Acoustic analysis of cattle (*Bos taurus*) mother–offspring contact calls from a source–filter theory perspective

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ABSTRACT

Cattle vocalisations have been proposed as potential indicators of animal welfare. However, very few studies have investigated the acoustic structure and information encoded in these vocalisations using advanced analysis techniques. Vocalisations play key roles in a wide range of communication contexts; e.g. for individual recognition and to help coordinate social behaviours. Two factors have greatly assisted our progress in developing an understanding of animal vocal communication. Firstly, more rigorous call analysis methods allow us to describe the variation in the vocal parameters in unprecedented detail. Secondly, the adoption of the "source–filter theory" of call production links the acoustic structure of vocalisations to the morphology and physiology of calling animals. Using these approaches, it is possible to quantify the potential for each acoustic component to carry information. In this study, we examined naturally occurring contact calls produced by crossbred beef cows and their calves under free-ranging conditions. Our main aims were to identify vocal parameters, which can be used to characterise cow and calf contact calls, and to describe variation in these parameters under relatively undisturbed conditions. Additionally, we aimed to provide information for future studies on potential acoustic indicators of animal welfare in cattle. We identified two different types of cow contact calls associated with different behavioural contexts, and with differing acoustic structures. Low frequency calls (LFCs) were produced by cows when they were in close proximity to their calves, in the first three or four weeks postpartum, and they were made with the mouth closed or only partially open (fundamental frequency (F0) = 81.17 ± 0.98 Hz). By contrast, high frequency calls (HFCs) were produced by cows when they were separated from their calves (e.g. not in visual contact) and preceded nursing (F0 = 152.8 ± 3.10 Hz). Calf calls were produced when separated from their mothers and preceded suckling (F0 = 142.8 ± 1.80 Hz). A detailed analysis of cow LFCs and HFCs, and of calf calls, showed that all three types of calls are individually distinctive. We also show that calf calls encode age, but not sex. Although it has previously been suggested that cattle contact calls are individually distinctive, to our knowledge, our study

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is the first to use the most rigorous, modern methods to analyse their calls. This study represents an important advance in our knowledge cattle contact vocalisations, which is essential for future work on cattle communication and welfare.

1. Introduction

Vocal communication can convey different types of information and is thus used in many forms of social interactions (Fischer et al., 2002; Taylor et al., 2009; Theis et al., 2007). For example, vocalisations may encode individual identity of the producer (Briefer and McElligott, 2011a). There is also good evidence that vocal cues can inform receivers about physical attributes of the senders (McComb and Reby, 2005). For example, male deer rut vocalisations are used by conspecifics to infer body mass, age and social status (Briefer et al., 2010; Reby and McComb, 2003; Pitcher et al., 2014; Vannoni and McElligott, 2008, 2009), and goat (*Capra hircus*) kid calls reveal information about their sex, age and body weight (Briefer and McElligott, 2011b). These types of information are particularly useful when individuals range widely, because visual or olfactory signals are not always available (Sèbe et al., 2007).

Early research on mammal vocal communication, and particularly applied studies of vocalisations in an animal welfare context, generally focused on easily measured parameters of vocalisations, such as calling rate and behavioural responses of receivers (Grandin, 1998, 2001; Weary and Chua, 2000). These studies often relied on the descriptive analyses and/or classification of calls into types, according to different contexts (Byrne and Soumi, 1999; Marchant et al., 2001; McElligott and Hayden, 1999; Owings and Morton, 1998; Weary and Fraser, 1995). Recent developments in signal analysis techniques have led to major advances in our understanding of animal vocal communication (Boersma and Weenink, 2009; Taylor et al., 2010; Taylor and Reby, 2010). For example, the source–filter theory, which was originally developed to describe the link between parameters of the human voice and their mode of production, has recently been applied to animal vocalisations. This framework has allowed researchers to describe in detail the structure and variation of the acoustic parameters present in animal vocalisations (Briefer and McElligott, 2011b; Fant, 1960; Taylor and Reby, 2010; Titze, 1994).

The source–filter theory of voice production (Fant, 1960; Titze, 1994) states that mammal vocalisations are generated by vibrations of the vocal folds ("source"). This source sound is subsequently filtered by the vocal tract ("filter"). The source determines the fundamental frequency (also known as pitch; "F0"). Fundamental frequency can vary between individuals, as a result of differences in the way that larynx is operated, or because of variation in the morphology of callers (McComb and Reby, 2005; Reby and McComb, 2003). In the supra-laryngeal vocal tract (i.e. the tube that links the larynx to the mouth and nasal openings), certain frequencies of the source spectrum, which correspond to the vocal tract resonances, are selectively amplified or "filtered". The physical characteristics of the filter, such as length and shape of the cavities of the vocal tract, pharynx, mouth and nasal cavities, determine the frequencies of the formants and the relative energy distribution in the spectrum (McComb and Reby, 2005; Taylor and Reby, 2010).

Variation in vocal parameters related to the source or filter encodes information such as mate quality, social status, and individual identity. For example, fundamental frequency varies between individuals in fallow deer female contact calls (*Dama dama*, Torriani et al., 2006). Formant frequencies are important for individuality coding in African elephants (*Loxodonta africana*; McComb et al., 2003), whereas both source and filter-related parameters encode individual identity in goats (Briefer and McElligott, 2011a). Overall, the source–filter framework also has great potential as a valuable tool in animal applied sciences, helping to highlight animal welfare indicators in vocalisations (Briefer, 2012; Briefer et al., 2015; Manteuffel et al., 2004; Marchant-Forde et al., 2002; Watts and Stookey, 2000).

It is highly likely that the acoustic structure of cattle vocalisations provides information about the caller, such as age, sex and individuality, in the same way as vocalisations of other ungulates (Briefer and McElligott, 2011a,b; Fitch, 1997; Reby and McComb, 2003). It has previously been suggested that cattle vocalisations differ among individuals and populations (Hall et al., 1988; Kiley, 1972). Kiley (1972) suggested that cattle produce six different call types in various behavioural contexts. However, the proposed call classification of Kiley (1972) was limited by the technologies for sound recording and analyses that were available at that time.

The assessment of animal welfare is usually achieved through measurements of different physiological or behavioural indicators, in order to obtain information about how well or poorly animals are coping with their environment (Broom, 1986; Boissy et al., 2007). There is evidence suggesting that vocalisations in cattle may signal the physiological and emotional state of the producer (Watts and Stookey, 2000). For example, both cows and calves increase their calling rate after being separated from each other (Kohari et al., 2014; Weary and Chua, 2000), and during handling (Grandin, 1998, 2001; Watts and Stookey, 2001). Similarly, vocalisation structure may vary according to the stress levels of the producer (Stehulova et al., 2008; Thomas et al., 2001; Watts and Stookey, 1999). These studies have demonstrated the potential use of cattle vocalisations to assess stress and welfare (Manteuffel et al., 2004; Thomas et al., 2001; Watts and Stookey, 2000). Therefore, vocal parameters could serve as a useful non-invasive means to assess welfare in cattle (Briefer, 2012; Manteuffel et al., 2004; Weary and Fraser, 1995). However, in order to develop robust vocal welfare indicators, a comprehensive study of cattle vocalisations living in relatively undisturbed conditions (e.g. free-ranging) is required. First,

the acoustic parameters that allow the structure and information content of vocalisations to be characterised in detail must be identified. Second, a thorough description of the range of vocal parameters under free-ranging conditions is needed, in order to provide a reference point for future studies on vocal indicators of welfare.

In this study, we provide the first detailed description of the structure and information content of cow and calf vocalisations during mother–offspring communication, using the source–filter theory framework. We aimed to provide the methodology that could be applied in future studies investigating cattle vocalisations, including those examining communication in other behavioural contexts, and those specifically attempting to develop vocal indicators of animal welfare. We recorded and analysed contact calls of cows and calves that were outdoors, free-ranging and relatively undisturbed on a farm (no artificial manipulation or isolation involved in the recording process). We hypothesised that cow vocalisations would be individually distinctive, in order to allow mother–offspring recognition. We also hypothesised that source and filter-related parameters of calf vocalisations would change with age and show sex differences. This study represents an important advance that will assist future understanding of cattle vocal communication.

2. Methods

2.1. Subjects and study site

The study was carried out using two crossbred beef cattle herds (Herd 1: $n = 21$ adult females; Herd 2: $n = 23$ adult females) kept in two separated fields on a farm in Radcliffe on Trent (52°56′44″ N, 1°02′62″ W), Nottinghamshire, UK, from February to December 2010. The two fields were approximately 52 ha (Herd 1) and 23 ha (Herd 2), and were separated only by a road (3 m wide). We observed and recorded 344 mother–offspring contact calls (cows, $n = 205$ calls; calves, $n = 139$ calls) from 31 individuals ($n = 17$ cows and 14 calves). Recordings were carried out in each field independently. All individuals included in the study were free to roam in the fields with fresh grass and water ad libitum. All cows included in our study were multiparous. The studied calves were all born between February and July 2010 and were all sired by the same bull. The two herds were kept separately in their respective fields almost without interchange of animals, except in three cases, where the owners moved two animals from Herd 1 to Herd 2 and one animal from Herd 2 to Herd 1. All the calves included in the study were kept all year long in the same field as their mothers.

2.2. Sound recording and signal acquisition

Recordings of individual calves and cows were made opportunistically between 8 am and 5 pm. Calls were recorded at distances of 8–30 m from the vocalising animal with a Sennheiser MKH70 directional microphone, connected to a Marantz PMD660 digital recorder (sampling rate 44.1 kHz). Accurate individual identification was done using specific ID tags placed in the animals' ears by the farmers and recognition of coat markings. The exact ages of the calves on days when calls were recorded were known.

Recorded vocalisations were uploaded to a computer at a sampling rate of 44.1 kHz and saved in a WAV format at 16-bit amplitude resolution. We used Praat v.5.1.44 DSP Package (Boersma and Weenink, 2009) for the acoustic analyses. Calls were individually visualised on spectrograms in Praat (FFT method, window length = 0.1 s, time steps = 100, frequency steps = 250, Gaussian window shape, dynamic range = 40 dB). Vocalisations with high levels of background noise (as visualised on the spectrogram) were not considered for acoustic analysis.

2.3. Acoustic analyses

Cow and calf vocalisations are typically 1.3–1.5 s long, with a clear harmonic structure (Fig. 1a–c). Cow calls were divided in two different basic categories, according to the behavioural context observed during call production. These categories were adapted from previous studies of cow vocalisations (Kiley, 1972) and other ungulates (low/high frequency calls; Sèbe et al., 2010). Cow low frequency calls (henceforth "LFCs") were produced with the mouth closed or only partially opened. They were extremely quiet, being noticeable by hear to a casual observer only when produced indoors or from a very short distance (approximately 8–10 m) outdoors (Fig. 1a). They were produced during the first 3–4 weeks after the calves were born, during resting periods where mother and offspring were close to each other (e.g. Kiley, 1972; Sèbe et al., 2010). During these situations, we approached the animals at 8–10 m and were then able to hear and record the calls. By contrast, cow high frequency calls (henceforth "HFCs"), where the cow's mouth was fully opened for at least part of the call (the call sometimes started with the mouth only partially opened), were typically much louder, and were clearly audible in the field (Fig. 1b). In order to include only contact calls, cow HFCs were used in the study exclusively if they were produced by a cow when her own calf was in another part of the field, and when vocal production was followed by reunion with the calf and nursing. Similarly, we considered only those calf calls produced when their mothers were in another part of the field, and when vocal production was followed by reunion with the mother and suckling. Calf calls were similar in pitch to cow HFCs (both higher pitch than LFCs) and were produced with the mouth fully opened for at least part of the call (Fig. 1c). As with cow HFCs, the first part of the call was sometimes (ca. 30% of calls) produced with the mouth only partially opened.

In order to assess the basic acoustic parameters of cow and calf calls, the source-related vocal features were extracted (parameters related to the fundamental frequency, F0), together with filter-related features (formants) and intensity measures (42 parameters for cow LFCs and 45 for cow HFCs and calf calls; Table 1), all of which potentially contribute to vocal individuality (Taylor and Reby, 2010; Briefer and McElligott, 2011a), using a custom built programme in Praat v.5.1.44 (Reby and McComb, 2003). This programme batch-processed the analyses and then exported acoustic parameters, except for the filter-related features, which were manually and
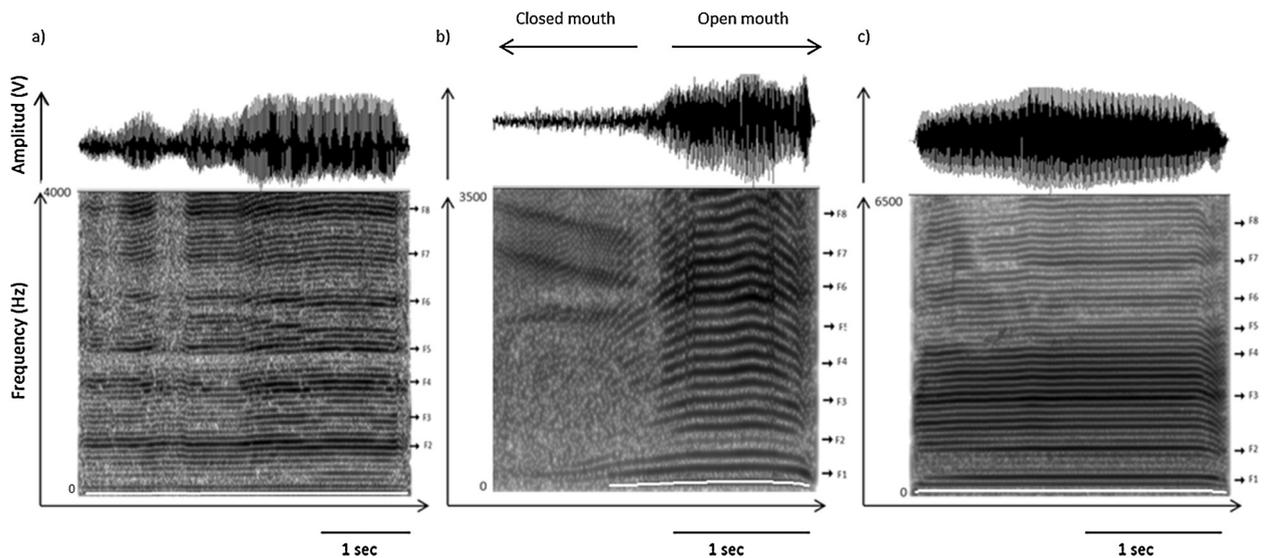
Fig. 1. Examples of oscillograms (above) and spectrograms (below) of cattle vocalisations. The white line at the bottom of each spectrogram indicates the fundamental frequency (F0). Frequency values of the formants are indicated by arrows on the right of the spectrogram. (a) Low frequency cow call produced with closed mouth (LFC). (b) High frequency cow call (HFC). The first part of the HFC was produced with the mouth partially closed, and then the second part with the mouth fully open (the arrows at the top indicate where the change occurs). For HFCs, we considered just the part with open mouth and the acoustic parameters described in this figure correspond exclusively to the acoustic analysis carried out on this part of the call. (c) Calf call (produced with opened mouth).

individually calculated in Praat (see ESM 1 for detailed Praat settings). For calls that were composed of a first part produced with the mouth fully or partially closed, we recorded the original total call length but, in order to calculate the other acoustic parameters in a standardised way,

we measured them only using the part of the call made with the mouth open. This was necessary because the extent of mouth opening influences the resonant properties of the vocal tract, and some formants can be modified or even suppressed in closed-mouth calls (Titze, 1994). For cow LFCs,

Table 1
Abbreviations for the vocal parameters analysed in cow and calf calls.

Abbreviation	Parameter
F0Start (Hz)	Frequency value of F0 at the start of the call
F0End (Hz)	Frequency value of F0 at the end of the call
F0Mean (Hz)	Mean F0 frequency value across the call
F0Min (Hz)	Minimum F0 frequency value across the call
F0Max (Hz)	Maximum F0 frequency value across the call
TimeF0Max (%)	Percentage of the total call duration when F0 is maximum
F0AbsSlope (Hz/s)	F0 mean absolute slope
F0Var (Hz/s)	Cumulative variation in the F0 contour in Hertz divided by call duration
FMRate (s^{-1})	Number of complete cycles of F0 modulation per second
FMExtend (Hz)	Mean peak-to-peak variation of each F0 modulation
Jitter (%)	Mean absolute difference between frequencies of consecutive F0 periods divided by the mean frequency of F0
Shimmer (%)	Mean absolute difference between the amplitudes of consecutive F0 periods divided by the mean amplitude of F0
F1Mean, F1Min, F1Max (Hz)	Mean, minimum and maximum frequencies values of the first formant
F2Mean, F2Min, F2Max (Hz)	Mean, minimum and maximum frequencies values of the second formant
F3Mean, F3Min, F3Max (Hz)	Mean, minimum and maximum frequencies values of the third formant
F4Mean, F4Min, F4Max (Hz)	Mean, minimum and maximum frequencies values of the fourth formant
F5Mean, F5Min, F5Max (Hz)	Mean, minimum and maximum frequencies values of the fifth formant
F6Mean, F6Min, F6Max (Hz)	Mean, minimum and maximum frequencies values of the sixth formant
F7Mean, F7Min, F7Max (Hz)	Mean, minimum and maximum frequencies values of the seventh formant
F8Mean, F8Min, F8Max (Hz)	Mean, minimum and maximum frequencies values of the eighth formant
DfMin (Hz)	Minimum spacing of the formants
MaxVTL (s)	Maximum estimated vocal tract length
Q25% (Hz)	Frequency value at the upper limit of the first quartiles of energy
Q50% (Hz)	Frequency value at the upper limit of the second quartiles of energy
Q75% (Hz)	Frequency value at the upper limit of the third quartiles of energy
AmpVar (dB/s)	Cumulative variation in amplitude divided by the total call duration
AMRate (s^{-1})	Number of complete cycles of amplitude modulation per second
AMExtent (dB)	Mean peak-to-peak variation of each amplitude modulation
Dur (s)	Duration of the call

the amplitude of the first formant was low compared to the subsequent formants and the software could not track it accurately; therefore it was eliminated from the analysis.

2.4. Statistical analysis

Sample sizes for the different identified types of calls were as follows: for LFCs, $n = 8$ individuals, with 7–10 calls per individual; for HFCs, $n = 15$ individuals, with 7–10 calls per individual; for calf calls, $n = 14$ individuals, with 9–10 calls per individual. For individuals for which more than 10 good quality calls were available, in order to create a balanced design for the analysis, we randomly selected 10 calls. Calls were often produced in sequences with, on average, three (calves) or five (cows) calls per sequence, separated by periods of silence (average 2.7 s in cows, and 2.8 s in calves). In order to obtain a representative sample for each individual, we used either single isolated calls, or calls from sequences that were separated by at least three calls (i.e. usually the first and last call of a typical 5 cow – call sequence and just one from a typical calf sequence), because consecutive calls are more likely to be homogeneous (Briefer and McElligott, 2011b; Reby et al., 1998). We strongly recommend this approach for similar studies of vocalisations. Because the total number of cow HFC, cow LFC and calf calls differ, and because some parameters could not be measured in all the calls, sample sizes differ between parameters and among the various analyses (see Section 3).

Maximum estimated vocal tract length (MaxVTL), measured using the formants frequencies of the calls produced by 7 randomly selected calves and cows, were compared to actual head lengths measured on the same animals (ESM 1). Comparisons between MaxVTL and head length values were carried out using Spearman Rank correlations in R (R Development Core Team, 2009).

Individual distinctiveness of calls was determined for cow and calf contact calls by calculating the Potential for Individual Coding (PIC) for each measured parameter, and by performing a Principal Components Analysis (PCA; Johnson and Wichern, 1992), followed by a Multivariate Analysis of Variance (MANOVA; with Wilk's lambda estimate for F; Huberty and Olejnik, 2006) and a Discriminant Function Analysis (DFA; Tabachnick and Fidell, 2007). Cow LFCs, HFCs and calf calls were treated separately. We carried out PCA, MANOVA and DFA using SPSS v. 20.

To calculate PICs, coefficients of variation were first calculated between and within individuals (CVb and CVw, respectively) as follows:

$$CV = 100 \left(1 + \frac{1}{4n}\right) \left(\frac{SD}{\bar{x}}\right)$$

where SD is the standard deviation of the sample, $\bar{x}$ is the mean and n is the sample size (Sokal and Rohlf, 1995). PIC was then calculated as the ratio of CVb to the mean CVw for all individuals. For a given parameter, a PIC value greater than 1 indicates that this parameter has good potential for use in individual recognition because its intra-individual variability is smaller than inter-individual variability (Robisson et al., 1993).

PCA was used to reduce the number of predictors and eliminate redundancy due to the potentially high inter-correlation of the measured vocal parameters, as well as to examine clustering among parameters (Johnson and Wichern, 1992). Missing data, occurring when one vocal parameter in a given call could not be measured, were replaced by the average value of this parameter for the given individual (0.5% of values missing for calves, 1.0% HFCs and 0.06% LHCs). The principal components (PCs) with eigenvalues that exceeded Kaiser's criterion greater than 1 were retained, and were then used as input variables for the subsequent statistical analyses (see Briefer and McElligott, 2011a).

MANOVA with "individual" as a categorical fixed factor and "age" (in calves only) included as a covariate was performed in order to confirm statistical differences between PC scores of individuals, and to test for age effects. Univariate ANOVA (for cows) and ANCOVA (for calves), with the same factor and covariate (individual and age), were also performed for each PC to aid in the interpretation of the MANOVA results. Then, a DFA with one factor (individual) was used to quantify the extent to which individuals can be classified on the basis of their calls, and to identify which groups of variables (PCs) are most useful in this classification (Huberty and Olejnik, 2006; Johnson and Wichern, 1992). On the basis of the discriminant functions extracted from the DFA, each set of PC scores (corresponding to calls) was assigned to the appropriate individual (correct classification) or to another individual (incorrect classification). This allowed us to calculate the percentage of calls (represented by PC scores) correctly classified (CC). The results were cross-validated by performing a "leave one out" classification (McGarigal et al., 2000). We calculated the CC due to chance by applying a randomisation procedure. The expected level of correct assignment was averaged from DFAs performed on 1000 randomised permutations of the data set (McGarigal et al., 2000).

Conventional DFA only allows the inclusion of a single factor at a time, and differences among individual calves identified in our initial DFA could arise solely because of differences between males and females (Mundry and Sommer, 2007). To remove the potentially confounding effects of sex, two additional DFAs were carried out on male and female data separately. The CCs were calculated for these DFAs as previously described.

Further analyses were performed to check for effects of sex on vocalisations in calves. MANOVA with "sex" as a fixed factor was performed on the average PC scores per individual, in order to test for statistical differences between female and male calls. In order to determine whether the age-related changes in calf vocalisations are different between males and females, we performed a *T*-test on the slopes of the relationship between age and the first two PCs for each calf.

2.5. Ethics

Animal care and all experimental procedures were in accordance with the International Society for Applied Ethology guidelines. During the recordings, mothers and calves were never manipulated or isolated.

3. Results

The mean ± standard errors (SEM) values of all the acoustic parameters measured in cows (LFCs and HFCs) and calf calls are detailed in Table 2. Cow LFCs had a mean F0 of 81.1 ± 0.9 Hz, and their formant frequencies (F2–F8) ranged from 634.3 ± 6.6 Hz to 3224 ± 26.2 Hz. By contrast, cow HFCs had a mean F0 of 152.8 ± 3.1 Hz, and their formant frequencies (F1–F8) ranged 228.3 ± 1.8 to 3181 ± 2.6 Hz. The mean F0 of calf calls was 142.8 ± 1.8 Hz, and formant frequencies (F1–F8) ranged from 391.7 ± 5.3 to 5813 ± 68.7 Hz.

PICs for most vocal parameters analysed in cow calls (both LFCs and HFCs) and calf calls were greater than 1, except for TimeF0Max in calves, and FMRate in cow LFCs (Table 2). This indicates that most of the source- and filter-related parameters are likely to code for individuality in calf and cow calls. Mean estimated MaxVTLs were 41.26 cm (± 0.35) for cow LFCs, 42.32 cm (± 0.05) for cow HFCs and 23.40 cm (± 0.29) for calves. These values were highly correlated with the observed measures of calves and cows head lengths (Spearman rank correlation for cows: $n = 7$ values, $r = 0.91$, $p = 0.003$; and for calves: $n = 7$ values, $r = 0.85$, $p = 0.02$; see ESM 1).

The PCA generated nine PCs for both cow LFCs ($n = 8$ cows, 69 calls, 42 vocal parameters) and calf calls ($n = 14$ calves, 139 calls, 45 vocal parameters) with an eigenvalue greater than 1, and in both cases, these PCs explained over 84% of the variance in the original variables used to describe the calls (ESM 2, Table 1A and C for more details on the factor loadings of the vocal parameters on the principal components). The first three PCs together explained more than 60% of the variance in the original variables for both cow LFCs and calves. The first PC was strongly and positively correlated with all the parameters describing the frequencies of the formants, and the minimum spacing among formant frequencies, and negatively with the mean estimated vocal tract length (MaxVTL). The second PC correlated strongly and positively with the parameters describing the fundamental frequency (F0), (ESM 2, Table 1A and C). The third PC for cow LFCs correlated negatively with the energy quartiles (Q25%, Q50% and Q75%), while the same vocal parameters correlated positively with this PC for calf calls (ESM 2, Table 1A and C).

The results of the PCA for cow HFCs differed from those of LFCs. Twelve PCs with an eigenvalue greater than 1 were generated ($n = 15$ cows, 136 calls, 45 vocal parameters). Together, they explained 76% of the variance in the original variables used to describe the calls (ESM 2, Table 1B). As with the calf calls and cow LFCs, the first PC correlated strongly and positively with the mean and maximum formant frequencies, but it did not correlate with the minimum formant frequencies or MaxVTL. The second PC correlated positively with several attributes of the fundamental frequency contour (F0Start, TimeF0Max, F0AbsSlope), and it also correlated negatively with MaxVTL and some other parameters (ESM 2, Table 1B). The third PC was more like the second PC for calves and cow LFCs, in that it correlated positively with the fundamental frequency

(F0), although it also correlated with some formant frequencies (ESM 2, Table 1B).

There were significant differences among individual cows in PCs scores for LFCs (MANOVA: $F_{63,304} = 4.26$, $p < 0.0001$) and HFCs (MANOVA: $F_{168,1032} = 2.93$, $p < 0.0001$). There was a significant effect of the interaction between individual and age on calf calls, meaning that the vocalisations of individual calves changed in different ways as they got older (MANOVA: $F_{117,783} = 2.69$, $p < 0.0001$). This effect is particularly evident in PC1 (formant frequencies), which generally decreased with age (ANCOVA: $F_{1,111} = 299.67$, $p < 0.001$), but some individuals showed more rapid declines over time than others (ANCOVA: $F_{13,111} = 11.14$, $p < 0.001$; see the effect of age on DfMin as an example, Fig. 2a). In addition to the significant interaction between age and individual, there were significant main effects of individual calf (MANOVA: $F_{117,783} = 3.07$, $p < 0.0001$), and calf age on the PC scores (MANOVA: $F_{9,103} = 35.05$, $p < 0.0001$). The effect of age was largely restricted to PC1. However, there was no obvious change in PC2 (reflecting F0) over time (ANCOVA: $F_{1,111} = 3.05$, $p = 0.08$; see F0Mean as a function of age as an example, Fig. 2b). By contrast, there was no effect of sex on the characteristics of calf calls (MANOVA: $F_{1,4} = 1.87$, $p = 0.29$).

For Cow LFCs, the DFA produced five discriminant functions (DFs) which could be used to discriminate among individuals (see ESM 2, Table 2A–C for more details on the discriminant function coefficients). Similarly, for cow HFCs, the DFA produced six discriminant functions, and for calf calls, the DFA produced three discriminant functions. For cow HFCs and calf calls, DF1 was highly correlated with PC1 (i.e. formant frequencies), PC2 (i.e. attributes of the F0 contour), and for cow HFCs also with PC3 (i.e. F0; ESM 2, Table 2A and C). By contrast, for cow LFCs, DF1 correlated mostly strongly with PC3 (which in turn correlated with the energy quartiles; Q25%, Q50% and Q75%) and PC4 (which was correlated with other attributes of F0; ESM 2, Table 2B).

Cross-validated DFAs correctly classified 53.6% of LFC calls ($n = 8$ cows with 7–10 calls per individual, chance level = 12.5%; binomial test $p < 0.001$), 30.9% of HFC calls ($n = 15$ cows with 7–10 calls per individual, chance level = 6.67%; binomial test $p < 0.001$) and 23.7% of calf calls ($n = 14$ calves, with 9–10 calls per individual, chance level = 7.14%; binomial test $p < 0.001$). Plots of calls and cross-validated DFA further illustrate that cow LFCs are relatively more individually distinctive, while calf calls are relatively less individualised (Fig. 3a–c).

Two additional DFAs including female and male calf data separately (to remove the potentially confounding effect of sex in calf calls) produced (for both sexes) two discriminant functions, which can be used to distinguish individual calves (see ESM 2, Tables 3A and B for more details on the discriminant function coefficients). Cross-validated DFAs correctly classified 33.9% of female calf calls ($n = 6$ calves with 9–10 calls per individual, chance level = 16.69%; binomial test $p < 0.001$) and 31.3% of male calf calls ($n = 8$ calves, with 10 calls per individual, chance level = 12.5%; binomial test $p < 0.001$). No statistical differences were found when we compared the slopes of the relationships between age

Table 2

Mean vocal parameters and PIC values (mean ± SEM) for high and low frequency cow calls (HFCs and LFCs), and calf calls. See Table 1 for abbreviations of the vocal parameters.

Parameter	Cow LFCs			Cow HFCs			Calf calls		
	Mean	SEM	PIC	Mean	SEM	PIC	Mean	SEM	PIC
F0Start (Hz)	76.5	0.9	1.4	94.2	3.2	1.3	130.1	2.1	1.1
F0End (Hz)	80.0	1.1	1.5	145.4	3.6	1.2	129.8	2.1	1.1
F0Mean (Hz)	81.1	0.9	1.4	152.8	3.1	1.2	142.8	1.8	1.2
F0Min (Hz)	74.8	1.0	1.4	91.0	2.8	1.3	121.0	1.6	1.2
F0Max (Hz)	84.7	1.0	1.5	198.7	3.6	1.4	153.3	2.1	1.1
TimeF0Max (%)	66.7	2.7	1.0	73.6	1.5	1.1	65.4	1.7	0.9
F0AbsSlope (Hz/s)	18.8	1.6	1.3	150.9	6.7	1.2	55.7	3.2	1.1
F0Var (Hz/s)	12.9	1.3	1.2	132.4	6.0	1.2	35.9	2.1	1.0
FMRate (s^{-1})	1.7	0.1	0.9	2.1	0.1	1.0	1.2	0.0	1.0
FMExtend (Hz)	10.5	1.3	1.1	96.7	7.7	1.1	45.8	4.0	1.2
Jitter (%)	0.02	0.00	1.2	0.04	0.00	1.0	0.01	0.00	1.3
Shimmer (%)	0.17	0.00	1.1	0.17	0.00	1.0	0.15	0.00	1.0
F1Mean (Hz)	NA	NA	NA	228.3	1.8	1.0	391.7	5.3	1.1
F2Mean (Hz)	634.3	6.6	1.2	644.6	3.7	1.1	1162.0	16.0	1.1
F3Mean (Hz)	1064.0	11.7	1.1	1073.0	2.8	1.1	1939.0	24.6	1.1
F4Mean (Hz)	1513.0	16.1	1.2	1478.0	2.5	1.1	2722.0	34.2	1.1
F5Mean (Hz)	1930.0	20.1	1.2	1889.0	2.4	1.1	3499.0	42.3	1.1
F6Mean (Hz)	2384.0	23.0	1.1	2319.0	2.4	1.0	4280.0	50.3	1.1
F7Mean (HZ)	2819.0	25.2	1.1	2743.0	2.2	1.1	5050.0	60.4	1.1
F8Mean (Hz)	3224.0	26.2	1.2	3181.0	2.6	1.1	5813.0	68.7	1.1
F1Min (Hz)	NA	NA	NA	171.8	2.3	1.0	312.9	5.8	1.0
F2Min (Hz)	543.9	8.73	1.2	552.1	4.2	1.1	1018.0	15.6	1.0
F3Min (Hz)	961.2	12.6	1.1	971.3	3.8	1.1	1782.0	24.1	1.1
F4Min (Hz)	1403.0	17.0	1.2	1381.0	3.1	1.0	2561.0	33.8	1.1
F5Min (Hz)	1814.0	20.5	1.2	1788.0	2.9	1.0	3335.0	42.4	1.1
F6Min (Hz)	2273.0	23.7	1.1	2210.0	3.1	1.0	4108.0	49.5	1.1
F7Min (Hz)	2697.0	26.1	1.2	2630.0	2.9	1.0	4860.0	59.6	1.1
F8Min (Hz)	3099.0	27.5	1.1	3062.0	2.9	1.0	5627.0	68.3	1.1
F1Max (Hz)	NA	NA	NA	301.3	3.6	1.0	465.5	7.3	1.1
F2Max (Hz)	735.8	8.2	1.2	745.0	4.8	1.1	1311.0	17.3	1.1
F3Max (Hz)	1186.0	12.1	1.0	1174.0	4.1	1.0	2089.0	25.9	1.1
F4Max (Hz)	1631.0	17.4	1.1	1587.0	4.4	1.0	2891.0	35.2	1.1
F5Max (Hz)	2045.0	20.2	1.2	2005.0	4.1	1.0	3682.0	42.7	1.1
F6Max (Hz)	2494.0	23.5	1.1	2446.0	4.4	1.0	4467.0	51.3	1.1
F7Max (Hz)	2943.0	25.8	1.1	2870.0	4.4	1.0	5248.0	61.5	1.1
F8Max (Hz)	3365.0	26.1	1.2	3313.0	4.8	1.0	6022.0	69.3	1.1
DfMin (Hz)	426.3	3.7	1.1	413.5	0.5	1.1	763.5	9.1	1.1
MaxVTL (cm)	41.26	0.3	1.1	42.3	0.0	1.16	23.4	0.2	1.2
Q25% (Hz)	112.6	5.0	1.1	172.6	4.4	1.14	259.8	14.1	1.1
Q50% (Hz)	353.1	23.6	1.1	290.9	10.3	1.24	543.2	26.0	1.1
Q75% (Hz)	1227.0	92.2	1.0	595.7	32.1	1.29	1103.0	53.7	1.0
AmpVar (dB/s)	8.6	0.3	1.1	38.2	1.1	1.07	11.0	0.4	1.0
AMRate (s^{-1})	2.3	0.0	1.0	9.5	0.2	1.04	2.9	0.0	1.0
AMExtent (dB)	4.1	0.2	1.0	4.3	0.2	1.71	4.5	0.2	1.3
Dur (s)	1.3	0.0	1.2	1.2	0.0	1.28	1.4	0.0	1.1

and the first two PCs between males and females (PC1: $t = -0.11$, df = 12, $p = 0.20$; PC2: $t = -0.23$, df = 12; $p = 0.26$).

4. Discussion

We investigated the potential indicators of individuality in the acoustic parameters of cow and calf vocalisations. We also investigated the changes in vocal parameters of calves as they matured. We were able to distinguish two different types of cow contact calls, associated with different behavioural contexts, and with different acoustic parameters. Low frequency calls (LFCs) were produced with the mouth closed or only partially opened. These calls were only produced by mothers when they were in close proximity to their calves, during the first three or four weeks after birth. By contrast, high frequency calls (HFCs) and calf calls were always produced with the mouth fully opened for at least part of the call. Cows and calves produced contact calls when they became separated (i.e. in another part of the field). Such calls preceded reunion and nursing events. Both cow LFCs and HFCs, and calf calls, were individually distinctive. Nevertheless, there was considerable overlap in the acoustic properties of the calls of different individuals, especially among calves. Calf calls were also affected by age, but not by sex. These results represent the most rigorous and detailed description to date of cattle vocalisations in outdoor, free-ranging, relatively undisturbed conditions. They provide an important reference against which future studies can compare vocal parameters recorded under conditions of poor or good welfare. Our results thus represent an important advance in knowledge of cattle vocalisations, which will assist with their future potential use as non-invasive indicators of welfare (Briefer, 2012; Briefer et al., 2015; Manteuffel et al., 2004; Watts and Stookey, 2000).
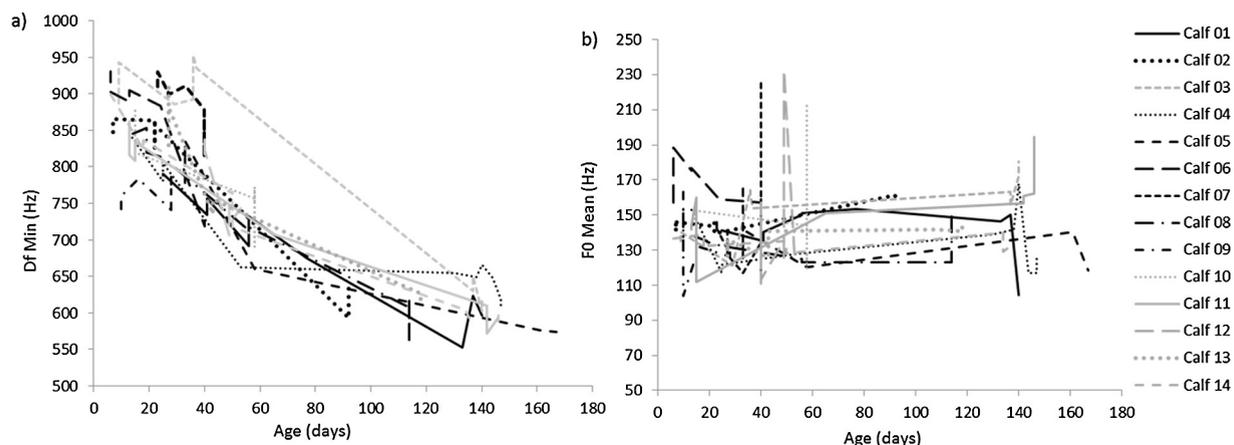
Fig. 2. (a) Effect of calf age on DfMin. Each line represents data from a different individual. ANCOVA with PC1 (which was strongly correlated with various formant characteristics, including DfMin) as the response variable showed that the effect of age and the interaction between age and individual were significant. (b) Effect of calf age on F0Mean. Each line represents data from a different individual. ANCOVA with PC2 (which was strongly correlated with F0) as the response variable showed that there was no significant effect of age.

In species that live in large social groups, individual recognition between parents and offspring using vocal cues is especially likely to occur, because of the high risk of confusion between individuals (e.g. goat, Briefer and McElligott, 2011a; sheep, Sèbe et al., 2007). Our results show that both cow and calf contact calls are individually distinctive. All acoustic parameters analysed (including both source- and filter-related factors) have the potential to be used for individual recognition, as their intra-individual variability is smaller than their inter-individual variability (PIC scores greater than 1). However, for cow HFCs and calf calls, the Discriminant Function Analysis (DFA) revealed that the most important factors for individual identity are the filter-related vocal parameters (formant frequencies). Indeed, the first principal component mostly correlated with formant measures that loaded highly on the first discriminant function of the DFA. By contrast, source-related parameters (fundamental frequency contour) and energy quartiles were the most important factors

for individual identity in cow LFCs. The individuality cues that we highlighted could potentially allow cows and calves to recognise each other vocally within social groups. Further playback experiments are needed to test whether conspecifics perceive and use these cues for individual recognition.

In the first study of cattle vocalisations of which we are aware, Kiley (1972) classified calls according to their acoustic parameters (F0, amplitude and tonality). Cow LFCs in our study (mean F0 = 81.17 ± 0.98 Hz) were consistent with what Kiley (1972) described as an "mm" call (mean F0 = 83 Hz). As in our study, this type of call was described as being produced with a closed mouth, and occurred exclusively when mothers and calves where next to each other (Kiley, 1972). Such calls have previously been suggested to play an important role in mother–offspring recognition in cattle (Barfield et al., 1994; Tucker, 2009; von Keyserlingk and Weary, 2007), and also in other ungulates (e.g. sheep, *Ovis aries*; Sèbe et al., 2010). Kiley (1972) also reported the
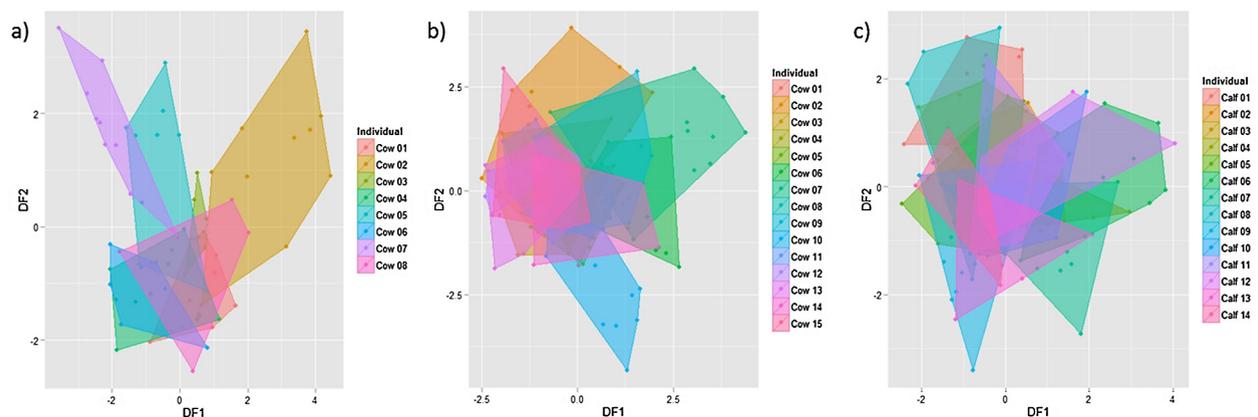

Fig. 3. (a) First two discriminant function scores for cow LFCs; *n* = 8 cows, with 7–10 calls per individual. Points represent individual calls, while polygons delineate areas of parameter space occupied by calls of different individuals. Cross-validated DFA classified 53.6% of calls correctly. (b) First two discriminant function scores for cow HFCs; *n* = 15 cows, with 7–10 calls per individual. Cross-validated DFA classified 30.9% of calls correctly. (c) First two discriminant function scores for calf calls; *n* = 14 calves, with 9–10 calls per individual. Cross-validated DFA classified 23.7% of calls correctly.

production of similar low frequency calls by calves, which contrasts with our findings. The higher frequency type of calls that Kiley (1972) described, which could correspond to the cow HFCs that we analysed, had a very broad frequency range (e.g. F0 ranged from 50 to 800 Hz) and were reported to be produced in almost any behavioural context (e.g. fear, isolation, pain, stress, etc.). Hence, they cannot easily be compared with the HFCs described here.

Although previous studies have suggested the existence of individual differences in cattle vocalisations (Barfield et al., 1994; Hall et al., 1988; Kiley, 1972), none have examined the acoustic characteristics in detail using the source–filter framework. Cow LFCs have relatively strong individuality (cross-validated DFA classified 53.6% of calls correct, chance level = 12.5%) and this is consistent with previous suggestions that cow LFCs are used for mother–offspring recognition (Barfield et al., 1994; Kiley, 1972; Tucker, 2009; von Keyserlingk and Weary, 2007). Similar classifications have been found in contact calls of other mammals (e.g. 69.9% in adult female goats, Briefer and McElligott, 2011a; 64% for adult females in Atlantic Walrus, *Odobenus rosmarus rosmarus*, Charrier et al., 2010; 60% for adult African elephants, Soltis et al., 2005). By contrast, cross-validated DFA of the cow HFCs classified only 30.9% of calls correctly (chance level = 6.67%). This suggests that HFCs may play a less important role in the recognition of mothers by calves than LFCs, which are typically produced by cows very soon after calving. Recognition by 24 h old calves of their own mother has been observed previously (Marchant-Forde et al., 2002). It is likely that early recognition of a mother's calls by offspring could be achieved through LFCs, as observed in other ungulates such as sheep (48 h old, mother–offspring recognition; Sèbe et al., 2010).

Although, we showed that calf vocalisations are individually distinctive, the cross-validated DFA of calf calls correctly classified only 23.7% of calls (chance level = 7.14%), which is relatively low. It is likely that calf vocalisations were changing over time as they grew larger. Given that our analyses were based on a sample of calls recorded over a long period (from 6 days up to 173 days old), age-related variation in call characteristics could partially mask the differences among individuals.

Age strongly affected the acoustic parameters of calf calls; PC1 (which correlated most strongly with formant frequencies) decreased as the calves got older. By contrast, there was no obvious effect of age on PC2, which correlated most strongly with F0. According to the source–filter theory, formant frequencies are determined by the length and shape of the vocal tract, mouth and nasal cavities (Fant, 1960; Titze, 1994). The vocal tract grows with the rest of the body as an animal matures and its length is directly dependent on body size (Briefer and McElligott, 2011b; Taylor and Reby, 2010). As a result, there is usually a negative relationship between the frequency spacing between successive formants and body size among adult individuals of several species (red deer, *Cervus elaphus*, Reby and McComb, 2003; fallow deer, Vannoni and McElligott, 2008), as well as in juveniles as they grow (goats, Briefer and McElligott, 2011b). The age-related changes in formant frequencies in calf calls that we found are thus probably the

result of the lengthening of the vocal tract during growth. Unlike filter-related formant frequencies, source-related parameters, and in particular F0 contour, are typically weakly correlated with body size (Fitch, 1997; Reby and McComb, 2003). Differences in source-related characteristics of the vocalisations are determined by variation in sub-glottal pressure and by the length and tension of the vocal folds (Titze, 1994). Because the tissues of the larynx are soft and unconstrained by skeletal structures, the sounds they produce do not vary predictably with body size (Fitch, 1997). This may explain the absence of an age effect on the acoustic parameters associated with F0 in calves.

Our study was carried out using animals that lived in large open fields, with relatively little human disturbance, and without artificial stressors such as social isolation. By contrast, the few studies that have previously investigated cattle vocalisations have been carried out in the context of intensive management (Grandin, 1998, 2001; Ikeda and Ishii, 2008; Thomas et al., 2001; Watts and Stookey, 1999, 2000, 2001; Weary and Chua, 2000). Furthermore, these previous studies only included a few vocal parameters (usually F0). For example, Thomas et al. (2001) reported that dairy calves had higher F0 when fed conventionally than when fed more milk and more often (126.6 ± 2.2 versus 109.0 ± 3.1 Hz). However, we found that the calves in our study, which were kept with their mothers during lactation period under semi-natural conditions, had on average even higher F0 (142.8 ± 1.80 Hz). Similarly, Ikeda and Ishii (2008) showed that vocalisations of a single cow in two different stressful conditions (hungry and separated from her calf), were acoustically different. Calls produced by a cow after separation from her calf had higher F0 (around 330 Hz) than those produced under hunger condition (around 250 Hz; Ikeda and Ishii, 2008). In our study, cows which had naturally become separated from their calves (without artificial isolation) had considerably lower F0 (HFCs = 152.8 ± 3.10 Hz), which probably represents better the natural frequency of cow contact calls than measurements in previous studies. Other studies measured some acoustic parameters in cattle calls during potentially painful contexts (e.g. prodding with electric prods; Grandin, 1998; in a stunning box; Grandin, 2001; and iron branding; Watts and Stookey, 1999). Unfortunately, none reported any F0 value or carried out formant analysis, to which we might compare our results.

5. Conclusion

Our study provides a very detailed description of the acoustic structure and information content of cow and calf contact calls in a relatively undisturbed farm setting. We found evidence for individuality cues in cow and calf vocalisations. We identified the key sources of individual variation in cow and calf contact calls, which include both source-related parameters (F0 and associated variables) and filter-related parameters (mostly describing formant frequencies). The acoustic features of calf calls were variable during development, probably due to the lengthening of the vocal tract as they grew. Therefore, some individuals showed more rapid declines in formant frequencies over time than others. The methodology employed in this study

could be applied in future studies investigating vocalisations in behavioural contexts other than mother–offspring communication, and provides a reference for studies seeking to develop vocal indicators of welfare in cattle.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.applanim.2014.11.017.

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