



**HAL**  
open science

## Context-related variation in the peripartum vocalisations and phonatory behaviours of Holstein-Friesian dairy cows

Alexandra C. Green, Cameron E.F. Clark, Sabrina Lomax, Livio Favaro,  
David Reby

► **To cite this version:**

Alexandra C. Green, Cameron E.F. Clark, Sabrina Lomax, Livio Favaro, David Reby. Context-related variation in the peripartum vocalisations and phonatory behaviours of Holstein-Friesian dairy cows. *Applied Animal Behaviour Science*, 2020, 231, pp.105089 -. 10.1016/j.applanim.2020.105089 . hal-03492532

**HAL Id: hal-03492532**

**<https://hal.science/hal-03492532>**

Submitted on 22 Aug 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Context-related variation in the peri-partum vocalisations and phonatory**  
2 **behaviours of Holstein-Friesian dairy cows**

3 Alexandra C. Green<sup>1,2</sup>, Cameron E.F. Clark<sup>1</sup>, Sabrina Lomax<sup>1</sup>, Livio Favaro<sup>2,3</sup>, David Reby<sup>2</sup>

4 <sup>1</sup>Livestock Production and Welfare Group, School of Life and Environmental Sciences, University  
5 of Sydney, Camden, Australia

6 <sup>2</sup>Equipe Neuro-Ethologie Sensorielle, ENES/CNRL, CNRS UMR5292, INSERM UMR\_S 1028,  
7 University of Lyon/Saint-Étienne, Saint-Étienne, France

8 <sup>3</sup>Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina  
9 13, 10123 Turin, Italy

10 \*Corresponding author: A. Green

11 Email address: [a.green@sydney.edu.au](mailto:a.green@sydney.edu.au) (A. Green)

12

13 **Abstract**

14 **Context-related information** can be reflected within mammalian vocalisations and could in turn be  
15 studied to benefit production animals. Whilst previous research has revealed **the contextual, and even**  
16 emotional content of goat, pig and horse vocalisations, cattle vocalisations remain relatively less  
17 explored. In this study we recorded the vocalisations and accompanying phonatory behaviours of 19  
18 Holstein-Friesian dairy cows (n = 10 primiparous, n = 9 multiparous) during the **peri-partum contexts** of  
19 parturition with dystocia and fence-line calf separation. Findings revealed that vocal structure was

20 context dependent, with parturition calls longer in duration, higher in fundamental frequency (F0) min  
21 and F0 start, containing more nonlinear phenomena and more minor F0 modulations. By contrast, calls  
22 during calf separation were distinguishable by their F0 contour, having a higher F0 mean and F0 max,  
23 and greater F0 var, F0 cv and F0 absolute slope. During parturition, primiparous cows emitted calls  
24 longer in duration, lower in F0 mean, and containing more F0 modulations than their multiparous  
25 conspecifics. Parturient cows expressed a greater number of open mouth calls, whereas mixed calls  
26 were more common in the calf separation context. Additionally, 82% of the primiparous and 10% of the  
27 multiparous cow vocalisations involved tongue exposure from the mouth during parturition, which may  
28 represent a visual indicator of compromised welfare. Overall, our results show that the **context-related**  
29 **variation is conveyed through an integration of vocal and visual sensory modalities, with the**  
30 **combination of an open mouth configuration, tongue protrusion, and spectral properties such as an**  
31 **overall lower F0 and longer duration during parturition likely enhancing vocal transmission over longer**  
32 **distances to inform more receivers about the urgency of this context.** Knowledge of these vocal and  
33 behavioural cues could be adopted on farm to determine the welfare of peri-partum cattle and are  
34 instrumental for future cattle bioacoustics research.

35

36 *Keywords:*

37 *Calf separation; parturition; vocal communication; welfare*

38

## 39 **1. Introduction**

40 There are many welfare challenges associated with the peri-partum period in cows (Rørvang et al.,  
41 2018). Parturition is painful for many mammalian species, particularly the first time or when foetal

42 expulsion is difficult (Barrier et al., 2012; Mainau and Manteca, 2011; Remnant et al., 2017). Moreover,  
43 in commercial farming environments, peri-partum cows may also be group housed to facilitate farm  
44 management, and this can lead to mismothering and agonistic social interactions (Rørvang et al., 2018).  
45 Within 24 hours post-partum, industry **common practice is** to separate the cow and calf to minimise the  
46 bond formation that occurs soon after birth (Hudson and Mullord, 1977), as well as associated distress  
47 responses from the cow (Flower and Weary, 2001; Lidfors, 1996; Stěhulová et al., 2008). Alongside this,  
48 herd sizes are increasing and individual animal attention from farmers is diminishing (Barkema et al.,  
49 2015). Thus, novel welfare assessment techniques are necessary to improve peri-partum farming  
50 practices and alert farmers to those animals requiring attention.

51 The study of vocal behaviour presents an opportunity to assess an individual's attributes non-invasively  
52 (Green et al., 2017). Mammalian vocalisations have been shown to contain dynamic cues to  
53 motivational state (Morton, 1977), **context (Taylor et al., 2009)** and more recently, emotions, aligning  
54 with the arousal/valence framework (Briefer, 2012; Scherer, 1986). Accordingly, there has been a surge  
55 in bioacoustics research surrounding the emotional content of livestock vocalisations, especially of goats  
56 (Baciadonna et al., 2019; Briefer et al., 2015b), pigs (Briefer et al., 2019; Leliveld et al., 2017; Linhart et  
57 al., 2015), horses (Briefer et al., 2015a) and recently cattle (Green et al., 2019). **Cattle have been**  
58 **recorded vocalising in the welfare-compromising contexts of** handling (Grandin, 2001), restraint and  
59 branding (Watts and Stookey, 1999), and with differing methods of calf separation (Ikeda and Ishii,  
60 2008; Weary and Chua, 2000). While some acoustic analyses have been undertaken to assess **context-**  
61 **related variation** (Weary and Chua, 2000; Yeon et al., 2006), cattle vocal research has traditionally  
62 focused on conspicuous vocal measures such as calling rate (Flower and Weary, 2001; Lidfors, 1996;  
63 Stěhulová et al., 2008) and the quantification of high-frequency call types (Johnsen et al., 2015), rather  
64 than the spectrographic features for a more comprehensive analysis of welfare state.

65 According to the source-filter theory of voice production (Fant, 1960), mammalian vocalisations  
66 commence in the larynx (source of the sound) through vibrations of the vocal folds, whose rate  
67 determines the fundamental frequency (F0), amplitude and duration of the sound (Taylor and Reby,  
68 2010). This sound is subsequently filtered through the supra-laryngeal vocal tract (filter of the sound)  
69 which is responsible for altering the formant frequencies and energy distribution of the sound (Taylor  
70 and Reby, 2010). The source-filter framework has been adopted over the last few decades to investigate  
71 static indexical and fluctuating motivational or emotional vocal cues in a range of mammalian species,  
72 including deer (Reby and McComb, 2003), primates (Gamba et al., 2011), goats (Briefer and McElligott,  
73 2011; Favaro et al., 2014), pigs (Briefer et al., 2019), and more relevantly cattle (Green et al., 2019;  
74 Padilla de la Torre et al., 2015). Animal exposure to a stressor results in changes in respiration, salivation  
75 and muscle tension through the triggering of the autonomic nervous system (Briefer, 2012). This in turn  
76 results in the animal altering its source and/or filter-related vocal features (Briefer, 2012; Scherer, 1986).  
77 Several F0-related vocal parameters have been associated with different production contexts (Mcgrath  
78 et al., 2017; Taylor et al., 2009; Yin and McCowan, 2004) and further, source-related vocal parameters  
79 including nonlinear phenomena, amplitude, F0 mean, F0 variability, and/or call duration have all been  
80 shown to increase alongside increasing situation urgency (Koutseff et al., 2017; Marx et al., 2003;  
81 Stoeger et al., 2012, 2011), likely mediated by changes in physiological arousal. Context-related vocal  
82 modulations triggered by differences in emotions and/or motivations seem to be shared homologously  
83 across mammalian species, likely due to commonalities in morphology, physiology and vocal production  
84 mechanisms (Briefer, 2012). Thus, the application of the source-filter theory will be helpful in  
85 deciphering the welfare-related context variation of cow vocalisations, along with their communicative  
86 functions.

87 Here we investigated the acoustic differences of Holstein-Friesian cattle vocalisations, produced during  
88 the peri-partum contexts of parturition with dystocia and fence-line calf separation. Moreover, both

89 primiparous and multiparous cows were observed to assess the effect of parity on peri-partum vocal  
90 responses. The accompanying phonatory behaviours at the time of each vocalisation including mouth  
91 configuration and tongue protrusion are also described, to determine the relationship between vocal  
92 production and other conspicuous behavioural parameters. We hypothesised that there would be  
93 context-related variability in the cow vocalisations and their underlying phonatory behaviours, which  
94 may reflect differences in motivations and emotions that the cattle were experiencing.

95

## 96 **2. Materials and methods**

### 97 *2.1. Animals and management*

98 The experiment was conducted in a maternity barn (Figure 1) at a large-scale commercial dairy farm in  
99 New South Wales, Australia between June and October 2018. The experiment was approved by the  
100 University of Sydney Animal Ethics Committee (Project number: 2016/1078). Nineteen primiparous and  
101 multiparous Holstein-Friesian cows were included in this experiment (n = 10 primiparous, n = 9  
102 multiparous, mean parity = 2.16, range = 1 - 5). These experimental cows were selected from a herd of  
103 maternity cows (n = ~ 120) which were all within two weeks of their intended date of parturition. From  
104 this herd, each focal cow was selected on her day of parturition, based on her expression of prepartum  
105 behaviour including increased vocal rate, restlessness, tail lifting, increased mucous production, looking  
106 at other calves and/or licking her amniotic fluid (Barrier et al., 2012). On this farm, the calving  
107 intervention criteria involved the farm staff checking the progress of the parturient cow every 30  
108 minutes (min) (including pushing, visibility of discharge, amniotic sac and/or feet). Farm staff assisted  
109 the cow when no progress was made for a minimum of 30 min. To minimise variability in calving  
110 procedures, only cows that required calving intervention for foetal expulsion were included in this study.  
111 Both parturition and subsequent calf separation were observed for all experimental cows from 06:30 –

112 14:30, with one cow recorded at a time. All cows were identifiable by their unique coat markings, ear  
113 tags and collar numbers. Given their daily handling, all cows were habituated to human presence.

114



115

116 Figure 1. Diagram of the maternity barn, containing Pen 1 (11.7 m x 57.0 m), the pen with the cattle  
117 crush (11.7 m x 2.7 m), Pen 2 (11.7 m x 9.2 m) and Pen 3 (11.7 m x 15.8 m), which are divided by a fence-  
118 line as seen in (Green et al., 2020, under review).

119

## 120 2.2. Housing and feeding

121 Pre-parturient cattle were introduced to the maternity barn once a week. Cattle were grouped by parity,  
122 with multiparous cows housed in a free-stall section (Pen 1) of up to 65 animals, and primiparous cows  
123 loosely housed in Pen 3 with up to 12 animals (Figure 1). The multiparous cows had access to 68 (34 x 2)  
124 free stalls which contained soft sand bedding that was raked daily. The majority of Pen 2 and Pen 3 were  
125 covered in soft sand bedding which was replaced weekly. The remainder of the barn had grated  
126 concrete flooring which was flushed daily. In their respective pens, all cows were offered a total-mixed  
127 ration diet *ad-libitum* at a feeding strip on the far side of the barn. All cows had unlimited access to  
128 water in troughs positioned throughout the maternity barn. At 07:00 and 15:00, cows that had calved  
129 that day were processed for milking and moved to a separate milking barn and herd.

130

131 **2.3. Recording conditions**

132 *2.3.1. Parturition*

133 The recording of parturition commenced when the cow expressed signs of the second stage of labour,  
134 including visibility of the amniotic sac and/or calf legs. Duration of recording varied between cows with  
135 calving duration longer for primiparous (mean = 89.9 min, range = 50 – 173 min) than multiparous  
136 (mean = 63.2 min, range = 24 – 127 min) cows. Despite the group-housing environment, during  
137 parturition, cows tended to isolate themselves from conspecifics by moving to a pen area free from  
138 disturbance. Calving intervention was provided by the experienced farm staff and involved using a  
139 calving jack whilst the cow was standing restrained in a head bail at the cattle crush (n = 5 primiparous,  
140 n = 8 multiparous cows) or calving ropes to pull the calf from the side lying cow (n = 5 primiparous, n = 1  
141 multiparous cows). Recording ceased when the calf was born. During parturition, vocalisations were  
142 mainly associated with the cow pushing out the calf, or when the farm staff assisted with calf pulling.  
143 High-quality recordings were available for 17 of the 19 experimental cows during parturition.

144 *2.3.2. Calf separation*

145 Calf separation involved the farmer moving the calf to the other side of a fence-line barrier between Pen  
146 2 and Pen 3 (Figure 1) where the calves and cows were housed, respectively. The focal cow was  
147 recorded for 60 min immediately after separation from her calf, with separation occurring soon after  
148 parturition (mean time = 108 min, range = 64 – 271 min). All cows could bond with their respective calf  
149 before separation commenced. Across the observation period, recording coincided with peak calving  
150 activity, meaning that Pen 2 contained multiple calves (mean = 5, range = 1 – 10). Calves had access to a  
151 heated shelter to maintain body temperature if needed. Pen 3 consisted of multiple cows including the  
152 post-partum focal cow and primiparous cows which were due to calve (mean = 7 cows, range = 4 – 10).



153 The focal cow and her respective calf maintained visual, auditory and some physical contact through the  
154 fence-line barrier for the recording session. During calf separation, vocalisations were mainly produced  
155 when the cow looked at the calf. Calves were transported twice daily at 10:00 and 15:00 h to a separate  
156 shed for individual housing.

157

#### 158 **2.4. Vocalisation recordings**

159 Vocalisations were recorded from the 19 cows across parturition and subsequent calf separation.

160 Vocalisations were captured from between 1 to 15 m from the focal cow using a Sennheiser ME67

161 directional microphone (frequency response: 40 – 20000 Hz, max SPL: 125 dB at 1000 Hz) powered by a

162 Sennheiser K6 power module (Sennheiser Electronic GmbH and Co, Wedemark, Germany). For shock

163 and wind-noise reduction, the microphone was covered with a Rycote Classic Softie Windshield and

164 attached to a Softie mount with pistol grip® (Rycote Microphone Windshields, Gloucestershire, United

165 Kingdom). Vocalisations were recorded onto a Marantz PMD661 MK2 digital solid-state recorder

166 (Marantz Professional, Cumberland, RI, United States) with stereo input (sampling rate: 44.1 kHz). Lower

167 and higher amplitude calls were captured using two recording volume gain settings concurrently and

168 these settings were adjusted manually to avoid signal saturation. Each vocalisation was stored as a

169 separate file in the .WAV uncompressed format at 16-bit amplitude resolution.

170

#### 171 **2.5. Vocalisation analyses**

172 A total of 393 vocalisations were analysed on the basis of good signal to noise ratio, including 214 from

173 parturition (n = 9 multiparous cows, n = 8 primiparous cows) and 179 from calf separation (n = 7

174 multiparous cows, n = 5 primiparous cows). Vocalisations were analysed using Praat v.6.0.31 (Boersma

175 and Weenink, 2009). Overall, we measured 12 acoustic parameters (Table 1) that could be robustly  
176 extracted from vocalisations produced in a commercial farming environment where ambient noise was  
177 an important component of the soundscape. Further, we selected parameters that would likely  
178 modulate with **increasing context-related urgency**. Full call duration was measured directly off the  
179 waveform, and the narrow band spectrogram of each call was visualised (FFT method, window length =  
180 0.1 s, time steps = 1000, frequency steps = 250, Gaussian window shape, dynamic range = 60 dB)  
181 displaying the first 2500 Hz of the call, to determine the proportion of nonlinear phenomena relative to  
182 the full call duration. We then ran a custom-built script to batch process the remaining acoustic analyses  
183 (Reby and McComb, 2003), which contained two distinct procedures to characterise the F0 contour and  
184 modulation events, respectively. In particular, a band-pass filter (pass Hann band, from frequency = 40  
185 Hz, to frequency = 2500 Hz, smoothing = 10 Hz) was firstly applied to each vocalisation to remove  
186 background noise produced by farm machinery and birds present in the maternity shed. The script  
187 procedure then involved extracting the F0 contour of each vocalisation ([Sound: To pitch (cc) command],  
188 time step = 0.01s, pitch floor = 45 Hz, pitch ceiling = 1000 Hz) to measure a range of F0-related  
189 parameters. These included F0 mean, F0 min, F0 max, F0 start, F0 end, F0 var, F0 cv and F0 absolute  
190 slope. We manually corrected spurious values and octave jumps by viewing the spectrogram and the  
191 associated F0 contour using the Pitch edit window [Inspect pitch object] (Reby and McComb, 2003). In  
192 the case of biphonation sidebands (Fitch et al., 2002), the F0 values were selected if they were clearly  
193 visible. Further, we 'unvoiced' any regions where the F0 values could not be accurately detected, for  
194 example, where deterministic chaos (Fitch et al., 2002) was present. The second procedure involved  
195 applying two distinct smoothing algorithms to the F0 contour, including (Smooth command in Praat,  
196 bandwidth = 25) followed by (Smooth command in Praat, bandwidth = 2), which suppressed the long-  
197 term and short-term F0 modulation events, respectively (Koutseff et al., 2017; Raine et al., 2018; Reby  
198 et al., 2016). Following the smoothing procedures, the inflection points were counted as a change in the

199 sign of the contour's derivative and divided by the total number of voiced segments in each recording.  
 200 This resulted in two distinct indexes of F0 modulation, including inflex25, which characterised minor  
 201 intonation events, and inflex2 which characterised major intonation events.

202

203 Table 1. Definitions and justification of the 12 vocal parameters measured in this study.

Parameter type	Vocal parameter	Definition	References to previous distress-related studies
<b>Temporal</b>	Full duration (s)	Total duration of the call (from start to end)	(Raine et al., 2018; Stoeger et al., 2012, 2011)
<b>F0 - contour</b>	F0 mean (Hz)	Mean F0 across the call	(Koutseff et al., 2017; Raine et al., 2019, 2018)
	F0 min (Hz)	Minimum F0 across the call	(Koutseff et al., 2017; Raine et al., 2019, 2018)
	F0 max (Hz)	Maximum F0 across the call	(Koutseff et al., 2017; Raine et al., 2019, 2018)
	F0 start (Hz)	F0 at the start of the call	(Koutseff et al., 2017)
	F0 end (Hz)	F0 at the end of the call	(Koutseff et al., 2017)
	F0 var (Hz/s)	Cumulative variation in the F0 contour in Hertz divided by call duration	(Briefer, 2012)
	F0 CV (Hz)	Coefficient of variation over the duration of the call	(Koutseff et al., 2017; Raine et al., 2019, 2018)
<b>F0 - modulation</b>	Abs F0 slope (Hz/s)	F0 mean absolute slope	(Briefer et al., 2019)
	Inflex 25	Index of minor F0 modulation	(Koutseff et al., 2017; Raine et al., 2019, 2018)
	Inflex 2	Index of major F0 modulation	(Koutseff et al., 2017; Raine et al., 2019, 2018)

<b>Nonlinear phenomena</b>	Nonlinear phenomena (%)	Proportion of the call that contains nonlinear phenomena including deterministic chaos (non-random broadband noise with no clear harmonic structure), biphonation sidebands (side frequencies which occur either side of the F0 and harmonics) and/or subharmonics (spectral components that are integer fractions of the F0)	(Koutseff et al., 2017; Raine et al., 2018; Stoeger et al., 2012)
----------------------------	-------------------------	---	---

204

205 **2.6. Behavioural observations**

206 A video camera (Sony HDR-AS300 action cam®, Sony Australia Limited, North Sydney, Australia) was  
 207 affixed along the fence-line to continuously record the focal cow behaviour during parturition and calf  
 208 separation. To relate behaviour with vocal production, video and audio were simultaneously recorded  
 209 and time stamped. To characterise the accompanying mouth and tongue positions of the cows during  
 210 vocal production, behavioural analysis software BORIS v.7.7.4 (Friard and Gamba, 2016) was used.  
 211 Mouth position upon vocalisation was recorded as either 1) closed, 2) mixed (including both closed and  
 212 open mouth components), or 3) open. The proportion of the call duration for which the mouth was  
 213 open was quantified and tongue exposure (tongue protruding and/or dorsally flexed inside of the  
 214 mouth) was additionally reported. Mouth position was recorded for all 393 vocalisations; however,  
 215 tongue position was only clearly visible in 295 of the vocalisations.

216

217 **2.7. Statistical analyses**

218 Statistical analyses were performed using R Studio v.1.2.1 335 (RStudio Team, 2020), an integrated  
 219 development environment for R (R Core Team, 2020). For the vocal data, we used the ‘lme4’ package  
 220 (Bates et al., 2015) to carry out linear-mixed effects models (LMMs) with each vocal parameter included  
 221 as the response variable. These models included the fixed effects of context (parturition or calf  
 222 separation) and parity (primiparous or multiparous), and their two-way interaction. Since cattle calls are

223 likely structured on a graded continuum (Kiley, 1972), the proportion of the call duration with the mouth  
224 open was included as a covariate in the model, as mouth configuration can influence F0-related  
225 parameters (Sebe et al., 2010). Additionally, to compensate for the variable duration of parturition  
226 amongst cows, time duration of both contexts was normalised to range between 0 and 1 with the time  
227 of each vocalisation included as a covariate. All fixed effects were checked for multicollinearity using the  
228 'VIF function' (Fox and Weisberg, 2018), with all considered to be non-collinear as they resulted in  
229 values of less than four. The random effect was cow ID to control for repeated measures from the same  
230 individuals. Residuals were graphically inspected, and to approximate normal distribution and  
231 homoscedasticity all vocal parameters bar *inflex2* and nonlinear phenomena were log transformed.

232 For the behavioural data, which included categorical response variables, we ran a series of generalised  
233 linear mixed models (GLMMs) with binomial distribution in 'lme4', implementing the 'all versus one'  
234 approach. The response was the behaviour of interest (closed, mixed, or open mouth) which was scored  
235 as 1, versus the other two behaviours of that category scored as 0. Fixed effects included context  
236 (parturition or calf separation) and parity (primiparous or multiparous) along with their two-way  
237 interaction, and the covariate of normalised time. The random effect was cow ID to control for repeated  
238 measures. As tongue exposure was produced exclusively during parturition, no further statistical tests  
239 were applied to this behavioural parameter.

240 To assess the significance of the fixed effects in both the vocal and behavioural datasets, we compared a  
241 full model including the fixed and random effects, to a null model, comprising the covariates and  
242 random effect for which we were controlling. Any non-significant interaction terms were dropped from  
243 the models, with models compared using Akaike's information criterion (AIC) (Akaike, 1974), with the  
244 lowest scoring AIC model selected. Models were fitted with maximum likelihood estimation and  
245 likelihood ratio tests were used to confirm the significance of the full models. We used Tukey adjusted

246 pairwise comparisons in the ‘emmeans’ package (Lenth et al., 2019) to compare results of parturition  
247 and calf separation, and we report the estimated marginal means, along with their standard errors on  
248 the response scale. The main effect of context is reported in instances where the context by parity  
249 interaction was not significant. Further, we only report on fixed effects which were of relevance to our  
250 hypothesis, i.e. we do not report on the values of the covariates. For all models, a probability  $< 0.05$  was  
251 considered statistically significant, and a statistical trend was considered at  $0.05 < p < 0.1$ .

252

### 253 **3. Results**

#### 254 *3.1. Vocal parameters during parturition and calf separation*

255 All 12 vocal parameters measured in this study were significantly affected by context, or a context by  
256 parity interaction (Table 2). Post-hoc comparisons of context showed that vocalisations produced during  
257 parturition had a greater prevalence of nonlinear phenomena as well as a higher F0 min and F0 start  
258 (Table 3). By contrast, vocalisations during calf separation had a higher F0 max, and a greater F0 var, F0  
259 cv and F0 absolute slope (Table 3). Additionally, these calf separation calls tended to have a higher F0  
260 end (Table 3). There was a significant context by parity interaction for four vocal parameters including  
261 full duration, F0 mean, minor F0 (inflex 25) and major F0 modulations (inflex 2) (Table 2). Within the  
262 parturition context, primiparous cows produced vocalisations with a longer duration, a lower F0 mean,  
263 and more major F0 modulations (inflex 2) than their multiparous conspecifics (Table 4). Primiparous  
264 parturition vocalisations also tended to have more minor F0 modulations (inflex 25). By contrast, there  
265 was no parity difference observed for any vocal parameter during calf separation (Table 4). Overall, for  
266 both primiparous and multiparous cows, parturition induced calls with a longer duration, lower F0 mean  
267 and more minor inflections (inflex 25) than subsequent calf separation (Table 4). Further, primiparous

268 cattle vocalisations contained more major inflections (inflex 2) during parturition than in subsequent calf  
 269 separation, however for multiparous cows, this difference was not significant (Table 4).

270

271 Table 2. Results of final model selection for LMMs and GLMMs using ANOVAs, comparing the full model  
 272 (with the fixed effects, covariates, and random effect) to the null model (with only the covariates and  
 273 random effect). Only the fixed effects relevant to our hypothesis are provided in the table and  
 274 significant P-values are highlighted in bold.

Parameter		Effect	df	X <sup>2</sup>	P-value
<b>Vocalisations</b>					
<b>Temporal</b>	Full duration (s)	Context * Parity	3	62.16	< <b>0.001</b>
<b>F0 - contour</b>	F0 mean (Hz)	Context * Parity	3	37.16	< <b>0.001</b>
	F0 min (Hz)	Context	2	9.77	<b>0.008</b>
	F0 max (Hz)	Context	2	28.57	< <b>0.001</b>
	F0 start (Hz)	Context	2	14.74	<b>0.001</b>
	F0 end (Hz)	Context	2	8.55	<b>0.01</b>
	F0 var (Hz/s)	Context	2	43.33	< <b>0.001</b>
	F0 CV (Hz)	Context	2	32.03	< <b>0.001</b>
	Abs F0 slope (Hz/s)	Context	2	35.23	< <b>0.001</b>
<b>F0 - modulation</b>	Inflex 25	Context * Parity	3	19.27	< <b>0.001</b>
	Inflex 2	Context * Parity	3	8.10	<b>0.04</b>
<b>Nonlinear phenomena</b>	Nonlinear phenomena (%)	Context	2	31.03	< <b>0.001</b>
<b>Behaviours</b>					

<b>Mouth position</b>	Closed mouth	Context	2	5.59	0.06
	Mixed	Context	2	26.97	<b>&lt; 0.001</b>
	Open mouth	Context * Parity	3	50.90	<b>&lt; 0.001</b>

275

276 Table 3. Estimated marginal means  $\pm$  SE of main effects along with their P-values derived from the  
 277 Tukey's post-hoc pairwise comparisons. The LMMs included each vocal parameter as the response  
 278 variable, the fixed effects of context and parity, the covariates of normalised time and proportion of the  
 279 mouth open, and the random effect of cow ID. Significant P-values are highlighted in bold.

<b>Vocal parameter</b>	<b>Parturition</b>	<b>Calf separation</b>	<b>t-ratio</b>	<b>P-value</b>
<b>F0 min (Hz)</b>	75.80 $\pm$ 2.38	70.60 $\pm$ 2.42	2.18	<b>0.03</b>
<b>F0 max (Hz)</b>	167.00 $\pm$ 9.52	218.00 $\pm$ 13.32	-4.99	<b>&lt; 0.001</b>
<b>F0 start (Hz)</b>	84.80 $\pm$ 3.58	75.70 $\pm$ 3.42	2.97	<b>0.003</b>
<b>F0 end (Hz)</b>	119.00 $\pm$ 4.89	130.00 $\pm$ 5.89	-1.88	0.06
<b>F0 var (Hz/s)</b>	99.20 $\pm$ 8.19	168.30 $\pm$ 15.19	-6.01	<b>&lt; 0.001</b>
<b>F0 cv</b>	0.15 $\pm$ 0.01	0.23 $\pm$ 0.02	-5.12	<b>&lt; 0.001</b>
<b>F0 abs slope</b>	118.00 $\pm$ 9.22	185.00 $\pm$ 15.92	-5.22	<b>&lt; 0.001</b>
<b>NLP (%)</b>	33.10 $\pm$ 4.39	16.70 $\pm$ 4.56	5.61	<b>&lt; 0.001</b>

280

281



282 Table 4. Estimated marginal means  $\pm$  SE of interaction effects along with their P-values derived from the  
 283 Tukey's post-hoc pairwise comparisons. The LMMs included each vocal parameter as the response  
 284 variable, the interaction between the fixed effects context and parity, the covariates of normalised time  
 285 and proportion of the mouth open, and the random effect of cow ID. Letters denote significant  
 286 differences ( $P < 0.05$ ) between parities in the same context, and P-values are reported for significant  
 287 differences at the contextual level (parturition versus calf separation). Significant P-values are  
 288 highlighted in bold.

Vocal parameter	Parity	Parturition	Calf separation	Parturition versus Calf separation	
				t-ratio	P-value
<b>Full duration (s)</b>	Primiparous	2.08 $\pm$ 0.14 <sup>A</sup>	1.18 $\pm$ 0.11	5.75	<b>&lt; 0.001</b>
	Multiparous	1.52 $\pm$ 0.10 <sup>B</sup>	1.17 $\pm$ 0.07	5.36	<b>&lt; 0.001</b>
<b>F0 mean (Hz)</b>	Primiparous	115.00 $\pm$ 7.84 <sup>A</sup>	177.00 $\pm$ 15.13	-5.01	<b>&lt; 0.001</b>
	Multiparous	144.00 $\pm$ 9.43 <sup>B</sup>	165.00 $\pm$ 10.82	-3.35	<b>&lt; 0.001</b>
<b>Inflex 25</b>	Primiparous	12.85 $\pm$ 1.34	7.24 $\pm$ 1.02	3.71	<b>&lt; 0.001</b>
	Multiparous	9.92 $\pm$ 0.97	8.42 $\pm$ 0.82	2.10	<b>0.04</b>
<b>Inflex 2</b>	Primiparous	1.06 $\pm$ 0.06 <sup>A</sup>	0.81 $\pm$ 0.10	2.15	<b>0.04</b>
	Multiparous	0.87 $\pm$ 0.06 <sup>B</sup>	0.88 $\pm$ 0.05	-0.14	0.89

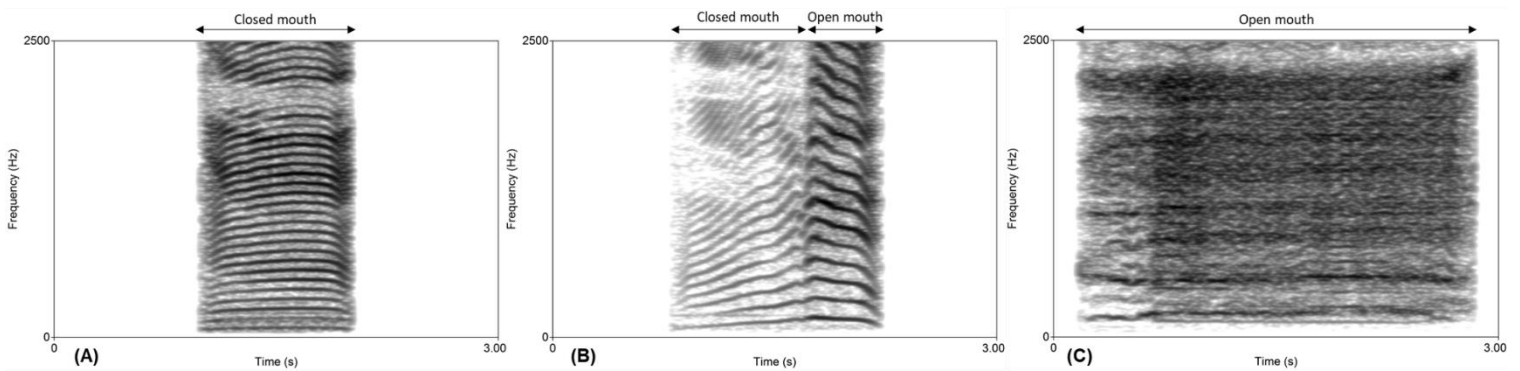
289

290

291 3.2. Phonatory behaviours during vocal production

292 The production of open mouth and mixed calls (Figure 2) was significantly impacted by context (Table 2).  
293 Both open and mixed calls were emitted upon exhalation, and closed mouth calls were emitted nasally.  
294 A greater percentage of mixed calls was observed during calf separation compared to parturition (Z ratio  
295 = -4.73,  $P < 0.0001$ ). By contrast, more open mouth calls were produced during parturition than calf  
296 separation for both primiparous (Z ratio = 4.77,  $P < 0.0001$ ) and multiparous cows (Z ratio = 3.02,  $P =$   
297 0.003). There was also a significant context x parity effect during parturition (Table 2), with primiparous  
298 cows producing more open mouth calls than multiparous cows (Z ratio = -2.92,  $P = 0.004$ ). During  
299 parturition, tongue exposure was observed during 82% of the primiparous cow vocalisations and just  
300 10% of the multiparous cow vocalisations, however this behaviour was not observed during calf  
301 separation by any cow. Further, tongue exposure was exclusively observed when the cows were  
302 emitting the vocalisation and at no other time during the observation period.

303



304

305 Figure 2. Narrow-band spectrograms of (A) a closed mouth vocalisation produced during parturition, (B)  
306 a mixed vocalisation comprising closed and open mouth components produced during calf separation,  
307 and (C) an open mouth vocalisation produced during parturition.

308

#### 309 4. Discussion

310 Despite ongoing discussions about the potential for vocalisations to assess animal welfare (Green et al.,  
311 2017; Manteuffel et al., 2004; Watts and Stookey, 2000), the information coded within cow vocalisations  
312 remains under-investigated. Here we show context-related variability in the acoustic features and  
313 phonatory behaviours of cow vocalisations recorded during parturition with dystocia and fence-line calf  
314 separation. First, we describe the acoustic and phonatory-behavioural characteristics of peri-partum  
315 cow vocalisations at the contextual level. We then discuss plausible reasons for their contextual  
316 differences related to their communicative function and potential motivational and emotional encoding.  
317 These findings contribute to the greater understanding of cattle vocal communication and are a step  
318 towards the creation of a tool to detect welfare changes aurally and visually on farm.

319 Parturient cow vocalisations were characterised by a longer duration, overall lower F0, a greater  
320 prevalence of nonlinear phenomena and more minor frequency modulations than calf separation calls.  
321 Further, primiparous parturient cows produced calls longer in duration, more frequency modulated and  
322 lower in F0 mean than their multiparous conspecifics. Presently, all cows had difficulty with foetal  
323 expulsion, requiring farming intervention to extract the calf. Moreover, the primiparous cows endured  
324 longer labour durations, which has previously been associated with more pain due to foeto-pelvic  
325 disproportion and greater effort placed into calving (Mainau and Manteca, 2011). Interestingly, the  
326 parturient cow vocalisations share features with the guttural, low F0 sounds of parturient women upon  
327 effort and exertion (McKay and Roberts, 1990). We suggest that the parturient cow vocal characteristics  
328 may reflect the intense musculature and energy expenditure during parturition, affecting sub-glottal  
329 pressure and muscular tension within the vocal apparatus (Taylor and Reby, 2010; Titze, 1994). By  
330 contrast, calf separation vocalisations could be discriminated by their distinctive F0 contour, being more  
331 harmonic and comprising a broader frequency range and greater variability around the F0. It has been

332 shown that more intense separation methods (e.g. separation from the calf after four days) are  
333 associated with calls of higher frequencies (Weary and Chua, 2000). Thus, the lack of parity effect on calf  
334 separation call structure may represent within-context similarities in arousal expression. Our results also  
335 align with the observations of Flower and Weary (2001), which found no behavioural differences  
336 between post-partum primiparous and multiparous cows undergoing immediate separation from their  
337 calves.

338 In our study, fundamental frequency related parameters (F0 mean, max, end, var, CV, absolute slope)  
339 were overall higher for calf separation than parturition and did not conform to the vocal arousal  
340 expression exhibited by other mammalian species (Briefer, 2012). In dogs, disturbance barks produced  
341 in more urgent situations (e.g. when a stranger rang a doorbell) were also lower in F0 parameters,  
342 despite mirroring higher arousal through their longer duration, more rapid repetitions and vocal  
343 roughness (Yin and McCowan, 2004). Cattle vocalisations are acoustically graded (Kiley, 1972) and in our  
344 study there was a high prevalence of intermediate call types which were ambiguous to visually classify.  
345 For this reason, we addressed contextually driven vocal variation independent of any empirical call type.  
346 Despite the ability to encode instantaneous dynamic information (Taylor and Reby, 2010), vocalisations  
347 are not always direct expressions of emotional state. Different parts of the acoustic continuum may  
348 serve different communicative functions in a variety of contexts, for example nasalised calls are often  
349 favoured for short-distance communication, and oralised calls for communication over longer distances  
350 (Padilla de la Torre et al., 2015). This could explain why it was difficult to compare the potential  
351 emotional encoding in vocalisations across contexts. The emotional information encoding in other  
352 mammalian species has been shown to differ between call types (Linhart et al., 2015; Maigrot et al.,  
353 2018), thus to more definitively attribute acoustic variations to emotional state, future cattle studies  
354 should analyse vocalisations most typical of the low- and high-frequency call structures (Padilla de la  
355 Torre et al., 2015) and exclude any intermediate call sub-types.

356 Acoustic variations can reflect the circumstances surrounding vocal emission (Owings and Morton,  
357 1998). Indeed, the present contrasting peri-partum acoustic features were most likely shaped by the  
358 different communicative functions of the vocalisations. Low-frequency vocalisations tend to propagate  
359 further than high-frequency vocalisations (Marten et al., 1977), with nonlinear phenomena enhancing  
360 the projection of formant frequencies over longer distances (Fitch et al., 2002). Therefore, parturient  
361 cows were likely vocalising over longer distances to their conspecifics, or to the farmer for help. In  
362 contrast, when separated, the cows were likely vocalising to their respective calves in close proximity  
363 across the fence-line. The calf separation calls emulate the high-frequency calls produced by free-  
364 ranging cattle initiating social contact (Padilla de la Torre et al., 2015), similar in their acoustic structure  
365 (F0 start, end, mean, min, max, absolute slope, var) and their mixed mouth configuration, suggesting  
366 that these separation calls play a communicative role in maintaining contact with the calf. Nonetheless,  
367 the acoustic characteristics of the peripartum vocalisations partially conform to Morton's motivational-  
368 structural rules, which state that mammals emit harsh, low-frequency, high-intensity vocalisations when  
369 in hostile contexts as opposed to tonal, high-frequency vocalisations when appeased or fearful (Morton,  
370 1977). The communicative functions of these certain acoustic characteristics could be verified through  
371 playback experiments of peri-partum vocalisations to signal receivers.

372 Just as acoustic properties can enhance the salience of the vocalisations for long distance  
373 communication, seemingly so too can the phonatory behaviours associated with vocal production.  
374 Parturient vocalisations were typically coupled with an open mouth configuration, and this was  
375 observed more frequently in the primiparous than multiparous cows. Mouth configuration has been  
376 used to empirically classify call types in cattle (Johnsen et al., 2015; Padilla de la Torre et al., 2015) and  
377 other ungulates (Briefer et al., 2019, 2015b), with evidence to suggest that the expression of different  
378 call types relates to different underlying motivational or emotional states (Maigrot et al., 2018; Morton,  
379 1977; Tallet et al., 2013). A greater production of open mouth calls also seems to correlate with

380 increasing distress during calf separation (Johnsen et al., 2015), which could reflect greater urgency  
381 during parturition compared to calf separation, especially for the primiparous cows.

382 Tongue protrusion was also observed exclusively during parturition solely at the time of vocal  
383 production. To the best of our knowledge, this behaviour has not been documented in other cattle  
384 studies, but in Iberian red deer stags, tongue protrusion is a conspicuous feature of acoustic rutting  
385 display and is a consequence of thyroid muscle contraction (Frey et al., 2012). While hypothesised to be  
386 energetically costly, tongue protrusion with an open mouth configuration may allow for the  
387 uninterrupted passage of an exhalatory air stream producing the vocalisation (Frey et al., 2012), which  
388 could mechanically function to project the vocalisation over longer distances. This could explain why  
389 there was a greater prevalence of tongue protrusion behaviour in the primiparous parturient cows,  
390 again reinforcing the notion that they perceived the context with greater urgency. Although we did not  
391 directly estimate the impact of tongue protrusion on vocal characteristics, the lower F0 mean of the  
392 parturient vocalisations, particularly those emitted by the primiparous cows, may have also been  
393 influenced by the tongue protrusion behaviour. Similarly, the common roars of Iberian Red stags which  
394 were produced with the tongue protruded, were lower in F0 than their non tongue-protruding harsh  
395 roar equivalents (Frey et al., 2012). Presently, both mouth configuration and tongue protrusion  
396 behaviour provided valuable information about contextual and parity-related effects in cows and are  
397 promising visual tools to assess welfare-related differences on farm. Further exploration of these  
398 phonatory behaviours and their impact on acoustic features is therefore warranted in a well-controlled  
399 experimental setting to validate our current suggestions.

400 Our findings are subject to some limitations. Due to the observational design of the present study, the  
401 two peripartum contexts differed in a number of aspects. The activity of the cow was higher during  
402 parturition, as cows expended strong muscular efforts to expel the calf. Also, the position of the cows

403 upon vocalising differed, with parturient cows either recumbent or restrained in a head-bail, compared  
404 to separated cows which were moving freely. This prevented the assessment of locomotion as a  
405 behavioural proxy of arousal (Leliveld et al., 2017; Maigrot et al., 2018), or heart rate as a physiological  
406 indicator of arousal (Briefer et al., 2015b, 2015a), as there was no previous habituation to the monitors.  
407 To overcome these limitations to unequivocally attribute acoustic differences to variations in emotional  
408 state, a controlled experiment should be performed in future. This could also involve comparing  
409 additional variables within each context, such as different methods of parturition (assisted versus  
410 unassisted) as well as different times (Flower and Weary, 2001; Lidfors, 1996; Weary and Chua, 2000) or  
411 degrees (Johnsen et al., 2015) of calf separation. By comparing calls with the same communicative  
412 function, this would assist in deciphering the precise vocal indicators of emotion in peri-partum cow  
413 vocalisations.

414

## 415 **5. Conclusions**

416 Vocalisations and associated phonatory behaviours can provide insight into the peri-partum farming  
417 context to which cows are exposed. In this study, we identified a series of robust vocal parameters that  
418 are not influenced by ambient noises produced on commercial dairy farms, and behavioural parameters  
419 that are conspicuous and easy to observe. The combination of an open mouth configuration, tongue  
420 protrusion and spectral properties such as an overall lower F0 and longer duration during parturition  
421 likely resulted in signal propagation over longer distances, thereby informing more receivers about the  
422 urgency of this context. We recommend assessing these measures further in a controlled experimental  
423 setting, to simultaneously determine behavioural and vocal encoding of emotions in peri-partum cows,  
424 for a more comprehensive understanding of their welfare state.

425

426 **Acknowledgements**

427 We are grateful to the undergraduate students who assisted with the data collection and farm staff who  
428 were so accommodating to this research. Special thanks to Peter Thomson for the statistical advice and  
429 Lena Lidfors for her behavioural expertise. Also, thank you to Frédéric Sèbe for assistance with filtering  
430 the vocalisations.

431

432 **Funding**

433 Author A.G was supported by an Australian Government Research Training Program (RTP) Scholarship.  
434 This research was partially supported by Dairy Australia to C.C and S.L and the University of Lyon's  
435 IDEXLYON project as part of the "Programme Investissements d'Avenir" (ANR-16-IDEX-0005) to D.R.

436

437 **Author contributions**

438 A.G, C.C, S.L designed the experiment. C.C and S.L sourced funding and provided resources and project  
439 administration. A.G collected the data. A.G, L.F, D.R conducted the acoustical and statistical analyses.  
440 A.G, L.F, D.R conceptualised the manuscript. A.G wrote the first draft of the manuscript. C.C, S.L, L.F, D.R  
441 contributed to subsequent drafts of the manuscript.

442

443 **References**

444 Akaike, H., 1974. A New Look at the Statistical Model Identification. IEEE Trans. Automat. Contr. 19,  
445 716–723. <https://doi.org/10.1109/TAC.1974.1100705>



446 Baciadonna, L., Briefer, E.F., Favaro, L., McElligott, A.G., 2019. Goats distinguish between positive and  
447 negative emotion-linked vocalisations. *Front. Zool.* 16, 1–11. [https://doi.org/10.1186/s12983-019-](https://doi.org/10.1186/s12983-019-0323-z)  
448 0323-z

449 Barkema, H.W.W., von Keyserlingk, M.A.G., Kastelic, J.P., Lam, T.J.G.M., Luby, C., Roy, J.-P., LeBlanc,  
450 S.J.J., Keefe, G.P.P., Kelton, D.F.F., 2015. Invited review: Changes in the dairy industry affecting  
451 dairy cattle health and welfare. *J. Dairy Sci.* 98, 7426–45. <https://doi.org/10.3168/jds.2015-9377>

452 Barrier, A.C., Haskell, M.J., Macrae, A.I., Dwyer, C.M., 2012. Parturition progress and behaviours in dairy  
453 cows with calving difficulty. *Appl. Anim. Behav. Sci.* 139, 209–217.  
454 <https://doi.org/10.1016/j.applanim.2012.03.003>

455 Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting Linear Mixed-Effects Models Using lme4.  
456 *J. Stat. Softw.* 67. <https://doi.org/10.18637/jss.v067.i01>

457 Boersma, P., Weenink, D., 2009. Praat: doing phonetics by computer. <http://www.praat.org/>.

458 Briefer, E., McElligott, A.G., 2011. Indicators of age, body size and sex in goat kid calls revealed using the  
459 source-filter theory. *Appl. Anim. Behav. Sci.* 133, 175–185.  
460 <https://doi.org/10.1016/j.applanim.2011.05.012>

461 Briefer, E.F., 2012. Vocal expression of emotions in mammals: Mechanisms of production and evidence.  
462 *J. Zool.* 288, 1–20. <https://doi.org/10.1111/j.1469-7998.2012.00920.x>

463 Briefer, E.F., Maigrot, A.-L., Mandel, R., Freymond, S.B., Bachmann, I., Hillmann, E., 2015a. Segregation  
464 of information about emotional arousal and valence in horse whinnies. *Sci. Rep.* 4, 9989.  
465 <https://doi.org/10.1038/srep09989>

466 Briefer, E.F., Tettamanti, F., McElligott, A.G., 2015b. Emotions in goats: mapping physiological,

467 behavioural and vocal profiles. *Anim. Behav.* 99, 131–143.  
468 <https://doi.org/10.1016/j.anbehav.2014.11.002>

469 Briefer, E.F., Vizier, E., Gygax, L., Hillmann, E., 2019. Expression of emotional valence in pig closed-mouth  
470 grunts: Involvement of both source- and filter-related parameters. *J. Acoust. Soc. Am.* 145, 2895–  
471 2908. <https://doi.org/10.1121/1.5100612>

472 Fant, G., 1960. *Acoustic theory of speech production*, 2nd ed. Mouton.

473 Favaro, L., Briefer, E.F., McElligott, A.G., 2014. Artificial neural network approach for revealing  
474 individuality, group membership and age information in goat kid contact calls. *Acta Acust. United*  
475 *with Acust.* 100, 782–789. <https://doi.org/10.3813/AAA.918758>

476 Fitch, W.T., Neubauer, J., Herzog, H., 2002. Calls out of chaos: the adaptive significance of nonlinear  
477 phenomena in mammalian vocal production. *Anim. Behav.* 63, 407–418.  
478 <https://doi.org/10.1006/anbe.2001.1912>

479 Flower, F.C., Weary, D.M., 2001. Effects of early separation on the dairy cow and calf: 2. Separation at  
480 day 1 and 2 weeks after birth. *Appl. Anim. Behav. Sci.* 70, 275–284. [https://doi.org/10.1016/S0168-](https://doi.org/10.1016/S0168-1591(00)00164-7)  
481 [1591\(00\)00164-7](https://doi.org/10.1016/S0168-1591(00)00164-7)

482 Fox, J., Weisberg, S., 2018. *An R Companion to Applied Regression*, Third. ed. Sage.

483 Frey, R., Volodin, I., Volodina, E., Carranza, J., Torres-Porras, J., 2012. Vocal anatomy, tongue protrusion  
484 behaviour and the acoustics of rutting roars in free-ranging Iberian red deer stags (*Cervus elaphus*  
485 *hispanicus*). *J. Anat.* 220, 271–292. <https://doi.org/10.1111/j.1469-7580.2011.01467.x>

486 Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio  
487 coding and live observations. *Methods Ecol. Evol.* 7, 1325–1330. <https://doi.org/10.1111/2041->

488 210X.12584

489 Gamba, M., Favaro, L., Torti, V., Sorrentino, V., Giacoma, C., 2011. Vocal tract flexibility and variation in  
490 the vocal output in wild indris. *Bioacoustics* 20, 251–266.

491 <https://doi.org/10.1080/09524622.2011.9753649>

492 Grandin, T., 2001. Cattle vocalizations are associated with handling and equipment problems at beef  
493 slaughter plants. *Appl. Anim. Behav. Sci.* 71, 191–201. <https://doi.org/10.1016/S0168->

494 1591(00)00179-9

495 Green, A., Clark, C., Favaro, L., Lomax, S., Reby, D., 2019. Vocal individuality of Holstein-Friesian cattle is  
496 maintained across positively and negatively valenced farming contexts. *Sci. Rep.* 9, 1–9.

497 <https://doi.org/https://doi.org/10.1038/s41598-019-54968-4>

498 Green, A.C., Johnston, I.N., Clark, C.E.F., 2017. Invited review: The evolution of cattle bioacoustics and  
499 application for advanced dairy systems. *Animal* 1–10.

500 <https://doi.org/10.1017/S1751731117002646>

501 Green, A.C., Lidfors, L.M., Lomax, S., Favaro, L., Clark, C.E.F., 2020. Vocal production in postpartum dairy  
502 cows: Temporal organization and association with maternal and stress behaviors. *J. Dairy Sci.*

503 Hudson, S.J., Mullord, M.M., 1977. Investigations of maternal bonding in dairy cattle. *Appl. Anim. Ethol.*  
504 3, 271–276. [https://doi.org/10.1016/0304-3762\(77\)90008-6](https://doi.org/10.1016/0304-3762(77)90008-6)

505 Ikeda, Y., Ishii, Y., 2008. Recognition of two psychological conditions of a single cow by her voice.

506 *Comput. Electron. Agric.* 62, 67–72. <https://doi.org/10.1016/j.compag.2007.08.012>

507 Johnsen, J.F., Ellingsen, K., Grøndahl, A.M., Bøe, K.E., Lidfors, L., Mejdell, C.M., 2015. The effect of  
508 physical contact between dairy cows and calves during separation on their post-separation

509 behavioural response. *Appl. Anim. Behav. Sci.* 166, 11–19.  
510 <https://doi.org/10.1016/j.applanim.2015.03.002>

511 Kiley, M., 1972. The Vocalizations of Ungulates, their Causation and Function. *Z. Tierpsychol.* 31, 171–  
512 222. <https://doi.org/10.1111/j.1439-0310.1972.tb01764.x>

513 Koutseff, A., Reby, D., Martin, O., Levrero, F., Patural, H., Mathevon, N., 2017. The acoustic space of  
514 pain: cries as indicators of distress recovering dynamics in pre-verbal infants. *Bioacoustics* 4622, 1–  
515 13. <https://doi.org/10.1080/09524622.2017.1344931>

516 Leliveld, L.M.C., Döpjan, S., Tuchscherer, A., Puppe, B., 2017. Vocal correlates of emotional reactivity  
517 within and across contexts in domestic pigs (*Sus scrofa*). *Physiol. Behav.* 181, 117–126.  
518 <https://doi.org/10.1016/j.physbeh.2017.09.010>

519 Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2019. Package “emmeans.”

520 Lidfors, L.M., 1996. Behavioural effects of separating the dairy calf immediately or 4 days post-partum.  
521 *Appl. Anim. Behav. Sci.* 49, 269–283. [https://doi.org/10.1016/0168-1591\(96\)01053-2](https://doi.org/10.1016/0168-1591(96)01053-2)

522 Linhart, P., Ratcliffe, V.F., Reby, D., Spinka, M., 2015. Expression of emotional arousal in two different  
523 piglet call types. *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0135414>

524 Maigrot, A., Hillmann, E., Briefer, E., 2018. Encoding of Emotional Valence in Wild Boar (*Sus scrofa*) Calls.  
525 *Animals* 8, 1–15. <https://doi.org/10.3390/ani8060085>

526 Mainau, E., Manteca, X., 2011. Pain and discomfort caused by parturition in cows and sows. *Appl. Anim.*  
527 *Behav. Sci.* 135, 241–251. <https://doi.org/10.1016/j.applanim.2011.10.020>

528 Manteuffel, G., Puppe, B., Schön, P.C., 2004. Vocalization of farm animals as a measure of welfare. *Appl.*  
529 *Anim. Behav. Sci.* 88, 163–182. <https://doi.org/10.1016/j.applanim.2004.02.012>

530 Marten, K., Quine, D., Marler, P., 1977. Sound transmission and its significance for animal vocalization -  
531 II. Tropical forest habitats. *Behav. Ecol. Sociobiol.* 2, 291–302. <https://doi.org/10.1007/BF00299741>

532 Marx, G., Horn, T., Thielebein, J., Knubel, B., Von Borell, E., 2003. Analysis of pain-related vocalization in  
533 young pigs. *J. Sound Vib.* 266, 687–698. [https://doi.org/10.1016/S0022-460X\(03\)00594-7](https://doi.org/10.1016/S0022-460X(03)00594-7)

534 Mcgrath, N., Dunlop, R., Dwyer, C., Burman, O., Phillips, C.J.C., 2017. Hens vary their vocal repertoire and  
535 structure when anticipating different types of reward. *Anim. Behav.* 130, 79–96.  
536 <https://doi.org/10.1016/j.anbehav.2017.05.025>

537 McKay, S., Roberts, J., 1990. Maternal and Caregiver Perceptions of the Meaning of Maternal Sounds  
538 During Second Stage Labor. *J. Nurse. Midwifery.* 35, 266–273.

539 Morton, E.S., 1977. On the Occurrence and Significance of Motivation-Structural Rules in Some Bird and  
540 Mammal Sounds. *Am. Nat.* 111, 855–869.

541 Owings, D.H., Morton, E.S., 1998. The roles of assessment and management in communication, in:  
542 *Animal Vocal Communication: A New Approach.* Cambridge University Press, Cambridge, p. 71.

543 Padilla de la Torre, M., Briefer, E.F., Reader, T., McElligott, A.G., 2015. Acoustic analysis of cattle (*Bos*  
544 *taurus*) mother–offspring contact calls from a source–filter theory perspective. *Appl. Anim. Behav.*  
545 *Sci.* 163, 58–68. <https://doi.org/10.1016/j.applanim.2014.11.017>

546 Raine, J., Pisanski, K., Bond, R., Simner, J., Reby, D., 2019. Human roars communicate upper-body  
547 strength more effectively than do screams or aggressive and distressed speech. *PLoS One* 14,  
548 e0213034. <https://doi.org/10.1371/journal.pone.0213034>

549 Raine, J., Pisanski, K., Simner, J., Reby, D., 2018. Vocal communication of simulated pain. *Bioacoustics*  
550 4622, 1–23. <https://doi.org/10.1080/09524622.2018.1463295>

551 Reby, D., Levréro, F., Gustafsson, E., Mathevon, N., 2016. Sex stereotypes influence adults' perception of  
552 babies' cries. *BMC Psychol.* 1–12. <https://doi.org/10.1186/s40359-016-0123-6>

553 Reby, D., McComb, K., 2003. Anatomical constraints generate honesty: acoustic cues to age and weight  
554 in the roars of red deer stags. *Anim. Behav.* 65, 519–530. <https://doi.org/10.1006/anbe.2003.2078>

555 Remnant, J.G., Tremlett, A., Huxley, J.N., Hudson, C.D., 2017. Clinician attitudes to pain and use of  
556 analgesia in cattle: Where are we 10 years on? *Vet. Rec.* 181, 1–7.  
557 <https://doi.org/10.1136/vr.104428>

558 Rørvang, M.V., Nielsen, B.L., Herskin, M.S., Jensen, M.B., 2018. Prepartum Maternal Behavior of  
559 Domesticated Cattle: A Comparison with Managed, Feral, and Wild Ungulates. *Front. Vet. Sci.* 5.  
560 <https://doi.org/10.3389/fvets.2018.00045>

561 R Core Team, 2020. R: A Language and Environment for Statistical Computing.

562 RStudio Team, 2020. RStudio: Integrated Development Environment for R.

563 Scherer, K.R., 1986. Vocal Affect Expression - a Review and a Model for Future Research. *Psychol. Bull.*  
564 99, 143–165.

565 Sebe, F., Duboscq, J., Aubin, T., Ligout, S., Poindron, P., Sèbe, F., Duboscq, J., Aubin, T., Ligout, S.,  
566 Poindron, P., 2010. Early vocal recognition of mother by lambs: contribution of low- and high-  
567 frequency vocalizations. *Anim. Behav.* 79, 1055–1066.  
568 <https://doi.org/10.1016/j.anbehav.2010.01.021>

569 Stěhulová, I., Lidfors, L., Špinko, M., 2008. Response of dairy cows and calves to early separation: Effect  
570 of calf age and visual and auditory contact after separation. *Appl. Anim. Behav. Sci.* 110, 144–165.  
571 <https://doi.org/10.1016/j.applanim.2007.03.028>

572 Stoeger, A.S., Baotic, A., Li, D., Charlton, B.D., 2012. Acoustic Features Indicate Arousal in Infant Giant  
573 Panda Vocalisations. *Ethology* 118, 896–905. <https://doi.org/10.1111/j.1439-0310.2012.02080.x>

574 Stoeger, A.S., Charlton, B.D., Kratochvil, H., Fitch, W.T., Stoeger, A.S., Charlton, B.D., 2011. Vocal cues  
575 indicate level of arousal in infant African elephant roars. *Acoust. Soc. Am.* 130, 1700–1710.  
576 <https://doi.org/10.1121/1.3605538>

577 Tallet, C., Linhart, P., Policht, R., Hammerschmidt, K., Šimeček, P., Kratinova, P., Špinko, M., 2013.  
578 Encoding of Situations in the Vocal Repertoire of Piglets (*Sus scrofa*): A Comparison of Discrete and  
579 Graded Classifications. *PLoS One* 8. <https://doi.org/10.1371/journal.pone.0071841>

580 Taylor, A.M., Reby, D., 2010. The contribution of source-filter theory to mammal vocal communication  
581 research. *J. Zool.* 280, 221–236. <https://doi.org/10.1111/j.1469-7998.2009.00661.x>

582 Taylor, A.M., Reby, D., McComb, K., 2009. Context-Related Variation in the Vocal Growling Behaviour of  
583 the Domestic Dog (*Canis familiaris*). *Ethology* 115, 905–915. <https://doi.org/10.1111/j.1439-0310.2009.01681.x>

584

585 Titze, I.R., 1994. Principles of voice production. Prentice-Hall Inc.

586 Watts, J.M., Stookey, J.M., 2000. Vocal behaviour in cattle: The animal's commentary on its biological  
587 processes and welfare. *Appl. Anim. Behav. Sci.* 67, 15–33. [https://doi.org/10.1016/S0168-1591\(99\)00108-2](https://doi.org/10.1016/S0168-1591(99)00108-2)

588

589 Watts, J.M., Stookey, J.M., 1999. Effects of restraint and branding on rates and acoustic parameters of  
590 vocalization in beef cattle. *Appl. Anim. Behav. Sci.* 62, 125–135. [https://doi.org/10.1016/S0168-1591\(98\)00222-6](https://doi.org/10.1016/S0168-1591(98)00222-6)

591

592 Weary, D.M., Chua, B., 2000. Effects of early separation on the dairy cow and calf 1. Separation at 6 h, 1

593 day and 4 days after birth. *Appl. Anim. Behav. Sci.* 69, 177–188. <https://doi.org/10.1016/S0168->  
594 1591(00)00128-3

595 Yeon, S.C., Jeon, J.H., Houpt, K.A., Chang, H.H., Lee, H.C., Lee, H.J., 2006. Acoustic features of  
596 vocalizations of Korean native cows (*Bos taurus coreanea*) in two different conditions. *Appl. Anim.*  
597 *Behav. Sci.* 101, 1–9. <https://doi.org/10.1016/j.applanim.2006.01.013>

598 Yin, S., McCowan, B., 2004. Barking in domestic dogs: Context specificity and individual identification.  
599 *Anim. Behav.* 68, 343–355. <https://doi.org/10.1016/j.anbehav.2003.07.016>

600