Non-song social call bouts of migrating humpback whales

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The use of stereotyped calls within structured bouts has been described for a number of species and may increase the information potential of call repertoires. Humpback whales produce a repertoire of social calls, although little is known about the complexity or function of these calls. In this study, digital acoustic tag recordings were used to investigate social call use within bouts, the use of bouts across different social contexts, and whether particular call type combinations were favored. Call order within bouts was investigated using call transition frequencies and information theory techniques. Call bouts were defined through analysis of inter-call intervals, as any calls within 3.9 s of each other. Bouts were produced significantly more when new whales joined a group compared to groups that did not change membership, and in groups containing multiple adults escorting a female and calf compared to adult only groups. Although social calls tended to be produced in bouts, there were few repeated bout types. However, the order in which most call types were produced within bouts was non-random and dependent on the preceding call type. These bouts appear to be at least partially governed by rules for how individual components are combined.
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[WWA]   Pages: 3042–3053

I. INTRODUCTION

The social calls of animals are generally studied by breaking down vocalizations into their individual components or call types. The production of individual call types within a species' communication repertoire may be tightly constrained to specific social and behavioral contexts, with different call types conveying specific information, such as alarm calls, individual or group identity calls, or group foraging calls (e.g., Bohn *et al.*, 2008). Calls presumably need to vary in structure to convey different information, leading to a number of different call types in a call repertoire. In general, little communication complexity has been attributed to non-human animal call systems (see review by Seyfarth and Cheney, 2010). Rather than increasing the number of different call types in a repertoire, another way of increasing the potential for complexity in a communication system is to combine individual stereotyped call types into structured call sequences. These call sequences may make up a "call bout," depending on the interval of time between adjacent calls.

The majority of research on call bouts has focused on the stereotyped sequences of calls produced by many species as song displays (e.g., in song birds, see review by Catchpole and Slater, 1995; in some primate species, Marler and Tenaza, 1977; Geissmann and Orgeldinger, 2000; in marine mammals such as humpback whales, *Megaptera novaeangliae*, Payne and McVay, 1971). These song sequences are highly stereotyped in most species and may serve a number of functions, including mate attraction and male-male competition, and song displays tend to be sex specific and related to breeding. In contrast to song displays, social calls are typically produced by both sexes, are produced as single calls or in short bouts, and function to communicate information both within and between social groups in a number of different contexts (Lynch, 1996). The structure, function, and complexity of social calls have been less well studied, but a number of species have been shown to combine a small set of call types into structured bouts of calls produced by one individual (e.g., titi monkey, *Callicebus moloch*, Robinson, 1979; Mexican chickadee, *Poecile sclateri*, Ficken *et al.*, 1994; black-capped chickadee, *Poecile atricapillus*; Mexican free-tailed bat, *Tadarida brasiliensis*, Bohn *et al.*, 2008) or more than one individual in call

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0001-4966/2015/137(6)/3042/12/$30.00   © 2015 Acoustical Society of America

matching interactions (e.g., killer whales, *Orcinus orca*, Miller *et al.*, 2004).

Male humpback whales are well known for producing complex and highly structured song displays to which all males within a population generally adhere (Payne and McVay, 1971). One of the aspects of complexity in humpback whale song is the hierarchical structuring of songs from basic calls or "units." These are combined to form short "phrases," which are repeated to form "themes" (Payne and McVay, 1971). Several different themes, usually sung in a particular order, make up a song type. Further complexity arises because of the constant changing of song types through the gradual evolution, replacement or addition of units, phrases and themes, with changes quickly adopted across all members of a population (Winn and Winn, 1978; Payne and Payne, 1985; Noad *et al.*, 2000). The changes to the song are generally undertaken without loss of the basic hierarchical structure that governs how different calls or units are combined to make songs. As humpback whale song displays change rapidly over time but the social context in which song is used remains the same (i.e., as a male breeding display, Payne and McVay, 1971; Winn and Winn, 1978; Tyack, 1981), the actual information conveyed in the song is thought to be in the complexity and novelty of the changing display rather than in individual units that make up the song (Tyack, 1981). Therefore the units within a song may convey little semantic meaning (Tyack, 1983).

In contrast, humpback whales' social sounds, which are defined as surface-generated percussive sounds and any vocalizations lacking the structure of song (Thompson *et al.*, 1977; Tyack, 1983; Silber, 1986), are produced by males, females, and calves. Social sounds tend to be produced in social groups, although single animals also produce social sounds (Dunlop *et al.*, 2008). Social sounds are commonly heard on the feeding grounds (Thompson *et al.*, 1977; Mobley *et al.*, 1988; Stimpert *et al.*, 2011), breeding grounds (Silber, 1986; Zoidis *et al.*, 2008), and whilst on migration (Dunlop *et al.*, 2007; Dunlop *et al.*, 2008). These sounds may convey specific semantic meanings as they are used to communicate within a wide array of social contexts, such as during feeding by groups (Thompson *et al.*, 1977; Mobley *et al.*, 1988), in aggressive interactions between competing males (Silber, 1986; Dunlop *et al.*, 2008), and in the maintenance of contact between a female and her calf (Dunlop *et al.*, 2007; Dunlop *et al.*, 2008; Zoidis *et al.*, 2008). Previous research on migrating whales from the east Australian population by Dunlop *et al.* (2007) categorized a repertoire of 34 different social sounds, including 32 social calls, using the acoustic features of individual sounds.

The majority of research conducted on humpback whale social calls has focused on individual call types, although Thompson *et al.* (1986) noted that feeding humpback whale groups off south-east Alaska tended to produce calls in sets of sounds rather than as isolated calls. Silber (1986) found that calls were often produced within variable multi-call sequences in multi-animal groups that were composed of different numbers and types of calls. Similarly, Cerchio and Dalheim (2001) noted that "cry" call types were commonly produced as repetitions of the same call type. However, a quantitative assessment of the production of social calls within bouts has not previously been investigated in humpback whales. Humpback whales' use of social calls in bouts is of particular interest given males' ability to produce complex song sequences, as well as the potential for social and contextual information to be conveyed by social calls. The well documented social call repertoire of migrating east Australian humpback whales (Dunlop *et al.*, 2007; Dunlop *et al.*, 2008; Rekdahl *et al.*, 2013) provides an ideal opportunity to further investigate whether humpback whales, like some social terrestrial species, also produce their calls within ordered call bouts.

The objectives of this study were to investigate (1) whether humpback whales commonly produce their social calls in call bouts, (2) whether some call types are produced more often within bouts than other call types, (3) compare the use of call bouts within different group compositions, such as single adults or female/calf (FC) groups, and (4) test whether the use of call bouts was linked to changes in groups' social structure (defined by group composition). In addition, (5) whether the ordering of calls within bouts is random or could be governed by structural rules for how they are combined were explored. In this paper, surface-generated percussive sounds were excluded and sounds used in the analysis are referred to as "social calls."

II. METHODS

A. Data collection

The data were collected during the September/October southward migration in 2004 and 2010, from waters off Peregian Beach, 130 km north of Brisbane (26°29′S, 153°06′E), Australia. The behavioral and acoustic data were collected as part of the Humpback whale Acoustic Research Collaboration (HARC) project in 2004 and the Behavioral Responses of Australian Humpback whales to Seismic Surveys (BRAHSS) project in 2010. HARC and BRAHSS had many data collection platforms that were used in this paper and will only be touched on briefly; for more detailed methods see Noad *et al.* (2004) and Dunlop *et al.* (2007, 2008).

The acoustic recordings were collected using Digital Acoustic Tags (DTAGs) (Johnson and Tyack, 2003). A DTAG was attached with suction cups directly to a whale and therefore provided a detailed acoustic recording from the group that included the tagged whale (the focal group). The DTAGs were deployed either from a 5.6 m research vessel using a 14 m cantilevered pole (2004 and 2010) or from a 6 m research vessel using a 6 m hand pole (2010). The tags sampled at 64 kHz with 16 bits per sample. The tags also contained a 400 Hz Butterworth high-pass filter to minimize low frequency flow noise. In 2004, once an individual within a group was tagged, the group composition was recorded and then the boat generally left the whale to be tracked by a land station. In 2010, once a whale was tagged, the group containing the tagged whale was then followed by the tagging vessel (focal follow), from which detailed, individual-level, behaviors were noted.

During both years, all groups within the study area (within a radius of approximately 10 km) were ad lib sampled by a land-based team. The land-based observation platform was located on Emu Mountain, which was directly adjacent to the study area and reached an elevation of 73 m. All passing groups (including the group containing the tagged whale) were tracked using a theodolite (Leica TM 1100 in 2004 and Leica TC 407 in 2010; Leica Geosystems AG, Heerbrugg, Switzerland) connected to a notebook computer. *Cyclopes* software (E. Kniest, University of Newcastle, Australia) used the bearing and angle of declination from the theodolite to calculate and display on a map the positions of whale groups in real time. Each theodolite fix was time-stamped and the group composition, behavior (e.g., breach, blow, tail slap, etc.) and information on the social context, such as group splitting and joining, were recorded with each fix. *Cyclopes* enabled accurate tracking of whales and also calculated distances from all other groups in the area. This provided information on the movements and behaviors of the focal (tagged) group as well as on other groups concurrently in the area.

The group composition categories used in the analysis included the following: adult groups (AAs), FC, female/calf/escort (FCE), female/calf/female/calf/multiple escort (2F2CEE), and female/calf/multiple escort (FCEE). AAs contained two or three whales of unknown sex but did not contain a calf. Social context was defined as whether groups were stable, were joined by other whales, or whales split from the group during the period of observation (Dunlop *et al.*, 2008). Whales were considered to be part of the same group if they remained within 100 m of each other and displayed synchronous surfacing behavior. Groups were recorded to have "joined" when the number of animals in a group increased and whales surfaced synchronously within 100 m of each other. Conversely, groups were recorded to have "split" when the number of animals decreased and the two groups surfaced greater than 100 m from each other.

B. Terminology

Call—refers to a single, continuous non-song vocal sound (as determined by the human ear) surrounded by intervals of silence.

Call type—calls were divided into a number of different call type categories based on spectrographic and auditory differences between different calls, e.g., "wop," "grunt," etc.

Call bout—a sequence of calls that may have been of the same or different call types, in which calls were separated by no more than 3.9 s from another call (similar to a "Phrase" in humpback whale song or a "Bout" in bat acoustic research; Bohn *et al.*, 2008). [See below for the determination of this bout end criterion (BEC).]

Call bout type—a bout of specific call types that occurred in a specific order.

Long bout—bout that contained more than four calls; call bouts may have been composed of the same or different call types.

Short bout—bout that contained four or fewer call types; call bouts may have been composed of the same or different call types.

C. Classification of calls and statistical analysis of call types

A total of 34 DTAG recordings were aurally and visually inspected for social calls by a single observer (MR). Twenty-six DTAG recordings (12 from 2004, 14 from 2010) were used in the final analysis. Data were excluded from 8 DTAGs due to poor signal-to-noise ratio (SNR), probably as a result of the calls being produced by groups other than the tagged focal group. The spectrograms of social calls were produced using *Adobe Audition* software (v1.5, Adobe Systems) with a 4096 point fast Fourier Transform, 75% overlap, 50 s window, yielding 15.625 Hz frequency resolution. Once a social call was located, the start and end times of the call in the recording were noted manually and the call was categorized qualitatively, where possible, using the catalogue of calls outlined by Dunlop *et al.* (2007) and Rekdahl *et al.* (2013). Dunlop *et al.* (2007) and Rekdahl *et al.* (2013) measured parameters of all social calls and performed both discriminant function analysis and principal components analysis (Dunlop *et al.*, 2007) or classification tree analysis (Rekdahl *et al.*, 2013) to quantify call categories. In the process of assigning calls to call types for this paper, it was noted that a number of calls commonly found in the recordings did not fit any of the previously defined call types. As these were common call types produced within bouts they were included in the analysis.

Although each DTAG was placed directly onto an individual whale, it is possible that calls within bouts may have been produced by nearby animals or two different animals within the same group. Therefore a number of criteria were used to limit the dataset to include bouts that were more likely to have been produced by a single individual in the group or at least from individuals within the focal group. First, any bouts where there were clearly two animals producing calls (characterized by overlapping calls) were excluded (to reduce the chances that call within bouts came from two different animals). Second, bouts where all sounds had obviously low SNRs (initially characterized by a qualitative assessment of call amplitude during the initial manual scan of data and validated through detailed measurements of a subset of data outlined below) were assumed to come from animals other than the tagged animal or group and were also excluded.

To calculate the SNR, received levels (RLs) of calls were measured in 1/3 octave band levels (dB re 1 μPa) over the range of 55 Hz to 2.25 kHz within a subset of bouts (Included, $N = 35$ bouts, 131 calls; Excluded, $N = 20$ bouts, 57 calls) using SpectraPLUS (Sound Technology, Inc., State College, PA). A noise correction was applied to the measurements by calculating the mean square voltage for at least 2 s of noise and subtracting this from the calculation of mean square voltage of the signal for each 1/3 octave band (see Dunlop *et al.*, 2013 for detailed methodology). The subsequent values were summed across 1/3 octave bands over the

55 Hz to 2.25 kHz bandwidth and converted to decibels (10 log of the sum) to calculate the broadband signal levels. The resulting RLs are not absolute measures and are only reported to describe differences between calls within a bout. Noise was measured over the same bandwidth and subtracted from the signal to calculate the SNR of calls. A histogram of the highest SNR values from both included and excluded bouts is displayed (Fig. 1); the bimodal distribution validated the 10 dB cutoff value for exclusion of bouts. Bouts were excluded if no sound within the bout had an SNR of over 10 dB (the highest SNR was 7 dB).

Bouts were included as long as at least one sound within the bout had an SNR of over 10 dB, however, the SNR of calls within bouts included in the analysis varied considerably [0–38 dB (Fig. 1)]. The source level of humpback whales social calls has been shown to vary by 60 dB re 1 μPa @ 1 m and the same call has been shown to vary in level by up to 58 dB re 1 μPa @ 1 m (Dunlop *et al.*, 2013). With such a large range in humpback whale social call levels, unequal SNRs within a bout was not thought to necessarily indicate that two different animals were producing the calls. As such, this was not a criterion for excluding bouts.

D. Call bout definition

A script was written in Perl (v 5.10.1) that calculated the durations of individual calls and the times between the adjacent calls (inter-call interval) from a spreadsheet containing start and end times of all calls from each year. The inter-call intervals were then used in an analysis to statistically calculate the bout criterion interval.

A number of statistical methods have been developed for splitting behaviors into bouts, which define a BEC based on the distribution of behaviors within behavioral states [i.e., log survivorship analysis, Slater and Lester, 1982; log-frequency analysis, Sibly *et al.*, 1990; maximum likelihood estimation method (MLM), Langton *et al.*, 1995; Luque and Guinet, 2007]. In all methods, the distributions of intervals between behaviors are considered to be a mixture of two or more Poisson processes, which at the smallest scale separate
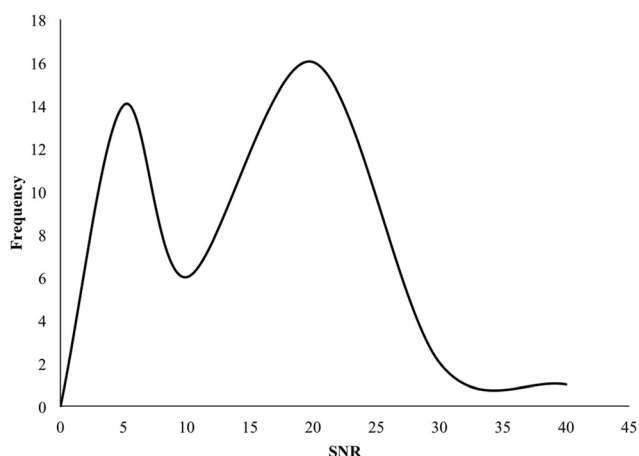

FIG. 1. Histogram of SNR measurements from the calls with the highest SNR for a subset of included and excluded bouts. The bimodal distribution centered on 10 dB support the exclusion value of 10 dB for bouts with no calls above 10 dB.

behaviors within bouts (fast processes) and, at the larger scale, separate different groups of behaviors or bouts (slow processes). A "broken-stick" model can then be fitted to the data that determines the point at which the two lines generated by the fast and slow processes meet (see Slater and Lester, 1982; Sibly *et al.*, 1990 for detailed explanations of methodology). Sibly *et al.* (1990) developed the log-frequency method, which calculates the BEC by fitting a non-linear curve to the logarithm of behavior interval frequencies in a histogram (arranged from smallest to largest intervals; Sibly *et al.*, 1990). Four parameters are then estimated from the fast and slow processes, which are the number of inter-call intervals occurring in both the fast and slow processes and the probabilities of a behavior occurring in the fast and slow processes per unit time. These parameters are used to calculate the BEC (Sibly *et al.*, 1990).

A MLM was used to calculate the BEC, as this method accounts for a number of causes of subjectivity that affect the methods described above (see Langton *et al.*, 1995; Luque and Guinet, 2007). Four starting parameters were initially calculated from the call interval data by fitting a "broken stick" model to the data as described in the paragraph above (Sibly *et al.*, 1990). However, a maximum likelihood estimation of all the observed data was used to generate the model parameters, rather than fitting a curve to a histogram of observed data (as in Sibly *et al.*, 1990), which removed any subjectivity involved in the choice of histogram bin widths (Langton *et al.*, 1995). These four parameters were then used to calculate a single mixing parameter, calculated from the proportions of fast and slow processes, which reduced the four model parameters to three (the number of inter-call intervals occurring in both the fast and slow processes and the mixing parameter, Langton *et al.*, 1995). The final maximum likelihood estimates for the model parameters were obtained from these parameter estimates and used to calculate the BEC. How well the model fit the observed data was assessed by plotting the observed cumulative frequency distribution of intervals to those of the fitted model (Langton *et al.*, 1995; Fig. 2). The "bouts2MLE" method within the DiveMove package was used (Luque, 2012) in R (R Development Core Team, 2012), which utilizes the methods outlined by Langton *et al.* (1995) and Luque and Guinet (2007) to calculate the BEC. In addition, the "bouts2NLS" method within DiveMove was used to calculate a BEC using the method outlined by Sibly *et al.* (1990) in order to ensure the MLM model was a better approach for defining a BEC for our data. Only recordings in which all call intervals could be accurately determined were used for the analysis and only call intervals less than 4000 s were used to reduce any potential bias introduced by including long intervals.

Once all the calls were labeled as belonging within bouts or as single calls based on the calculated BEC, various parameters were calculated using a Perl script (v5.10.1). These included the duration of each bout, the types and numbers of call types produced as single calls (not in a bout), the types and number of call types produced in bouts, the average intervals between sound types within bouts, the total number and types of bouts produced more than once, and the
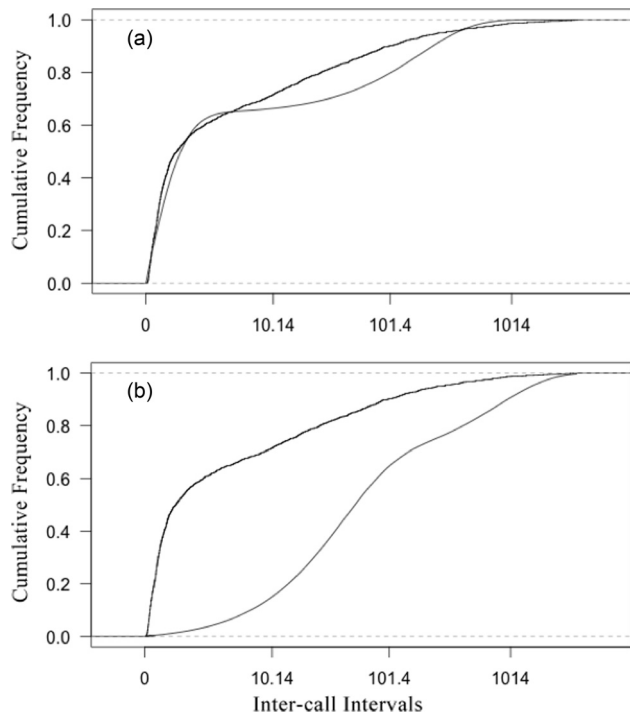
FIG. 2. Cumulative frequency distribution estimated through the MLM method (a) was a better fit with observed data than the log frequency method (b). The gray line—expected distribution and the black line—observed distribution.

TABLE I. Group composition and social context categories, total number of groups in which these group compositions and social contexts were observed, and the total number of hours of recording used in the behavioral analysis.

Group composition	No. of groups recorded	Hours of recording (hrs:mins)
AA	6	3:07
FC	11	4:08
FCE	9	2:58
FCEE	5	2:08
2F2CEE	4	2:15
Social context	No. of groups recorded	Hours of recording (hrs:mins)
Stable	26	12:15
Join	12	1:30
Split	10	1:05

total number of unique bouts (particular groups of calls only found once). The average number of calls per bout was 4.6, and guided the designation of calls into short bouts (≤ 4 calls) and long bouts (>4 calls) for further analysis.

E. Analysis of whether the production of call bouts was related to social context

In order to investigate whether the social context influenced the use of call bouts, a number of variables were recorded. The recordings were divided into 5 min time periods starting when the first social call was heard in the recording. The "group ID" was assigned at the start of the recording and did not change throughout the recording. For each 5 min time period, observations on group composition and the group's social context (whether whales were joining the group, splitting from the group, or the group remained stable) were noted as predictor variables (Table I). The total numbers of bouts ("all bouts"), short bouts ("short bouts," ≤ 4 calls) and long bouts ("long bouts," >4 calls) were noted as response variables. If a group was joined by whale(s) or had whale(s) split from the group, then from the time that the join or split was recorded, the behavior was considered to be a join or split 10 min either side of the behavioral state change based on the assumption that 10 min either side of the join or split would be coincident with the most significant behavioral changes. The data were split into 5 min time periods for the analysis and, if any of the predictor variables changed within any 5 min time block (i.e., there were two behavioral states corresponding to that 5 min period), the entire 5 min time period and corresponding information on bouts were excluded from the analysis. Bouts were assigned

to 5 min periods based on whether they started within the 5 min period regardless of whether the end of the bout was in that or the following 5 min period. All information on behaviors and corresponding bouts was extracted from the data set using a Ruby script (v1.9.2).

Generalized linear mixed models (GLMMs) were generated using R (R Development Core Team, 2012). GLMMs account for issues of non-independence of data by incorporating random effects as well as issues with non-normally distributed data by specifying the sample distribution and using link functions (see review by Bolker et al., 2008). As the data used were count data with many zeros, the glmmADMB package (Fournier et al., 2011) was used to generate the models. This package specifically accounts for the problems of count responses and zero inflation by using a Poisson distribution with a point mass at zero. A GLMM was fitted to each response variable (all bouts, short bouts, and long bouts) using "group ID" as the random effect (to account for repeated measures within each group) and the number of whales in each group as an offset (to account for group size as a potential influence on bout behavior). Predictor variables were group composition (AA, FC, FCE, 2F2CEE, FCEE) and social context ("stable," join, split). A null model with no predictor variables was compared to one including group composition and social context using the repeated measures analysis of variance function in R, which generates maximum likelihood estimates and associated p-values. The model that showed significant improvement was chosen ($p < 0.05$). The residuals of each model were checked for homoscedasticity and errors were checked for normality. Within-model z values and associated p values are also reported for specific comparisons.

F. Call order within bouts

There are two general methods for analyzing the organizational structure within sequences of events: chi-square tests (X^2) and information theory techniques (Chatfield and Lemon, 1970). These methods are similar (see review by Chatfield and Lemon, 1970), although X^2 tests allow for more detailed investigation of specific associations of calls

within bouts. Both methods were therefore used to explore whether calls are ordered into structured bouts in humpback whales.

1. Information theory

Information theory techniques were used to calculate the amount of uncertainty in predicting which call type followed another call type within a bout. Information theory has been utilized by a number of studies looking at sequences of events (e.g., Shannon, 1948; Chatfield and Lemon, 1970; McCowan *et al.*, 1999; Riesch *et al.*, 2008), including the structure of humpback whale song (Suzuki *et al.*, 2006; Miksis-Olds *et al.*, 2008). Information theory investigates the degree of diversity and organizational structure in a sequence of events by quantifying the amount of entropy that is lost in a system through knowledge of repertoire diversity (zero-order approximation of entropy), the frequency of occurrence of all behaviors (e.g., words or calls) in a repertoire (first-order approximation of entropy), and the conditional probabilities for which behaviors are combined (second-, third-, fourth-order, etc., approximation of entropy or $n - 1$ order Markov chain) (Shannon, 1948).

The zero-order model is a measure of repertoire diversity and is measured as

$$H_0 = \log_2 N,$$

where N is the overall number of call types in the repertoire (in this study $N = 23$ call types identified). The measure of the zero-order approximation of the system assumes that all calls in the repertoire are equally likely to occur and are independent of each other.

A first-order model takes into account the frequency of occurrence of each call type in the repertoire and is calculated by

$$H_1 = -\sum_i^N P(i) \log_2 P(i),$$

where $P(i)$ is the probability of occurrence of the call type (i) and N is the overall number of call types in the repertoire. The first-order entropy starts to investigate the internal structure in the communication repertoire. If the probability of occurrence is equal for all calls then $H_1 = H_0$.

A second-order model determines the conditional probabilities between any two call types within the repertoire (equivalent to a first-order Markov chain analysis). The second-order approximation is calculated by

$$H_2 = -\sum_{i,j}^N P(i) P_i(j) \log_2 P_i(j),$$

where $P_i(j)$ is the probability of call type j's frequency of occurrence given the preceding call type i has occurred. N is the number of call types in the repertoire. If the two events are completely independent (non-conditional) then $H_2 = H_1$.

The zero- and first-order approximation calculations give an indication of repertoire size and structure, whereas the second-order approximation describes the sequential dependencies between two calls in a sequence. If there is dependence on call frequencies (first-order) and the way that calls are combined (second-order), then the amount of entropy (or randomness) will decrease with successive orders.

2. Chi square analysis

For all call bouts, the call transitions (whether from one call to another of the same type or of a different type) were tallied and placed in a contingency table using a Perl (v5.10.1) script. A total of 1249 call transitions were counted and the observed transition counts were compared to the expected transition counts for all call types using an X^2 test conducted in R (R Development Core Team, 2012). The expected transition counts were calculated from the observed transition counts by dividing the row total by the column total in the matrix. As many of the expected values were below 5, which can lead to unreliable results (Everett and Hothorn, 2010), the sampling distribution was simulated using Monte Carlo methods by generating 20 000 permutations based on the observed data (Hope, 1968). Additional X^2 tests were also run to investigate whether any particular call types were more likely to follow themselves or any other call types significantly more than expected, with the expected distribution generated by Monte Carlo simulation.

III. RESULTS

Acoustic and behavioral data were analyzed from 72 h and 26 min of recordings from 35 groups. A total of 2426 individual calls were isolated, with each labeled as belonging to a bout (1942 calls) or being a single call (484 calls) and subjectively classified into a call type category. All calls grouped into 23 different call types that were all found in both years, with the exception of two call types, "ratchet" and "groan," that occurred at a low prevalence in only one or the other year. The BEC was calculated to be 3.9 s using the MLM method and 35.15 s using the log-frequency method. The estimated cumulative frequency distribution from the MLM model tended to fit that of the observed distribution with only slight departures and was in better agreement than the log-frequency method (Fig. 2). Thus, all calls that fell within 3.9 s from adjacent calls were considered to occur in bouts. The calculated BEC fit well with the observed distribution of calls in the recordings (see Fig. 3 for a typical temporal separation of calls in a recording).

A. Production of calls in bouts

Calls were produced more frequently in bouts (80% of total calls were produced in 346 bouts) than singularly (20% of total calls). All 23 call types were produced within bouts as well as heard as single call types. "Bop" (15.1% of total calls), "yap" (14.9% of total calls), "yelp" (13.9% of total calls), and "snort" (11.6% of total calls) were the most common call types produced within bouts (Table II). Two of the most common call types, yelp and yap (Fig. 3), were produced almost exclusively in bouts (>90% of calls found were in bouts for each of these call types).
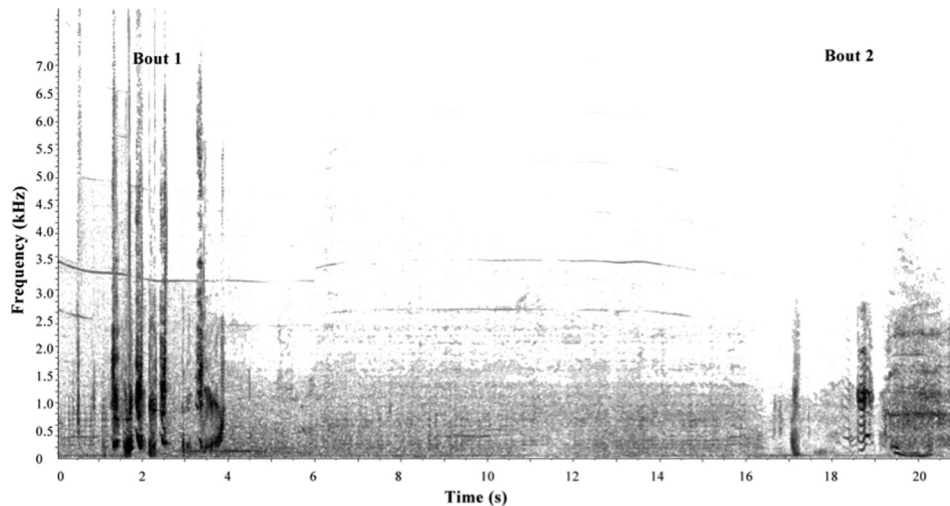
FIG. 3. Spectrogram of two call bouts determined by the BEC of 3.9 s. The two call bouts are separated by ∼13 s and are therefore two separate bouts. Bout 1 starting at 1.5 s is composed mostly of two of the most common call types in bouts—a yelp is followed by a yap, which is repeated and followed by another yelp and then a wop at 3 s. The two call bouts are labeled in the spectrogram Bout 1 and Bout 2.

Six new call types were identified and named that did not subjectively match any of the previously defined call type categories from this population (Dunlop *et al.*, 2007; Rekdahl *et al.*, 2013). One of these call types, the bop call, was the most common call type found to be produced within bouts [Fig. 4(b)]. The bop call was a broadband bop with a distinct amplitude onset that was less than 0.05 s in duration. The bop call occurred most commonly together with other bop calls [Fig. 4(b)], although it was also found commonly with snorts [Fig. 4(b)].

Using the bout criterion interval of 3.9 s to define bouts, there were 346 call bouts isolated from the two years of

recordings. Bouts contained from 2 to 26 calls with an average of 4.61 ± 4.72 (mean ± standard deviation). The average duration of bouts was 4.14 ± 3.25 s and the average interval between calls in a bout was 0.82 ± 0.83 s. Out of the 346 isolated bouts, only 27 bout types were heard more than once and in multiple recordings (collectively totaling 113 bouts). The other 233 bout types were each found only once in all recordings. The most common bout types were simple two call bouts with "purr, roar" ($N = 27$ found in 8 groups), "bop, bop" ($N = 21$ found in 8 groups)m and "snort, bop" ($N = 4$ found in 2 groups) produced most often [examples of these calls are displayed in Figs. 3(a) and 3(b), respectively].

B. Bout production within different group compositions and social contexts

The total number of bouts, short bouts, and long bouts produced within 5 min time periods were used as the response variables in GLMMs. The models containing the predictor variables [social context (stable, join, split) and group composition (FC, FCE, 2F2CEE, FCEE, AA)] showed significant improvement over the null models [all bouts: Log Likelihood -309.39, degrees of freedom (df) $= 4$, $p = 0.02$; short bouts: Log Likelihood -240.25, df $= 4$, $p = 0.04$; long bouts: Log Likelihood -185.68, df $= 4$, $p = 0.02$], demonstrating that both social context and group composition were important determinants of when bouts were produced.

Bouts in general were produced significantly more when groups were "joining"' relative to stable groups [$z = 3.38$, $p = 0.0008$, Fig. 5(a)], with no difference found between either of these categories and groups that were splitting. This increased production of bouts when groups were joining relative to stable pods also occurred for short bouts [$z = 4.16$, $p < 0.0001$, Fig. 5(b)], but the production of long bouts did not appear to be influenced by the groups' behavioral states [Fig. 5(c)]. FCEE groups tended to produce all bouts, short bouts, and long bouts significantly more relative to AAs (of unknown sex that did not contain a calf) [all bouts, $z = 2.87$, $p = 0.004$; short bouts, $z = 2.34$, $p = 0.02$; long bouts, $z = 2.44$, $p = 0.01$; Figs. 5(a)–5(c)], with no difference found among any other group compositions.

TABLE II. Total number and percentage of each call type recorded as occurring as part of a bout or as a single call. The total percentage of each call type produced as part of a bout is also displayed.

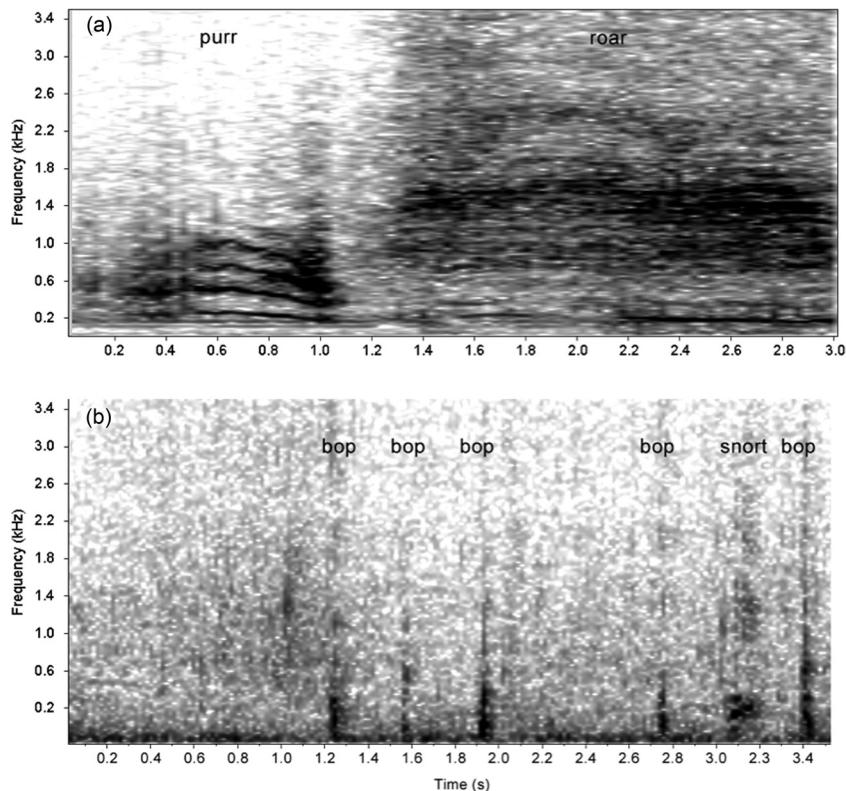| Call type	No. in bout	No. as single call	% bout	% single	% calls produced within a bout
Bop	294	89	76.8	23.2	15.1
Yap	290	9	97.0	3.0	14.9
Yelp	270	3	98.9	1.1	13.9
Snort	226	65	77.7	22.3	11.6
Roar	107	42	71.8	28.2	5.5
Purr	86	23	78.9	21.1	4.4
Moan	82	32	71.9	28.1	4.2
Squeal	75	13	85.2	14.8	3.9
Cry	75	24	75.8	24.2	3.9
Wop	70	48	59.3	40.7	3.6
Grumble	66	22	75.0	25.0	3.4
Bark	53	35	60.2	39.8	2.7
Whoop	52	27	65.8	34.2	2.7
Ratchet	34	12	73.9	26.1	1.8
Composite	26	10	72.2	27.8	1.3
Squeak	28	2	93.3	6.7	1.4
Whistle	27	2	93.1	6.9	1.4
Thwop	19	13	59.4	40.6	1.0
Trill	18	5	78.3	21.7	0.9
Pulses	16	4	80.0	20.0	0.8
Grunt	14	1	93.3	6.7	0.7
Groan	9	1	90.0	10.0	0.5
Growl	5	2	71.4	28.6	0.3
Total	1942	484			100

FIG. 4. Spectrograms of (a) purr,roar call bout type and (b) a bout of four bop call types followed by a snort followed by another bop. The calls are labeled above the relevant sound in the spectrograms. Note the difference in time scales.

C. Relative RL of calls within bouts

The maximum difference between the RLs of calls within bouts ranged from ~1 to 18 dB depending on the bout. The majority of call bouts (77%) were comprised of calls with less than 10 dB difference between sounds and 91% were less than 12 dB.

D. Ordering of call types within bouts

The order in which call types were positioned in a bout relative to the following call type differed significantly from the expected random distribution ($X^2 = 59.81$, $N = 1249$, $p < 0.0001$). In addition, for 21 of the 23 call types found within bouts, the transition to a subsequent call type differed significantly from the expected random distribution (results only displayed for the common call types; Table III).

Due to the small sample size, the organizational structure of humpback whale social call bouts could only be investigated as far as the sequential dependencies between two call types within bouts (second-order entropy/first-order Markov chain). The entropic slope of humpback whale social bouts decreased steadily between orders (Table IV), suggesting there was a degree of structure and order to how calls were composed within bouts.

IV. DISCUSSION

The results from this study have clearly shown that east Australian humpback whales frequently combine social calls into bouts, and that these bouts are produced more often in particular, types of social groups and social contexts. Previous research on humpback whale social vocalizations described the common use of multi-call sequences, which

varied in the number and types of calls used (Silber, 1986). Here, further quantitative evidence has been provided to demonstrate that the use of call bouts in humpback whales occurs commonly, and that the composition of calls within bouts is generally variable (223 bout types heard only once, compared to 27 bout types heard at least twice). However, further analysis into call order within bouts showed that the transitions from one call type to another within call bouts were non-random, demonstrating some level of order in how calls are combined into call bouts in humpback whales.

While our analysis of call bout order demonstrated that calls were often produced within structured bouts, whether or not bouts are produced by one or more individuals could not be determined conclusively. To minimize the chance that bouts were from more than one individual, all bouts containing overlapping social calls (indicating at least two different individuals were vocalizing at once) and any call bouts where there were noticeably large amplitude differences between different calls in the bout, were excluded from the analysis. However, measurement of the RLs of a subset of bouts showed that although there was generally less than 10 dB difference between calls within a bout, there were at times up to an 18 dB difference between calls within bouts. This may indicate that either there were multiple animals in close proximity producing calls in a call response interaction or, that bouts were produced by a single individual but that calls are produced at different amplitudes within the bout.

A number of species have been shown to produce calls in call-counter call interactions. Miller et al. (2004) demonstrated that bouts of stereotyped calls produced by killer whales are typically composed of vocal exchanges of matching call types between different individuals. Similarly, sequences of calls in fin whales (*Balaenoptera physalus*) can
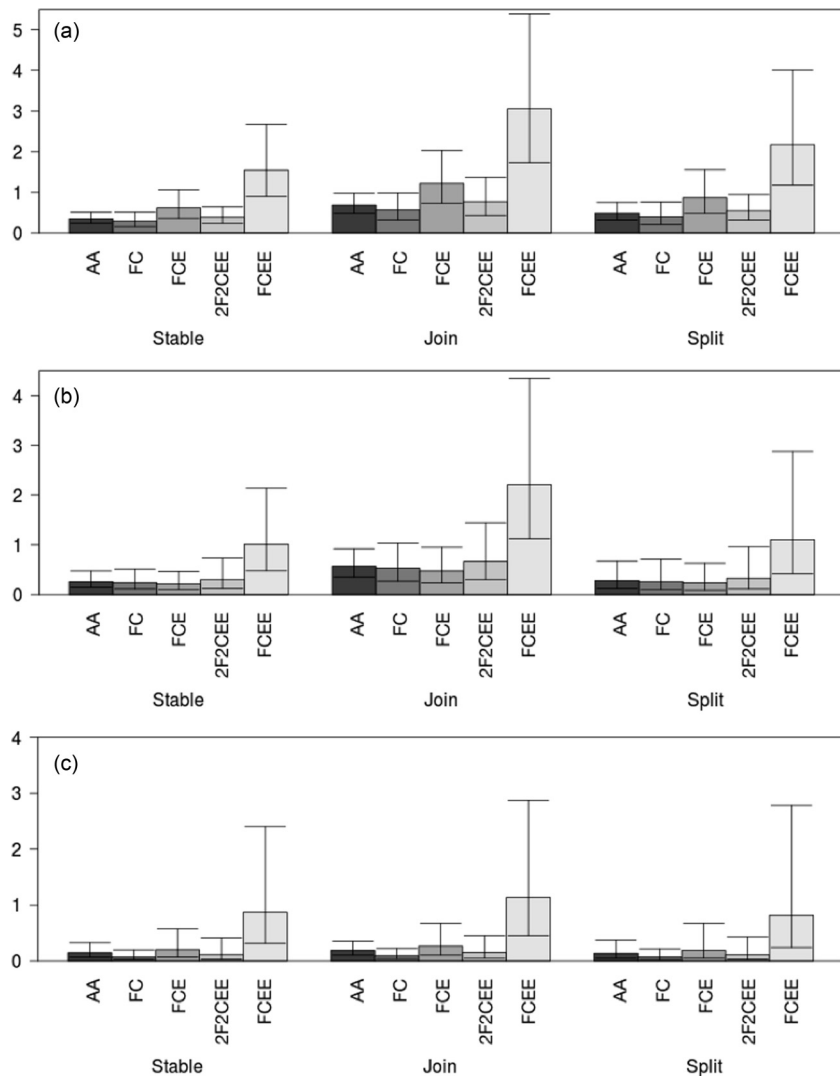
FIG. 5. Mean (±standard error of the mean) numbers of (a) all bouts, (b) short bouts, and (c) long bouts produced per 5 min sampling period during stable, joining, and splitting group behavioral states in AA, FC, FCE, 2F2CEE, and FCEE groups. Note: *y* axes are on different scales.

be composed of call-counter call interactions that may function in maintaining group cohesion or as contact calls (Sirovic *et al.*, 2013). In this study, whether call bouts are produced by a single animal cannot be determined conclusively and the lack of ability to spatially separate the calls precluded any analysis of call-counter call interactions. However, the relatively short duration used to define call

TABLE III. Chi square results comparing the expected and observed transition patterns for each call type are displayed to determine if the observed transition to the same call type, or to any other call type, differed significantly from the expected random distribution within a bout. Only the most significant results for the common call types are displayed.

Chi square analysis			
Call type (Preceding call)	N	X^2	p
Snort	139	139.15	<0.0001
Grumble	33	117.29	<0.0001
Yap	230	210.34	<0.0001
Yelp	247	267.52	<0.0001
Bop	150	327.96	<0.0001
Squeal	47	51.49	=0.008
Purr	58	405.50	<0.0001
Moan	36	104.35	<0.0001

bouts and the limitations placed on which call bouts were analyzed restricted the analysis to call bouts that were considered "likely"' to have been produced by a single individual.

The difference in relative received call levels within the subset of calls measured in this study may instead reflect intrinsic variability in the production of different call types or changes due to behavioral or environmental factors. Miller (2006) found that killer whales change the intensity of their calls depending on behavioral context, thereby changing the active communication space of their calls. Recently, Risch *et al.* (2014) found that acoustically tracked Atlantic minke whales (*Balaenoptera acutorostrata*) produce distinct pulsed call sequences with noticeable source level differences (∼12 dB) between pulsed calls within a sequence. Risch *et al.* (2014) suggested that these differences may be an inherent characteristic of call production by

TABLE IV. Approximations of entropy of humpback whale social calls.

Entropic approximation	Humpback whale social calls
Zero-order	4.59
First-order	3.85
Second-order	2.61

the individual, or alternatively may be a function of sound propagation due to depth in the water column possibly due to dive behavior during call production. Similarly, Dunlop et al. (2013) found the humpback whale social vocalization repertoire ranged in source levels (root-mean-square) from 124 to 184 dB re 1 mPa @ 1 m, and that average source level measurements differed among different call types and in different social groups. The large range in average source levels of different call types in the humpback whale repertoire may explain the variation in relative RL measurements found in this study, as all bouts measured were composed of multiple different call types and produced by different social groups. Regardless of whether call bouts in humpback whales are produced by a single individual or multiple individuals in a call response interaction, the finding that call bouts can be composed of calls following a particular order is still intriguing and provides the basis for further research into the function of these call combinations in social interactions.

For call bouts to convey meaning, calls produced within a bout should be non-random and have some kind of order (Riesch et al., 2008). In our study, the degree of order in which some call types were combined into bouts suggests that humpback whales follow rules for how calls are combined, at least to some extent. Thus, the rules governing call order within humpback whale call bouts may have similarities to the rudimentary syntax-like rules discovered in the social call systems of a number of other species (e.g., titi monkey, Robinson, 1979; Mexican chickadee, Ficken et al., 1994; killer whale, Riesch et al., 2008; Mexican free-tailed bat, Bohn et al., 2008). However, the combination of call types within bouts appeared to be somewhat open ended and more flexible than found in many of these species. In some species, research has suggested that an entire sequence of calls is the unit of perception rather than the individual calls that make up the sequence (e.g., cotton-top tamarin, Ghazanfar et al., 2001). Bohn et al. (2008), for example, found that Mexican free-tailed bats convey meaning in the stereotyped nature of their call sequences rather than in the individual call types, as calls were always found within bouts and in the same order. In contrast, the lack of stereotyped, predictable types of call bouts suggests that both the individual calls and how they were combined within bouts may have conveyed the information, rather than information being encoded only by the entire call bouts.

Investigating the social communication system of a species from a structural perspective provides valuable insight into the possible functions of specific calls and the amount of complexity in a system. The use of information theory to measure the amount of repetition and diversity of a communication repertoire has been attempted for a number of different species (e.g., the whistles of dolphins *Tursiops truncatus*, McCowan et al., 1999; the song of humpback whales, Suzuki et al., 2006; Carolina chickadee *Poecile carolinensis* calls, Freeberg and Lucas, 2012). The majority of these studies utilized model-based estimations of entropy rather than model-free "true" calculations of entropy, which are more accurate (see Suzuki et al., 2006). As animal call sequences are generally short in duration and produced sporadically, it may only be possible to calculate "estimations"

of entropy using the relative frequency of calls occurring in a finite set of observations. Humpback whales' social call sequences are also generally short in duration and occur sporadically, which led us to utilize a model-based estimation of entropy. Although there may be some degree of error in using estimations, there is still merit in utilizing this method as an initial investigation into the degree of order present in animal communication systems (see McCowan et al., 1999; Freeber and Lucas, 2012). In this paper, the use of chi square tests on the transitional probabilities between two call sequences supported the finding from the entropy calculations that some level of order occurs in humpback whales' social call sequences. However, further research addressing some of the limitations in using model-based estimations of entropy should be attempted before definitive conclusions can be drawn about the degree of complexity in humpback whales' social call sequences.

A significant part of investigating rule structure in communication systems is determining whether different call combinations convey different meanings to conspecifics. However, humpback whales are generally only visible for a small proportion of the time when at the surface and the majority of calls are produced while under water. Therefore attributing specific social and behavioral functions to different call combinations is difficult. Semantic information for different combinations of calls has been demonstrated to occur in some primate species for which detailed behavioral observations are easier to obtain (e.g., Campbell's monkeys, *Cercopithecus campbelli campbelli*; Ouattara et al., 2009). Male Campbell's monkeys combine six stereotyped call types to produce nine unique sequences that convey information to conspecifics about such things as group cohesion and travel (Ouattara et al., 2009). In the present study, the potential for contextual differences in the use of call bouts could only be explored broadly. The fact that call bouts were produced more in particular, types of social groups and social contexts suggests that producing calls in bouts is an important aspect of the communication of information in these contexts. Silber (1986) found that the use of social vocalizations increased significantly when new whales joined a group. In the present study, short call bouts in particular, were produced significantly more in joining interactions, which may indicate these are important for mediating the joining of new members into a group. However, the small sample sizes in our study limited the number of behavioral context categories that could be investigated as well as investigations into the types of bouts that may have been used in different contexts. Thus, further research is required to determine whether there is semantic meaning in how calls are combined within bouts within different social and behavioral contexts.

The results from this study have demonstrated that humpback whales often produce social calls in bouts that are composed of a number of different call types ordered in a non-random manner. Further research into vocal exchanges between tagged individuals within social groups combined with call source level measurements from acoustically and visually tracked individuals would provide valuable information on the behavioral functions of call bouts and whether

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some call bouts may be call-response interactions. Recent research has demonstrated that accelerometer data from DTAG recordings can be used to distinguish the calling behavior of tagged individuals from that of surrounding whales (Goldbogen *et al.*, 2014); using such data would be an important next step in further investigation of the use of social calls within bouts in humpback whales. Finally, focusing on specific call orders within bouts in different populations, how repeated call bouts vary among individuals, and the social and behavioral contexts to the use of these call bouts might uncover more of the communication abilities of humpback whales and enable comparisons with other species.

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