

Temporal stability and change in the social call repertoire of migrating humpback whales

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Quantifying the stability of a species vocal repertoire is fundamental for further investigations into repertoire function and geographic variation. Changes to the repertoire of sounds used in the song displays of male humpback whales have been well studied. In contrast, little is known about the stability of this species' non-song vocal calls. The stability of the social call repertoire of east Australian humpback whales was investigated from 1997, 2003–2004, and 2008. Out of 46 qualitatively defined call types, 19 were classified as “song-unit calls” that tended to change with the song, and 15 were “inconsistent” and only found in one or two years. Twelve call types were “stable” and present in all years and were commonly produced (64.2% of calls). Stable calls tended to vary in some of the measured call parameters but there was no clear trend between years. This result could indicate that minor changes to calls are not permanent, but reflect individual differences in call production or the graded nature of calls within different social environments. This research has clearly identified stable calls in the call repertoire of humpback whales and while their function is not well understood, their stability suggests an important role in social interactions.

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I. INTRODUCTION

Investigating the stability of a communication system over time can provide valuable insights into the social and physical processes shaping the evolution of vocal signals (Tyack and Sayigh, 1997; Rendell and Whitehead, 2005), and is a crucial first step in determining the functions of vocal signals and/or repertoire function (Pozzi *et al.*, 2010). Temporal changes in communication systems have been documented across a wide range of mammalian and avian taxa, such as marine mammals (e.g., harp seal *Pagophilus groenlandicus*, Serrano and Terhune, 2002; killer whale *Orcinus orca*, Ford, 1991; sperm whale *Physeter macrocephalus*, Rendell and Whitehead, 2005; humpback whale *Megaptera novaeangliae*, Winn and Winn, 1978), primates (e.g., common chimpanzee *Pan troglodytes schweinfurthii*, Mitani and Gros-Louis, 1998) and birds (e.g., black-capped chickadee *Poecile atricapillus*, Baker and Gammon, 2006). Changes to vocal signals can occur through the loss or acquisition of entire call types from a species' repertoire (call repertoire change), and/or through modification over time of certain structural characteristics of calls, such as duration or frequency characteristics of the sound (fine-scale variability within call type categories) (e.g., killer whale vocal repertoires, Ford, 1991; Deecke *et al.*, 2000). Both kinds of variability may occur due to interactions with the social and physical environment (e.g., Daniel and Blumstein, 1998; Parks *et al.*, 2007), genetic or cultural drift over time (e.g.,

Lynch, 1996; Deecke *et al.*, 2000), or a complex interaction of the above factors (Griebel and Oller, 2008).

The stability of a species' call repertoire may relate to the functions of specific calls within a species' social environment. For example, calls functioning to maintain territories and/or attract females may change over time depending on interactions with conspecifics. Village indigobirds (*Vidua chalybeata*) and yellow-rumped caciques (*Cacicus cela*) modify their song displays over time based on social competition amongst males and sexual selection (Payne, 1985). In species that have variable repertoires, there may be selection pressure to conform to novel sound types, leading to modifications over time. In contrast, calls functioning to maintain contact among social group members, and coordinate group dynamics, are more likely to remain stable. Killer whales, for example, produce “discrete” calls, which generally persist in the repertoire over long time periods (Ford, 1991; Deecke *et al.*, 2000; Riesch *et al.*, 2006). Killer whales live in stable matrilineal social groups, and these calls are generally pod specific or shared among acoustic clans and thought to function in group cohesion (Ford, 1991). Presumably, if specific call types or a call repertoire had an important function in social interactions, it would be disadvantageous for those to change over time (Riesch *et al.*, 2006). The persistence of stable calls within repertoires may occur through conformity-enforcing behavior (Lachlan *et al.*, 2004), in which incorrect copying of stable call types leads to ineffective communication between signaler and receiver and thus negative consequences for the signaler. Individual call types within call repertoires, however, may still be subject to variability in their fine-scale structural parameters over time,

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even though the overall call contour may remain stable (e.g., as found in killer whale discrete calls; [Deecke et al., 2000](#)).

Fine-scale structural variability within call type parameters (e.g., in call frequency or duration) may occur due to a number of reasons, such as cultural drift (e.g., [Lynch, 1996](#); [Deecke et al., 2000](#)), genetic differences (e.g., [Janik and Slater, 1997](#)), social influences (e.g., [Owings and Morton, 1998](#)), or evolution in response to changing environments (e.g., [Morton, 1977](#)). Changes to call parameters may be permanent (as may occur through cultural or genetic drift), or they may be short-term shifts in call parameters (as may occur in response to changing social environments). Cultural drift, through copying error, is considered to be a factor in the modification of some of the killer whales' discrete calls and "whistles" over time ([Ford, 1991](#); [Deecke et al., 2000](#)). However, these calls may also be affected by short-term shifts in response to changing social environments ([Ford, 1991](#)); for example, the addition of broadband or harsh elements to call types may reflect the motivational or emotional state of the signaler ([Owings and Morton, 1998](#)). Changing acoustic environments can also lead to changes in call parameters, such as the increase in call frequency of North Atlantic and Southern right whales (*Eubalaena glacialis* and *Eubalaena australis*), which may be in response to increased ambient noise levels over both short and long time scales ([Parks et al., 2007](#)). The differences shown in the stability of call repertoires and/or call types across a range of species appear to reflect call use within different social and physical environments. Therefore, understanding these levels of stability is an important first step in determining the function of signals within a species' social and physical environment ([Pozzi et al., 2010](#)).

Humpback whales are a model species in which to investigate stability and variation in vocalizations. Humpback whale song is one of the best examples of a changing vocal display, in which an apparent quest for novelty drives continuous population-wide changes to the males' song ([Noad et al., 2000](#); [Cerchio et al., 2001](#)). Songs are composed in a hierarchical manner, with individual sound types or units sung in a specific order to create phrases, which are then repeated to create a number of different themes, and sets of themes are repeated to form a song ([Payne and McVay, 1971](#); [Payne et al., 1983](#)). Changes to song generally occur through modifications or replacements of units within phrases and at times, entire themes ([Winn and Winn, 1978](#); [Payne et al., 1983](#)), which are transmitted horizontally within the population via vocal learning ([Payne et al., 1983](#); [Noad et al., 2000](#); [Garland et al., 2011](#)). Humpback whales also produce "social sounds" ([Winn et al., 1979](#); [Tyack, 1983](#); [Silber, 1986](#); [D'Vincent et al., 1985](#); [Thompson et al., 1986](#); [Dunlop et al., 2007](#); [Dunlop et al., 2008](#); [Stimpert et al., 2007](#); [Stimpert et al., 2011](#)), but there has been comparatively little research on the structure, function, and stability of these calls.

In contrast to song, social sounds are produced by males, females, and calves and are thought to be important in closer-range social interactions ([Winn et al., 1979](#); [Tyack, 1983](#); [Dunlop et al., 2007](#); [Dunlop et al., 2008](#); [Zoidis et al., 2008](#)). Social sounds are defined as vocalizations that lack

the rhythmic pattern and repetition of song ([Tyack, 1983](#); [Silber, 1986](#)) and include surface-generated sounds (e.g., breaching, pectoral, and tail slapping; [Dunlop et al., 2007](#)). This paper provides an analysis of vocal social sounds referred to hereafter as "social calls." [Dunlop et al. \(2007\)](#) found that a number of social calls were similar to song units, suggesting these social calls may also change over time and contribute to temporal instability in the social call repertoire. Other social calls were isolated that were found to be produced within specific social contexts ([Dunlop et al., 2008](#)). If particular calls are used in specific contexts it seems likely that some level of stability is required to maintain call function.

In this paper, we investigated the stability of the social call repertoire of humpback whales by addressing four aims. (1) We describe a call repertoire for the east Australian population during migration for the years 1997, 2003–2004, and 2008 and identify call types that persisted in the call repertoire over these years. (2) We explore the relationship between the song and social call repertoires over the study period. (3) We use quantitative methods to compare the qualitatively assigned social call categories and to validate call classification. (4) We investigate the stability of measured call parameters of common and stable call types in the call repertoire.

II. METHODS

A. Data collection

Song and social call recordings were collected during the September/October southward migration of humpback whales on the east coast of Australia. Social calls and song units were isolated from recordings collected in 1997, 2003, 2004, and 2008 and song units were also isolated from recordings collected in 1996, 1998, 2002, 2005, 2007, and 2009. Recording locations were within 600 km of each other, between Harvey Bay, Queensland (25°00'S, 153°00'E), and Byron Bay, northern New South Wales (28°43'S, 153°37'E).

Recordings were collected using a single hydrophone suspended from a boat, or from a moored radio-linked, hydrophone buoy array. The single hydrophone recordings were collected using either a (i) Cleavite CH17 or GEC Marconi SH101X hydrophone with external 40 dB gain pre-amplifier connected to a Sony digital audio tape (DAT) recorder (32 kHz sample rate, 12 bit) or (ii) High Tech HTI-96-MIN hydrophone with built in 40 dB gain pre-amplifier, connected to an M-Audio Microtrack digital recorder [waveform audio files (WAV), 22 or 44.1 kHz sample rate, 16 bit]. The DAT recordings were re-sampled to a desktop computer for analysis using a Soundblaster sound card while the Microtrack recordings were copied to a computer as intact WAV files.

The moored hydrophone-buoy systems were comprised of a surface buoy containing a custom-built pre-amplifier (+20 dB gain) and 41B sonobuoy VHF radio transmitter (AN/SSQ-47A). The signals from the buoys were transmitted in real-time to shore via the VHF sonobuoy transmitters and received at a shore station using a Yargi antenna

attached to a type 8101, four-channel sonobuoy receiver. The hydrophones used were either GMC-Marconi SH101X hydrophones connected to a RANRL +40 dB pre-amplifier, with recordings made on either an analog four-track Tascam 424 tape recorder or a Sony DAT recorder, or High Tech HTI-96-MIN hydrophones with built-in +40 dB pre-amplifier, recording directly to a computer using a National Instruments E-series data acquisition card running *ISHMAEL* software (Mellinger, 2001), usually at a sampling rate of 22 kHz, 16 bit depth on each channel. The hydrophone buoy system comprised from one to five hydrophone buoys anchored in 18–28 m of water. The buoys were positioned at a distance of 1.5 to 3 km offshore depending on the number and arrangement of the buoy system (see Dunlop *et al.*, 2007 for detailed methodology on the hydrophone buoy configuration and setup). The frequency response of the different systems used over the 12 years of data collection was, at worst, 30–20 kHz \pm 3 dB measured across the entire recording system including the hydrophone buoy radio link.

Social calls had to have a “good” signal-to-noise ratio (SNR) of at least 10 dB above background noise to be used in the final analysis with the entire call clearly distinguishable from background noise to enable accurate measurement of call parameters. The SNR of a subset of calls from each year were calculated using SPECTRAPLUS (Pioneer Hill Software) to validate the qualitative assessment of good call quality. Both song and social calls were opportunistically collected from these recordings with no concurrent behavioral observations of the vocalizing or singing individual/group. All calls deemed to have a good SNR were isolated from the recordings and used for further analysis. Only social call types found in more than one recording from different days, or more than 4 h apart in the same recording, were included in the analysis. As whales were moving through the study area, a minimum of 4 h or more between social calls in a recording was considered sufficient to attribute any calls to a new individual/group. If call types were found in only one group in one year, but were heard across multiple years, they were included in the analysis. This was to ensure that the call types utilized in the analysis were from multiple different groups, and representative of the call repertoire of the population, rather than being aberrant individual call types.

B. Qualitative classification of calls

Qualitative call classification was carried out by aural and visual classification of calls into call types based on spectrographic characteristics. Spectrograms of calls were produced using Spectrogram 14 (R. Horn, Visualization Software) with 4096 point fast Fourier transforms (FFT) and 5.4 Hz frequency resolution (used for lower frequency sounds), or Raven 1.3 (Cornell Lab of Ornithology) with 1024 point FFTs, Hamming window, 21 Hz resolution and 75% overlap (used for higher frequency sounds). Initial classification of calls was carried out by a single observer (MR), using a catalogue of social calls heard in the east Australian population during migration, initially outlined by Dunlop *et al.* (2007). The data collected in 2003 and

2004 were the same sounds used by Dunlop *et al.* (2007), although all call classifications and call measurements were checked by MR (re-measured or re-classified where necessary) and call classification was standardized to ensure consistency. Due to limited sample sizes in both 2003 and 2004 for some call types, all data were pooled from these two adjacent years and are hereafter referred to as 2003–2004 data. All call types in the qualitatively determined catalogue were divided into three types: stable if they were present in all three sets of data (1997, 2003–2004, and 2007), inconsistent if they were only present in one or two years, and song-unit calls if they were similar to units of the song, regardless of the number of time periods in which they were heard.

C. Comparison of song units and social calls

Humpback whale song units from the study population between 1996 and 2009 were identified for comparison with the social call catalogues of 1997, 2003–2004, and 2008. The song type of the east Australian population has undergone considerable change over this 1996 to 2009 period, with the song type undergoing at least four complete replacements where the song bore no similarities to the previous years song (Garland *et al.*, 2011). We therefore decided that it was appropriate to only compare song units from years directly surrounding the study years to investigate similarities between song units and social calls. Song units were isolated from 1996–1998 for comparison to the social call repertoire of 1997, from 2002–2005 for comparison to the social call repertoire of 2003–2004 and from 2007–2009 for comparison to the social call repertoire of 2008. Individual units were classified into “types” based on aural and visual differences, as has been described in other studies of humpback whales’ songs (e.g., Payne and McVay 1971; Noad *et al.* 2000; Garland *et al.* 2011). A representative sample of unit types was taken from a pool of at least two singers in each year in question to compare to the social call repertoire. Matching of social calls to song units was carried out subjectively by comparing calls visually using spectrograms as well as aurally to assess similarity.

D. Quantitative classification of calls

Variables were measured and extracted by hand from the spectrographic samples of all social calls for statistical analysis. Measurements were made on the fundamental frequency of the sound for harmonic sounds, or the lowest frequency component of the call for dense harmonic sounds that contained a significant broadband component. Temporal parameters measured included the duration of the signal, number of inflections and number of call repetitions if the calls were always produced as a repetition of the same call type (see Table I). Call repetitions were counted where call types were consistently repeated. Call repetitions were typically clear groupings of the same call type that occurred with \sim 2-s intervals between adjacent calls. The frequency parameters measured included frequencies at the start and end of the sound, minimum and maximum frequencies, peak frequency, frequency trend ratio, and frequency range

TABLE I. Description of measured variables used in analyses characterizing different call types.

Measurement	Description
Duration (s)	Total call duration
Number of inflections	The number of times the call changes from ascending to descending frequency or vice versa
Number of call repetitions	Number of repeats of the same call type (only if always produced as call repetitions)
Log minimum frequency (Hz)	Minimum frequency of the fundamental frequency
Log maximum frequency (Hz)	Maximum frequency of the fundamental frequency
Log start frequency (Hz)	Start frequency of the fundamental frequency
Log end frequency (Hz)	End frequency of the fundamental frequency
Log peak frequency (Hz)	Frequency of the spectral peak
Frequency range (as ratio)	Maximum frequency/minimum frequency
Frequency trend (as ratio)	Start frequency/end frequency

(see Table I). Frequency measurements were converted to a logarithmic scale for further analysis to account for the logarithmic rather than linear perception of pitch by mammals (Richardson *et al.*, 1995). This was also taken into account by using a ratio of frequencies for “frequency range” and “frequency trend” rather than the differences of frequencies (e.g., a one octave range in frequencies would give a consistent frequency range of two instead of being an absolute value relative to the frequencies used if simply using the difference between frequencies).

The call types in the qualitatively assigned call type catalogue, created from spectral and aural inspections of spectrograms, were tested quantitatively using classification tree or recursive partitioning analysis (Rpart; R Development Core Team, 2012). When classifying the original social sound repertoire for this population, Dunlop *et al.* (2007) utilized both principal component analysis (PCA) and discriminant function analysis (DFA) to validate the qualitatively classified call categories. Dunlop *et al.* (2007) advocated using DFA over PCA as they argued that reducing the variables to a small number of factors (as done by PCA) loses important acoustic information that may discriminate between different sound types. DFA uses a linear combination of values (canonical functions) from two or more independent, discriminating variables that best group cases into their *a priori* assigned classes. There are, however, many assumptions that must be met for DFA to be utilized, including normal distributions of discriminating variables, uncorrelated discriminating variables, homogeneity of variances and independence of samples. DFA is also sensitive to outliers (McGarigal *et al.*, 2000). Classification trees, by contrast, offer many advantages over DFA because they do not assume any specific distributions of variables, are not influenced by outliers and correlated or collinear variables act to strengthen the analysis by providing additional information through the generation of surrogate variables (Breiman *et al.*, 1984). In

addition, all variables are considered at each split in the tree and the variable containing the most information relating to the split is used, solving the problems found with the PCA and DFA analysis. As we wanted to consider all measured variables when classifying calls (Table I), and many of the assumptions of DFA were not met for our data, we used classification trees to provide statistical validation for the *a priori* classification scheme.

The classification trees, which were performed first on all call types and then on just the subjectively classified stable call types, were produced by specifying criteria about when a node (a grouping of calls) should be split. For the initial split, all calls were considered and split into two nodes, and so on, until either all calls were used, or the node could not be split further due to its containing too few cases. The splitting criterion used was the Gini index, which is a commonly used measure of impurity or “goodness of split” (Breiman *et al.*, 1984). All variables were considered separately in each splitting decision and ranked according to the Gini index. The split that minimized the impurity (splitting error) of the node, using the chosen variable, was then selected. As data could continue to be split until each case occupied its own node, decisions about when to stop growing the tree were made by overgrowing the tree, and then pruning upwards until reaching the tree with the lowest true misclassification rate (Breiman *et al.*, 1984). Cross validation (V-fold cross validation with 50 subsets) was performed before pruning to ensure the best predictive tree was chosen with the smallest estimated error. The smallest tree was selected based on the 1 SE rule specified by Breiman *et al.* (1984), which chooses the smallest tree within 1 SE of the tree with the least classification error.

E. Fine-scale parameter analysis of stable call types

A subset of identified stable call types was chosen for further analysis using linear mixed models to investigate the fine-scale stability of measured parameters. The call types were chosen based on whether they had sufficient sample sizes in all years and were correctly classified by the classification tree (Fig. 1). Models were fitted with the nlme package in R (R Development Core Team, 2012), using the restricted maximum likelihood (REML) method, as this method is less sensitive to outliers, which were an issue in the data. Mixed models were used because they take care of the non-independence of data by modeling the random effect (Crawley, 2007). The variables “log minimum frequency,” “log maximum frequency,” “log peak frequency,” “duration,” and frequency range were used as response variables in the models. The first three of these satisfied the assumption of Gaussian distribution. Both duration and frequency range were non-normally distributed, so were logged to achieve a normal distribution. These five response variables were chosen, as they characterize the structure of calls within call type categories. Variables that were important for discriminating between call types, such as “number of call repetitions” and “number of inflections,” were not included in the models, as these variables are

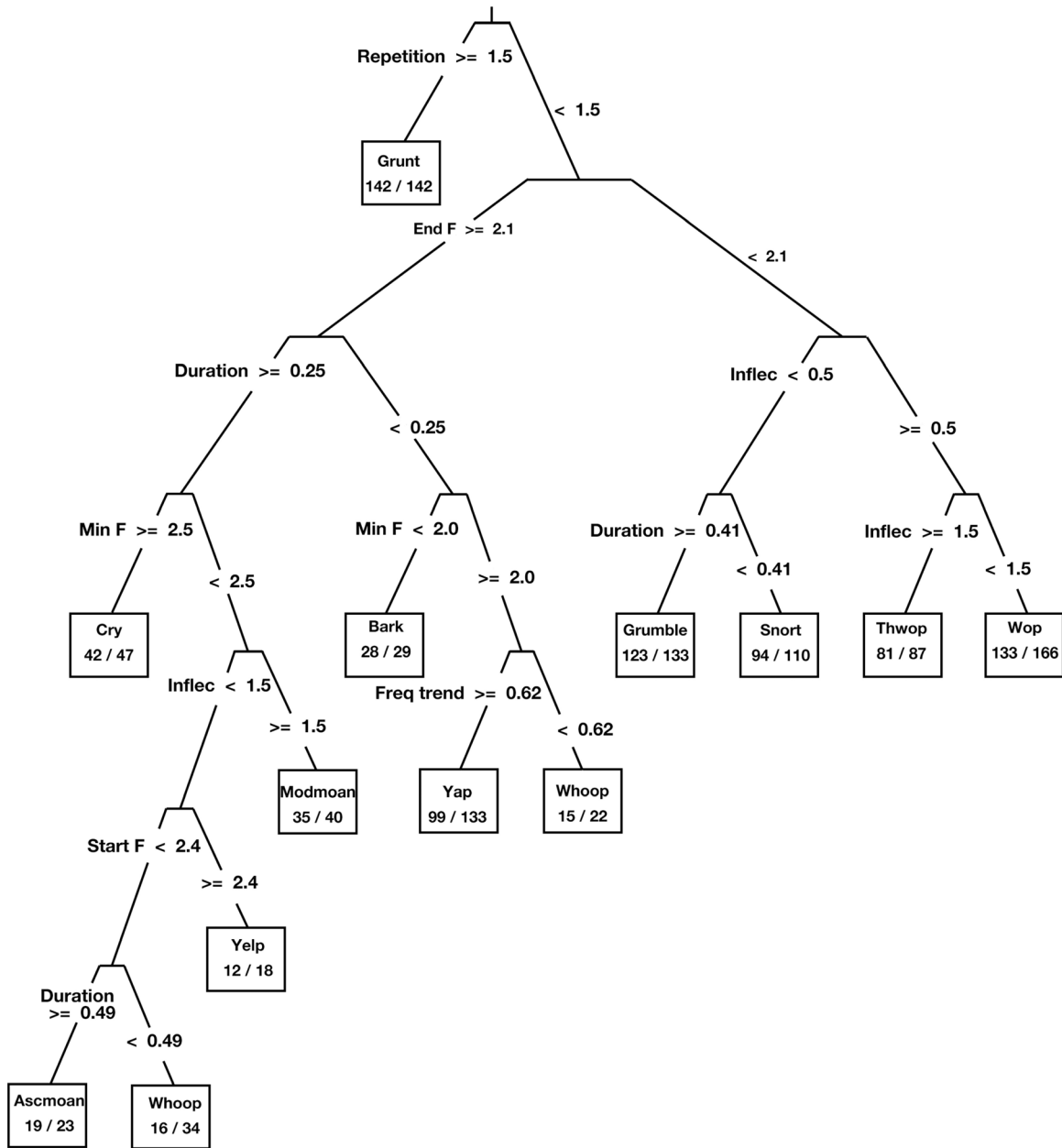


FIG. 1. Classification tree for all stable call types. The variables used to split the tree into two branches are displayed, along with the decision criterion next to the variable (<, > or =). The abbreviations used for variables are: Repetition = number of call repetitions, End F = log end frequency, Min F = log minimum frequency, Start F = log start frequency, Inflec = number of inflections, and Freq trend = frequency trend. Abbreviations used for call types: Ascmoan = ascending moan and Modmoan = modulated moan. The terminal node boxes displays the total number of correct classifications (below the call type). There is one more terminal node than in the original classification tree, with the whoop call type appearing in two places on the tree. Note: frequency measurements are displayed in kHz.

unlikely to change within call type categories. “Year” (1997, 2003–2004, 2008) was considered as the fixed effect and “recording number” (in which particular call types were heard) was included as a random effect in the models. The residuals of each model were checked for homoscedasticity, and errors were checked for normality. We found that the majority of models violated the assumption of homoscedasticity, with unequal variances between different years. In order to account for heteroscedasticity in the models, we re-ran all models using the function “varIdent,” which weighted the models based on each year’s variance structure. The initial model used 1997 as the reference year, and the model was then “releveled” using 2003–2004 as the reference year, to compare between 2003–2004 and

2008. The output of the models produced *t*-values and associated *p*-values that were considered significant at $p < 0.05$.

III. RESULTS

A. Determining the repertoire of call types and assessing the temporal stability of call types

A total of 1534 calls from 80 recordings were isolated from all years (1997, 211 calls from 25 recordings; 2003–2004, 577 calls from 32 recordings; 2008, 746 calls from 23 recordings). These were then subjectively categorized into 46 different call types (Table II). Out of the 46 call types only 12 were each subjectively judged to be similar enough to be categorized into the same broad call type categories

TABLE II. Total numbers of recordings and total numbers of calls (in brackets) for stable and inconsistent call categories across years (1997, 2003–2004, 2008). Shaded cells indicate calls that were not found in those years. Abbreviations: desc = descending and asc = ascending.

Call	Total # recordings (# calls)	1997	2003–2004	2008
Stable				
asc moan	8 (25)	1 (5)	1 (3)	6 (17)
bark	16 (63)	2 (2)	10 (50)	4 (11)
cry	26 (51)	13 (25)	5 (13)	8 (13)
grumble	31 (160)	4 (4)	18 (72)	9 (84)
grunt	21 (147)	8 (16)	7 (90)	6 (41)
mod moan	16 (37)	5 (5)	5 (14)	6 (18)
thwop	25 (87)	2 (2)	11 (67)	7 (18)
snort	29 (110)	3 (10)	16 (44)	10 (56)
whoop	7 (38)	4 (33)	1 (3)	2 (2)
wop	32 (134)	3 (5)	17 (64)	12 (65)
yap	17 (105)	4 (16)	3 (6)	10 (83)
yelp	5 (28)	2 (5)	1 (10)	2 (13)
Inconsistent				
bellow	4 (4)		4 (4)	
blow	4 (10)		2 (6)	2 (4)
creak	2 (7)	1 (3)	1 (4)	
desc groan	5 (20)			5 (20)
growl-purr	2 (6)	1 (2)		1 (4)
horn	5 (18)		5 (18)	
n groan	5 (23)			5 (23)
n moan	12 (17)	6 (9)		6 (8)
rasp	5 (34)	1 (4)		4 (30)
scream	4 (11)	1 (2)		3 (9)
short moan	6 (8)		6 (8)	
snort-grunt	2 (4)			2 (4)
snort train	3 (23)	3 (23)		
squeal	2 (2)			2 (2)
whistle	2 (6)			2 (6)

across the 11-year time period. These 12 call types collectively comprised 64.2% of all calls recorded and were identified as the core group of stable calls across all years. These stable call types included “cry,” “ascending moan,” “bark,” “grumble,” “grunt,” “modulated moan,” “snort,” “thwop,” “whoop,” “wop,” “yap,” and “yelp” (Table II).

There were 15 call types not recognizable as song units and found in at least two groups, but found in only one or two years (see Table II). These call types were considered to be inconsistent. Inconsistent call types were relatively uncommon (12.6% of all calls), and were generally only produced in a small number of recordings.

B. Exploring the relationships between the song and social call repertoires over the study period

There were 19 calls types (23.2% of total calls) considered to be subjectively similar to units of the song, which we have termed song-unit calls (see Tables II and III). These were typically similar to song units from whales in either the same or previous years, but rarely matched sounds used in the song in the following year. For example, in the 2003–2004 social call repertoire, there were a number of song-unit call types (e.g., “purr”) that were similar to units of the song sung in 2002 (Table III). The song-unit calls were usually lost from the social call repertoire during the 4–6 year gaps between the study periods and there were no song-unit calls that occurred in all years (Tables II and III).

C. Quantitative classification of calls to compare with the qualitatively assigned social call repertoire

The classification tree of calls, utilizing all variables, separated the majority of calls into the same categories as in

TABLE III. All social call types classified as “song-unit” calls are displayed (total number of recordings and calls in brackets), with the year(s) when they were found in the social call repertoire. Cells shaded in gray show the year(s) when units were found in the song that were very close to the corresponding song-unit social call type. Abbreviations: desc = descending and asc = ascending.

Song-unit call type #recordings (#calls)	Year recorded in social call repertoire	1996	1997	1998	2002	2003	2004	2005	2007	2008	2009
		Song	Song	Song	Song	Song	Song	Song	Song	Song	Song
desc cry 2 (7)	1997										
desc moan 4 (9)	1997										
trill 4 (7)	2003–2004, 2008										
growl 4 (19)	2003–2004, 2008										
purr 7 (27)	2003–2004										
sigh 1 (2)	2003–2004										
groan 9 (25)	2003–2004										
croak 3 (15)	2003–2004										
siren 2 (5)	2003–2004										
trumpet 4 (27)	2003–2004										
violin 3 (12)	2003–2004										
desc squeak 2 (10)	2003–2004										
squeak 3 (6)	2003–2004										
desc shriek 3 (7)	2003–2004										
asc shriek 1 (2)	2003–2004										
asc grumble 8 (132)	2008										
desc groan 5 (20)	2008										
desc moan 4 (9)	2008										
mod cry 1 (2)	2008										

the qualitatively determined catalogue (81% correct classification against 20.8% expected by chance). All variables were used in this classification at some point in the splitting process. There were more splits and terminal nodes than resulted from the qualitative classification, with 56 terminal nodes (call categories), as opposed to the 46 subjective call categories. The variables most important in splitting call categories appeared to be the “number of call repetitions,” duration, “number of inflections,” log maximum frequency, and frequency range. Although there was a high level of agreement between the two systems of classification, they were not in complete agreement.

A separate classification tree analysis was also run including just the 12 subjectively classified stable call types. The classification tree classified 85.2% of calls correctly against 10.9% expected by chance, and again used all variables in generating the classification tree, with the exception of frequency range. There were 13 terminal nodes (call categories) identified, with the call category whoop split into two different branches of the tree, explaining the additional call category (see Fig. 1). The decision to split whoops into two

different branches was made early in the splitting process based on differences in the variable duration. This could indicate that duration is not an important characteristic of whoops or that the classification of whoop calls needs further consideration. The variables duration and number of inflections were used in a number of splitting decisions, suggesting they are important variables in call discrimination.

D. Investigation of the stability of measured call parameters of common and stable call types in the call repertoire

Six of the stable call types (cry, yap, grumble, snort, grunt, wop; Fig. 2) were selected (due to sufficient sample size in all years) to investigate the stability of measured call parameters between 1997, 2003–2004, and 2008. All call types showed significant differences in at least one of the measured variables between years (Table IV). There was little consistency in which of the measured parameters changed over time, with the exception of frequency range, which was significantly different in all calls tested across years. For all

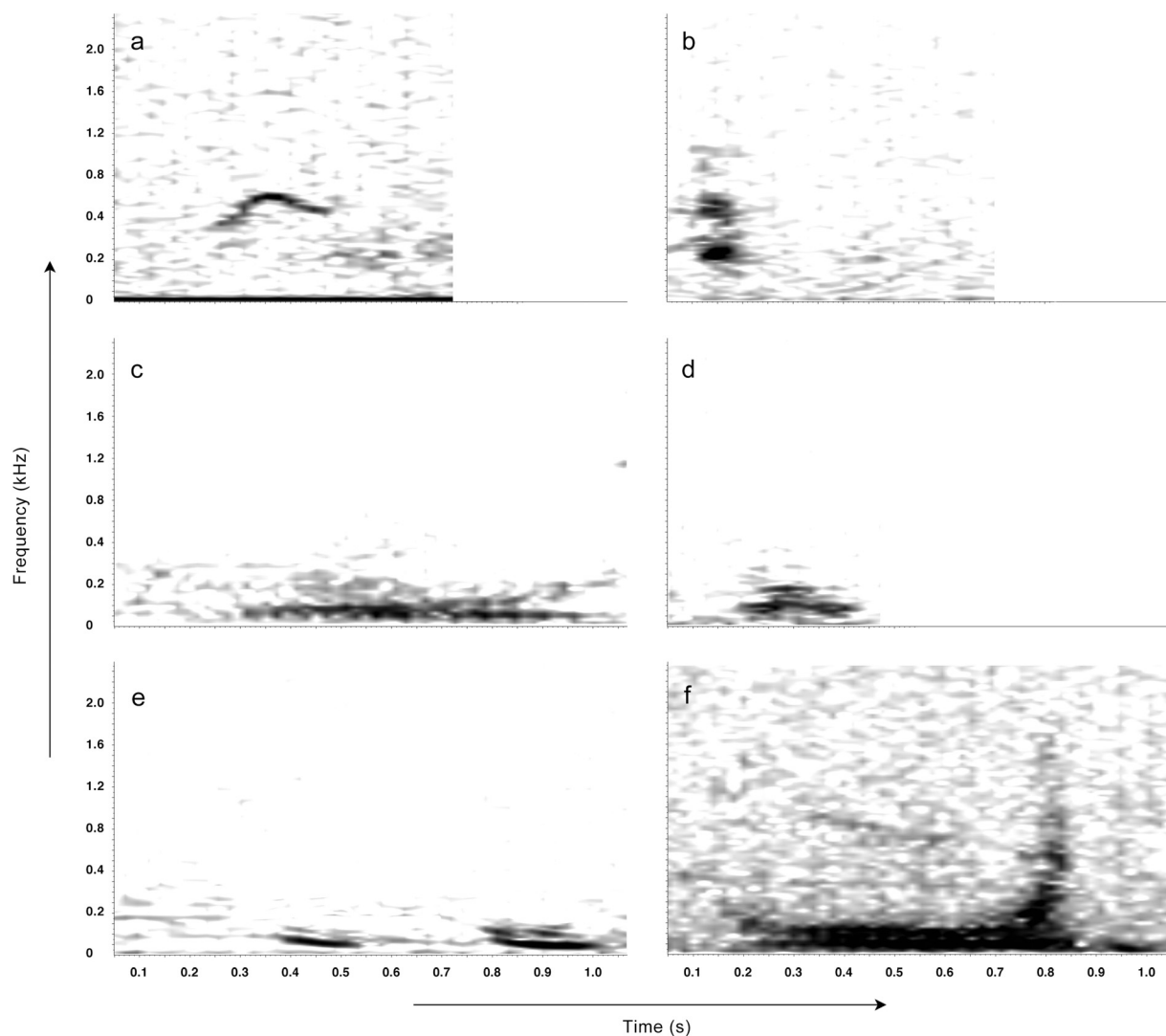


FIG. 2. Spectrograms of the six stable call types used for investigating temporal stability of measured call parameters (a) cry, (b) yap, (c) grumble, (d) snort, (e) grunt (repetitions at approximately 0.4 and 0.8 s), and (f) wop.

calls types, except for wops, there were some stable parameters that did not change significantly over time (Table IV).

IV. DISCUSSION

Humpback whales have long been known for their continually changing songs. The current study demonstrates, for the first time, that there is a core group of 12 stable call types commonly used in the social call repertoire of the east Australian humpback whales. Previous research undertaken on the east Australian population of humpback whales in 2002–2004 found a diverse social call repertoire that included song-unit social calls, as well as calls that differed from components of song (Dunlop *et al.*, 2007; Dunlop *et al.*, 2008). In our study, social calls recorded during four years over an 11-year period were investigated and a diverse social call repertoire was found, with the stable call types among the most commonly

produced calls. The finding of stable social calls as well as more labile social calls demonstrates that humpback whales have a complex communication repertoire.

Among marine mammals, Tyack (1999) suggested there is a correlation between a species' social system and ways in which they communicate. Baleen whales, for example, have few long-term associations and produce complex breeding displays. Killer whales, on the other hand, live in stable social groups and produce relatively stereotyped calls that tend to be specific to particular groups. We have shown in our study, that humpback whales also produce an array of stable social calls, which are presumably used to mediate social interactions. Humpback whales were previously considered to have few stable relationships (Clapham *et al.*, 1992); however, there have been reports of long-term associations on the feeding grounds (Weinrich, 1991; Ramp *et al.*, 2010). Humpback whales on migration frequently associate within groups (Dunlop *et al.*, 2007). Although these groups are generally unrelated (with the exception of females and calves; Valsecchi *et al.*, 2002), social interactions are nonetheless likely to be mediated, at least in part, by social calls. In which case, some level of stability in the social call repertoire would presumably be beneficial for communicating within different social contexts, even in the absence of stable social relationships (e.g., to maintain contact, advertise reproductive status and intentions, solicit interactions, or to coordinate movement within or between groups). The stable social calls isolated in this study may be used to convey specific information within differing social and behavioral contexts and should be the focus of future research.

Although there were temporally stable call types identified in the repertoire of humpback whales in our study, the fine-scale structural parameters of these call types were nonetheless somewhat variable. Such variability, or grading, in the structure of calls within broadly defined call categories appears to be common among animals, and these gradations in call intensity may reflect social or environmental influences (review by Owings and Morton, 1998). Modifications to structural call parameters may occur slowly, with a clear trend or evolution of parameters through cultural drift or genetic differentiation (e.g., Lynch, 1996; Deecke *et al.*, 2000), or rapidly, in direct response to changing social and/or physical environments (e.g., Owings and Morton, 1998). If the social calls of humpback whales were changing due to cultural drift or genetic differentiation, then a clear trend in call parameter changes would be expected. However, the measured call parameters generally showed no clear trend over time and in addition, there was considerable within-call type variability. These factors suggest that temporal variability in the structural parameters of stable calls in this study may be due to direct interactions with changing social and physical environments, supporting the suggestion that social calls are graded in nature (Thompson *et al.*, 1986; Dunlop *et al.*, 2007). In this case, short-term shifts in call parameters may occur in different social and behavioral contexts, to reflect the emotional or motivational needs of the signaler (Morton, 1977; Owings and Morton, 1998).

TABLE IV. *P*-values and associated *T*-values and degrees of freedom for the selected stable call types from the mixed models using the variables minimum frequency (Min F), maximum frequency (Max F), peak frequency (PF), duration (Dur) and frequency range (FR) to investigate stability between 1997, 2003–2004, and 2008. All significant results ($p < 0.05$) are shaded in gray. The total number of recordings and calls (in brackets) are displayed for all years.

Call	Variable	1997 to 2003–2004			2003–2004 to 2008		
		T	DF	P	T	DF	P
Cry 1997 = 13 (25) 2003–2004 = 5 (13) 2008 = 8 (13)	Min F	-3.22	18	0.005	2.70	18	0.01
	Max F	-0.29	18	0.77	-0.21	18	0.83
	PF	0.01	18	0.98	-0.17	18	0.87
	Dur	5.94	18	0.0001	0.10	18	0.0001
	FR	-4.39	18	0.0003	4.08	18	0.0001
Grumble 1997 = 4 (4) 2003–2004 = 18 (72) 2008 = 9 (84)	Min F	-0.44	127	0.65	-1.63	128	0.10
	Max F	-5.04	127	0.0001	2.72	128	0.007
	PF	-1.60	127	0.11	-1.04	128	0.29
	Dur	-0.19	127	0.84	-6.39	128	0.0001
	FR	-6.08	127	0.0001	13.87	128	0.0001
Snort 1997 = 3 (10) 2003–2004 = 16(44) 2008 = 10 (56)	Min F	0.43	26	0.66	-2.28	26	0.03
	Max F	-1.64	26	0.11	1.11	26	0.27
	PF	0.19	26	0.84	-2.73	26	0.01
	Dur	-0.58	26	0.56	-1.20	26	0.24
	FR	-4.97	26	0.0001	15.5	26	0.0001
Grunt 1997 = 8 (16) 2003–2004 = 7 (90) 2008 = 6 (41)	Min F	-1.20	18	0.26	1.09	18	0.28
	Max F	-4.50	18	0.0003	3.94	18	0.0001
	PF	-0.62	18	0.53	-0.054	18	0.96
	Dur	0.28	18	0.78	0.34	18	0.73
	FR	-7.66	18	0.0001	11.49	18	0.0001
Wop 1997 = 3 (5) 2003–2004 = 17 (64) 2008 = 12 (65)	Min F	-0.65	31	0.51	-2.13	31	0.04
	Max F	-2.50	31	0.01	-1.03	31	0.30
	PF	0.05	31	0.93	-4.98	31	0.0001
	Dur	1.28	31	0.20	2.24	31	0.03
	FR	-3.80	31	0.0006	17.35	31	0.0001
Yap 1997 = 4 (16) 2003–2004 = 3 (6) 2008 = 10 (83)	Min F	0.38	14	0.71	-0.21	14	0.83
	Max F	1.61	14	0.13	-0.62	14	0.54
	PF	-47.4	14	0.0001	56.51	14	0.0001
	Dur	-2.85	14	0.01	1.77	14	0.09
	FR	-2.22	14	0.04	3.27	14	0.006

Another potential source of variability within call type categories is the expression of individual attributes of callers such as size, sex or identity. Some aspect of body size, for example, may be conveyed in the frequency of an animal's calls, with larger animals generally producing lower frequency calls (August and Anderson, 1987). If individual callers' attributes are conveyed in the vocal signals of humpback whales, then such individual differences may be another source of the within-call type variability found in the stable call parameters. There were some parameters that did not change over time within each of the call types (e.g., log maximum frequency in cry, snort, and yap). It is thus possible that some aspects of the calls are stable, across individuals, which may relate to signal efficacy. In order to determine which mechanisms are responsible for the variation in the stable calls we recorded, larger sample sizes and social context information are required to determine whether the observed variability is functional and conveys specific information to conspecifics.

The presence of a number of 'inconsistent' call types in the repertoire (15 out of 46 call types) may have various explanations. The inconsistent call types were found in low numbers, and therefore may in fact be stable call types that were not recorded in all years due to insufficient sample size. Similarly, if specific call types are used in specific social and behavioral contexts (and therefore serve particular purposes; Owings and Morton, 1998), those specific contexts may not have been sampled in some years. Another possibility is that some of the inconsistent calls may be extreme gradations of the stable call types, and on the continuum that characterizes graded calls. Although the inconsistent calls were deemed different enough to warrant separate classification, this distinction was only based on our subjective groupings. Without corresponding social context information, we have little understanding of the functional role of these inconsistent social calls and what their role is within the social call repertoire of humpback whales.

The classification of calls into call type categories, in general, is a somewhat arbitrary process, as there is little information about the biological significance of the distinction between categories. The use of classification trees in splitting calls into categories provides a useful tool in assessing differences between call groupings, and may be used to determine both broad and finer groupings (like those used in this study), which may be subsequently used to test correlations with social context in future studies. A number of studies of other species have reported similar within-call category variability (e.g., Ford, 1991; Serrano and Terhune, 2002; Riesch *et al.*, 2006), which nonetheless did not negate the classification of calls into call type categories. Further research into the behavioral significance of call type categories would help to elucidate whether call classification accurately reflects call function, and will further aid in defining a social call repertoire for humpback whales.

A number of song-unit calls were identified in each of the study periods, and although relatively uncommon, were found to change in accordance with the song repertoire. The song-unit calls generally occur in short bouts or sequences, and were often produced when individuals were joining a group of whales (Dunlop *et al.*, 2007). The function of these short

bouts of song units is still unknown. Tyack (1981) suggested that individual song units sung in humpback whale songs themselves do not convey information in a communication sense, but rather the information in song is conveyed by the entire sequence of units. Frankel *et al.* (1995), however, suggested that individual song units may convey information about the fitness of the individual, such as size, to conspecifics. If there is individual fitness information conveyed in certain song units, males may produce specific song units, or small bouts of song units (pseudo-song), in close range social interactions, to reinforce their superiority to females or any competing males in the group. Stripe-backed wrens (*Campylorhynchus nuchalis*) defend territories using song but produce shorter versions of the same sounds during close-range aggressive interactions (Morton, 1977). Dunlop *et al.* (2008) found that in migrating humpback whales, song-unit calls were more commonly produced by male-dominated groups. The possible function of song-unit calls, therefore, is probably closely linked to song in female attraction and/or male dominance sorting (Tyack, 1981; Darling *et al.*, 2006).

This study is the first to demonstrate that humpback whales use stable call types that persist over time as part of their social call repertoire. Although only about one quarter of call types were consistently part of the social call repertoire over the years studied, these calls were generally the most commonly used, suggesting an important communicative function. Much of the call repertoire instability was due to the 19 identified song-unit calls that changed in accordance with the song repertoire. There were also inconsistent calls, not present in the social call repertoire of all years, which may reflect gradation of call types through "expression of effect" (Morton, 1977), individual differences or low sample sizes. Similar factors may explain the variability found in some of the fine-scale structural parameters of the stable call types, although the cause of this structural variation needs to be explored before we can understand the significance of variation from a communication perspective (Owings and Morton, 1998). Nonetheless, the results from this study demonstrate that humpback whales' social call repertoires show both stability and variability on different levels, both in terms of call repertoire stability, and the structural stability of individual call types over time, which is analogous with many other animal communication systems. The identification of stable call types, in particular, contrasts with the labile nature of humpback whale song, and further demonstrates the complex nature of social communication in this species. They also provide opportunities to focus subsequent research into the function of these calls, and the fine-scale structural variability of these calls in different social and behavioral contexts.

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August, P. V., and Anderson, J. G. T. (1987). "Mammal sounds and motivation-structural rules: A test of the hypothesis." *J. Mammal.* **68**(1), 1–9.

Baker, M. C., and Gammon, D. E. (2006). "Persistence and change of vocal signals in natural populations of chickadees: annual sampling of the gargle call over eight seasons." *Behavior* **143**, 1473–1509.

Breiman, L., Friedman, J. H., Olshen, R. A., and Stone, C. J. (1984). *Classification and Regression Trees* (Wadsworth International Group, California), pp. 1–358.

Cerchio, S., Jacobsen, J. K., and Norris, T. F. (2001). "Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages." *Anim. Behav.* **62**, 313–329.

Clapham, P. J., Palsboll, P. J., Mattila, D. K., and Vasquez, O. (1992). "Composition and dynamics of humpback whale competitive groups in the West Indies." *Behaviour* **122**, 182–194.

Crawley, M. J. (2007). *The R Book* (Wiley, Chichester, UK), pp. 627–661.

Daniel, J. C., and Blumstein, D. T. (1998). "A test of the acoustic adaptation hypothesis in four species of marmots." *Anim. Behav.* **56**, 1517–1528.

Darling, J. D., Jones, M. E., and Nicklin, C. P. (2006). "Humpback whale songs: Do they organise whales during the breeding season?." *Behaviour* **143**, 1051–1101.

Deecke, V. B., Ford, J. K. B., and Spong, P. (2000). "Dialect change in resident killer whales: implications for vocal learning and cultural transmission." *Anim. Behav.* **40**, 629–638.

Dunlop, R. A., Noad, M. J., and Cato, D. H. (2008). "Non-song acoustic communication in migrating humpback whales." *Marine Mammal Sci.* **24**, 613–629.

Dunlop, R. A., Noad, M. J., Cato, D. H., and Stokes, D. (2007). "The social vocalization repertoire of east Australia migrating humpback whales (*Megaptera novaeangliae*)." *J. Acoust. Soc. Am.* **122**(5), 2893–2905.

D'Vincent, C. D., Nilson, R. M., and Haruna, R. H. (1985). "Vocalizations and coordinated feeding of the humpback whale in Southeastern Alaska." *Sci. Rep. Whales Res. Inst.* **36**, 41–47.

Ford, J. K. B. (1991). "Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia." *Can. J. Zool.* **69**, 1454–1483.

Frankel, A. S., Clark, C. W., Herman, L. M., and Gabriele, C. M. (1995). "Spatial distribution, habitat utilization and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii, determined using acoustic and visual techniques." *Can. J. Zool.* **73**, 1134–1146.

Garland, E. C., Goldizen, A. W., Rekdahl, M. L., Constantine, R., Garrigue, C., Daeschler Hauser, N., Poole, M. M., Robbins, J., and Noad, M. J. (2011). "Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale." *Curr. Biol.* **21**, 687–691.

Griebel, U., and Oller, K. (2008). "Evolutionary forces favoring communicative flexibility," in *Evolution of Communicative Flexibility: Complexity, Creativity, and Adaptability in Human and Animal Communication*, edited by K. Oller and U. Griebel (MIT Press, Cambridge, MA), pp. 9–41.

Janik, V. M., and Slater, P. J. B. (1997). "Vocal learning in mammals." *Adv. Study Behav.* **26**, 59–99.

Lachlan, R. F., Janik, V. M., and Slater, P. J. B. (2004). "The evolution of conformity-enforcing behavior in cultural communication systems." *Anim. Behav.* **68**, 561–570.

Lynch, A. (1996). "The population memetics of birdsong" in *Ecology and Evolution of Acoustic Communication in Birds*, edited by D. E. Kroodsma and E. H. Miller (Cornell University Press, Ithaca, NY), pp. 181–197.

McGarigal, K., Cushman, S. A., and Stafford, S. (2000). *Multivariate Statistics for Wildlife and Ecology Research* (Springer Verlag, New York), pp. 129–187.

Mellinger, D. K. (2001). "Ishmael 1.0 User's Guide," NOAA Technical Memorandum OAR PMEL-120.

Mitani, J. C., and Gros-Louis, J. (1998). "Chorusing and call convergence in chimpanzees: Tests of three hypotheses." *Behaviour* **135**, 1041–1064.

Morton, E. S. (1977). "On the occurrence and significance of motivation-structural rules in some bird and mammal sounds." *Am. Nat.* **111**(981), 855–868.

Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M.-N., and Jenner, K. C. S., (2000). "Cultural revolution in whale songs." *Nature* **408**, 537.

Owings, D. H., and Morton, E. S. (1998). *Animal Vocal Communication: A New Approach* (Cambridge University Press, Cambridge, UK), pp. 101–146.

Parks, S. E., Clark, C. W., and Tyack, P. L. (2007). "Short- and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication." *J. Acoust. Soc. Am.* **122**(6), 3725–3731.

Payne, K., Tyack, P., and Payne, R. (1983). "Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): A detailed analysis of two seasons in Hawaii," in *Communication and Behaviour of Whales*, edited by R. Payne (Westview Press Inc., Boulder, CO), pp. 9–57.

Payne, R. B. (1985). "Behavioral continuity and change in local song populations of village indigobirds (*Vidua chalybeata*)." *Z. Tierpsychol.* **70**, 1–44.

Payne, R. S., and McVay, S. (1971). "Songs of humpback whales." *Science* **173**, 585–597.

Pozzi, L., Gamba, M., and Giacoma, C. (2010). "The use of artificial neural networks to classify primate vocalizations: A pilot study on black lemurs." *Am. J. Primatol.* **72**, 337–348.

Ramp, C., Hagen, W., Palsboll, P., Berube, M., and Sears, R. (2010). "Age related multi year associations in female humpback whales (*Megaptera novaeangliae*)." *Behav. Ecol. Sociobiol.* **64**(10), 1563–1576.

R Development Core Team (2012). "R: A language and environment for statistical computing." R Foundation for Statistical Computing, Vienna, Austria.

Rendell, L. E., and Whitehead, H. (2005). "Spatial and temporal variation in sperm whale coda vocalizations: Stable usage and local dialects." *Anim. Behav.* **70**, 191–198.

Richardson, W. J., Greene, C. R. J., Malme, C. I., and Thomson, D. H. (1995). *Marine Mammals and Noise* (Academic, New York), pp. 31–58.

Riesch, R., Ford, J. K. B., and Thomsen, F. (2006). "Stability and group specificity of stereotyped whistles in wild killer whales, *Orcinus orca*, off British Columbia." *Anim. Behav.* **71**, 79–91.

Serrano, A., and Terhune, J. M. (2002). "Stability of the underwater vocal repertoire of harp seals (*Pagophilus groenlandicus*)." *Aquat. Mamm.* **28**(1), 93–101.

Silber, G. K. (1986). "The relationship of social vocalizations to surface behaviour and aggression in the Hawaiian humpback whale (*Megaptera novaeangliae*)." *Can. J. Zool.* **64**, 2075–2080.

Stimpert, A. K., Au, W. W. L., Parks, S. E., Hurst, T., and Wiley, D. N. (2011). "Common humpback whale (*Megaptera novaeangliae*) sound types for passive acoustic monitoring." *J. Acoust. Soc. Am.* **129**(1), 476–482.

Stimpert, A. K., Wiley, D. N., Au, W. W. L., Johnson, M. P., and Arsenault, R. (2007). "Megapclicks": Acoustic click trains and buzzes used during nighttime foraging of humpback whales (*Megaptera novaeangliae*)." *Biol. Lett.* **3**(5), 467–470.

Thompson, P. O., Cummings, W. C., and Ha, S. J. (1986). "Sounds, source levels, and associated behaviour of humpback whales, southeast Alaska." *J. Acoust. Soc. Am.* **80**, 735–740.

Tyack, P. L. (1981). "Interactions between singing Hawaiian humpback whales and conspecifics nearby." *Behav. Ecol. Sociobiol.* **8**, 105–116.

Tyack, P. L. (1983). "Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds." *Behav. Ecol. Sociobiol.* **13**, 49–55.

Tyack, P. L. (1999). "Communication and Cognition" in *Biology of Marine Mammals*, edited by J. E. Reynolds III and S. A. Rommel (Smithsonian Institution Press, Washington, DC), Chap. 7, pp. 287–323.

Tyack, P. L., and Sayigh, L. S. (1997). "Vocal learning in cetaceans" in *Social Influences on Vocal Development*, edited by C. T. Snowdon and M. Hausberger (Cambridge University Press, Cambridge, UK), Chap. 11, pp. 208–233.

Valsecchi, E., Hale, P., Corkeron, P., and Amos, W. (2002). "Social structure in migrating humpback whales (*Megaptera novaeangliae*)." *Mol. Ecol.* **11**, 509–518.

- Weinrich, M. T. (1991). "Long term stability in grouping patterns of humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine," *Can. J. Zool.* **69**, 3012–3019.
- Winn, H. E., Beamish, P., and Perkins, P. J. (1979). "Sounds of two entrapped humpback whales (*Megaptera novaeangliae*) in Newfoundland," *Mar. Biol.* **55**, 151–155.
- Winn, H. E., and Winn, L. K. (1978). "The song of the humpback whale *Megaptera novaeangliae* in the West Indies," *Mar. Biol.* **47**, 97–114.
- Zoidis, A. M., Smultea, M. A., Frankel, A. S., Hopkins, J. L., Day, A., McFarland, S. A., Whitt, A. D., and Fertl, D. (2008). "Vocalizations produced by humpback whale (*Megaptera novaeangliae*) calves recorded in Hawaii," *J. Acoust. Soc. Am.* **123**, 1737–1746.