 shows the relationship between H_{SW} and the song period. As a general trend, as the song period increased, the entropy decreased suggesting that longer songs are more predictable. The average amount of information per song (34.5 bits) is illustrated in Fig. 5 by the line $34.5=xy$.

IV. DISCUSSION

This work is consistent with the original proposal by Payne and McVay (1971), supported qualitatively by many

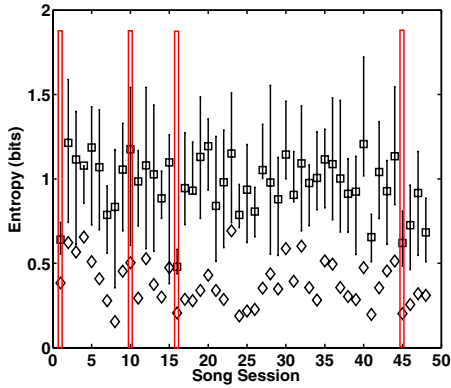


FIG. 4. (Color online) H_M values (squares) and H_{SW} values (diamonds) for all song sessions in Table I. The one-tailed 95% confidence intervals extending from each square indicate the lower limit on H_{SW} under the null hypothesis that the song was generated by a Markov source. The confidence intervals overlap with the H_{SW} value at song 15. The vertical bars indicate aberrant song sessions.

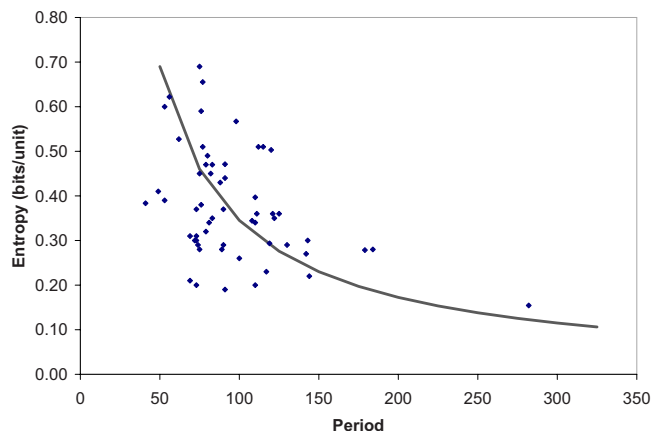


FIG. 5. (Color online) Source entropy as a function of song period. The solid line represents the best fit of a model where the average total information in a song (34.5 bits/song) is constant.

studies (e.g., Winn and Winn, 1978; Payne, 1983; Cato, 1991) and recently supported quantitatively by Suzuki *et al.* (2006), that the sequence of units of humpback song has a hierarchical structure. The periodicity of song within song sessions, ranging from 41 to 282 units, was illustrated in global autocorrelations (Fig. 2). Correlation analysis also indicated that humpback song is nonstationary; thus, there are more structural constraints in the whale song than the first-order or higher-order Markov models can accurately represent. Local stationarity was evident for lags less than 30 units, which supported the application of the SWML estimator. Bootstrap analysis of entropy values generated by the iid, first-order Markov model, and SWML estimator methods revealed that the SWML entropy estimates are significantly lower for the 2003 Australian humpback song produced during migration than both the iid and first-order Markov model estimates. The pattern of longer songs having lower entropy values and being more predictable is consistent with Guinee and Payne's (1988) suggestion that longer songs have a more redundant structure. This reduces the uncertainty about the next unit in any sequence and thus reduces the source entropy. Reducing the entropy while increasing the length of the song conserves the total information required to produce the song, at least in a loose sense. The proportion of aberrant song sessions composed approximately 8% of the song sessions analyzed; however, most of the aberrant song sessions yielded entropy estimates consistent with those of the typical song sessions recorded in the region.

Three of the four Australian migration songs classified as aberrant were due to low unit diversity. Although their entropy values did not differ from the values of the typical songs, their occurrence raises questions as to what the aberrant songs represent. It is possible that the aberrant songs are produced by juvenile males learning the song in which case they may be "age appropriate" rather than aberrant *per se*. Low unit diversity may also be a symptom of memory or language/speech disabilities similar to those occurring in humans (Cantwell and Baker, 1987; Gillam, 1998). As songs are believed to be an important element of the humpback mating system (Winn and Winn, 1978; Tyack, 1981; Darling

and Bérubé, 2001), how the production of aberrant song affects reproductive fitness is unknown.

It is interesting to compare the results from this analysis with those reported for Hawaiian humpbacks on the breeding grounds in Suzuki *et al.* (2006), even though these populations are both spatially and temporally distant from each other. There are statistically significant differences between the entropies ($p < 0.001$), song periods ($p < 0.001$), and alphabet sizes ($p < 0.001$) for the two populations (Wilcoxon rank-sum test for nonparametric data). The Australian songs had lower entropy values, shorter song periods, and smaller alphabet sizes. In addition, the average information content of the unit sequence in the 2003 eastern Australian humpback song produced during migration in this study (34.5 bits/song) was less than that reported by Suzuki *et al.* (2006) (130.3 bits/song) for humpback song produced on the breeding grounds of Hawaii in 1976–1978. In contrast, the redundancy ρ for the two populations was not significantly different (Wilcoxon rank-sum, $p = 0.20$).

There are several potential explanations for the difference in information content between the two songs. First, it is possible that song content and structure differ extensively between different humpback populations. In general, the 1976–1978 Hawaiian songs analyzed in Suzuki *et al.* (2006) both were longer and had higher entropies than the 2003 Australian songs analyzed here. Given that both the entropies and song lengths are significantly different between the populations, it is not surprising that the total information content of the songs differ. Either increasing the length of the song or the entropy of the song will increase the total number of bits per song. Additionally, the Hawaiian songs used a larger number of units. What warrants attention is that in spite of all these changes, the redundancy did not vary much. This implies that the larger values of H_{\max} for the Hawaiian songs also have proportionally larger entropies H . The entropy and correlation analyses indicate that both populations employ the same general structure for their songs, i.e., the hierarchical model proposed by Payne and McVay (1971). Given that both populations use the same general class of structure for their songs, the consistent redundancy estimates raise the interesting possibility that these temporally and spatially distinct groups have about the same level of structure constraints within their hierarchical songs. It would be interesting to compare with other populations to see if this is something fundamental in the song production centers of the humpback brain or simply coincidence. If song length and predictability are functions of population, while the redundancy remains roughly the same, the difference in selective pressures driving the difference in song structure between populations is of interest. Exploration of this would require quantitative analyses of songs from different populations over time and such studies, particularly including both Northern and Southern Hemisphere songs, have not yet been conducted.

A second explanation for these differences relating to possible song function is that differences in the unit sequence of song may be a result of seasonal behavior. The Hawaiian whales were recorded on the breeding grounds during winter, whereas the Australian whales were recorded during the

spring migration in transit to the feeding grounds. Change in song structure may reflect a shift in the seasonal behavioral state, which may or may not relate to differences in song function. That breeding ground song is innately more complex than migratory song, however, seems highly unlikely as there is no other evidence that the two are different. Indeed, in the South Pacific, east Australian migratory song and New Caledonia breeding ground song are usually almost identical despite being from different populations (Helweg *et al.*, 1998). If the breeding ground songs are longer, the song is often lengthened by repeating phrases more within a theme and not by adding units to phrases or new themes to the song. Migrating singers may sing shorter songs as a way of reducing the proportion of time singing compared with their counterparts on the breeding grounds if there is a greater cost in singing during migration. The increased energetic demands of actively swimming while singing during migration versus drifting on the breeding grounds (Noad and Cato, 2007) may have an effect, or migrating whales may minimize the time singing in order to minimize the delay in returning to the feeding grounds compared with the faster swimming nonsinging whales. However, a comparison of singing between the east Australian migration and the Hawaiian breeding grounds did not find a significant difference in the proportion of whales singing (Cato *et al.*, 2001), which suggests that there may be no significant difference in the proportion of time whales spent singing (assuming the proportions of singers in two populations were the same). Whales are also reported to sing on the feeding grounds (Clapham and Mattila, 1990; Clark and Clapham, 2004). Analysis of song from the same population during different seasons will be necessary to address the question of difference in song structure being attributed to seasonal behavior. As with innate population differences, however, song length itself is very unlikely to account for the full discrepancy between the east Australian and Hawaiian results.

A third explanation for the observed difference in entropy between the two songs is that it results from year by year variations in entropy within any population, and the Hawaiian song happened to be in a period of higher entropy and the Australian song in a period of lower entropy at the times of recording. The humpback whale song in any population changes with time, and this includes changes in pattern or structure. For example, recordings of migrating whales off the east coast of Australia indicated a period of relatively unstructured song in 1985 compared to songs in prior or following years, including a highly structured song in 1982 (Cato, 1991). Entropy analyses for a series of years for each of these populations would be required to determine the range in variation of entropy over a series of years and whether the differences between the two populations are significant compared to the temporal variation. This work illustrates the power of information entropy as a tool for objectively investigating the structure and information content of the sequence of units in humpback song. These techniques could be used to address temporal variation as suggested above and other interesting questions relating to humpback whale song.

Comparing the information and entropies between geographically and temporally distinct populations may be less informative than longitudinal studies of the same population. As reported above, less information was observed to be contained in the unit sequence of songs of migrating Australian whales in 2003 compared to Hawaiian whales on the breeding grounds in 1976–1978, while the redundancy of the songs was roughly constant. This indicates that there can be substantial variations in the information in the songs, which may be because of differences between populations, in behavior over the season, or as a result of year by year variation in the song. It raises questions associated with song function, selective pressures influencing whale song, and other potential avenues for information transfer within songs in addition to the unit sequence. Information theory techniques will be instrumental in quantitatively comparing song sequences produced among different populations, between whales during migration and at migration termini, and by whales in the same population in different years in order to address questions raised here. Exploration of song characteristics other than unit sequence and of the ability of these other characteristics to convey information through the underwater acoustic channel will further advance our understanding of humpback whale song.

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