

Invited review: The evolution of cattle bioacoustics and application for advanced dairy systems

A. C. Green^{1†}, I. N. Johnston² and C. E. F. Clark¹

¹Dairy Science Group, School of Life and Environmental Sciences, The University of Sydney, Camden, NSW 2570, Australia; ²School of Psychology, School of Life and Environmental Sciences, The University of Sydney, Camperdown, NSW 2006, Australia

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Vocalisations are commonly expressed by gregarious animals, including cattle, as a form of short- and long-distance communication. They can provide conspecifics with meaningful information about the physiology, affective state and physical attributes of the caller. In cattle, calls are individually distinct meaning they assist animals to identify specific individuals in the herd. Consequently, there is potential for these vocalisations to be acoustically analysed to make inferences about how individual animals or herds are coping with their external surroundings, and then act on these signals to improve feed conversion efficiency, reproductive efficiency and welfare. In the case of dairy farming, where herd sizes are expanding and farmers are becoming more reliant on technologies to assist in the monitoring of cattle, the study of vocal behaviour could provide an objective, cost effective and non-invasive alternative to traditional measures of welfare. The vocalisations of cattle in response to calf separation, social isolation and painful husbandry procedures, alongside changes to feeding and oestrous activity are here reviewed. For future application of sound technology, research is first necessary to analyse the acoustic structure of cattle vocalisations and determine the specific information they encode. This review draws together the latest research in field of cattle bioacoustics highlighting how the source–filter theory and affective state dimensional approach can be adopted to decode this information and improve on-farm management.

Keywords: cattle welfare, sound analysis, source–filter theory, vocal communication

Implications

The study of vocal behaviour not only allows researchers to learn more about the biology of a particular species, but attempts to interpret how animals are coping with their external surroundings. For dairy cattle, vocalisations could provide a novel way of interpreting how individuals or herds are dealing with farming practices such as calf separation, social isolation and painful husbandry procedures, alongside changes related to feeding and oestrus. This review explores published literature in cattle bioacoustics, highlighting how adopting theories from other mammalian species will benefit our understanding of cattle vocalisations and the associated opportunities to improve our dairy systems.

Introduction

The dairy industry has undergone profound changes in recent times as a result of the fluctuating demand for dairy and meat products worldwide, and reduced operating margins. To accommodate these changes, average herd sizes are

increasing with the emergence of farms operating with over 1000 head of cattle (Barkema *et al.*, 2015). Concurrently, skilled labour has become scarce meaning that attending to individual animals is difficult. Furthermore, farming practices are increasingly in the public eye due to greater levels of interconnectedness between consumers and producers and associated interest in provenance (Barkema *et al.*, 2015). To overcome this, there is often a reliance on technologies to assist with farm management to improve health and welfare at an individual animal level. Many of these technologies involve analysing cattle behaviour. For instance, we have already seen widespread adoption of on-collar or ear tag accelerometers in advanced dairy systems to predict oestrous, monitor lying, standing and walking activity as well as rumination (Clark *et al.*, 2015). This is because analysis of sensor-derived behaviour is objective, often minimally invasive, cost effective and can be conducted on the large scale. A recent behaviour of interest with relatively little applied use on farm is vocalisations.

Vocalisations are the sounds produced when a flow of aerodynamic energy from the lungs is converted into acoustic energy by the vocal folds and other laryngeal tissue

[†] E-mail: a.green@sydney.edu.au

(Bradbury and Vehrencamp, 1998). They are commonly expressed by gregarious species, including cattle, as a form of short- and long-distance communication. Although energetically costly, vocalisations can provide receivers with meaningful information about the physiology, motivational state, affective state and/or physical attributes of the sender (Watts and Stookey, 2000; Briefer, 2012) and accordingly be interpreted as 'commentary' on the animal's biological and welfare state (Watts and Stookey, 2000). Moreover, unlike tactile and olfactory signals which require direct or short-distance contact, and visual signals which can be blocked by intervening objects and rely on daylight, vocalisations can be expressed in a range of conditions (Bradbury and Vehrencamp, 1998). Vocalisations have been extensively studied in wild vertebrates, but considering there is interspecies variation in the degree to which vocalisations convey certain information (Bradbury and Vehrencamp, 1998), it is necessary to examine vocalisations at the species level.

This review first examines advancements in the field of bioacoustics, including applying the human-derived source-filter theory to explain vocal production and the concept of affective state to link vocal production with specific emotions. The distinctiveness of individual vocalisations are then highlighted as a mechanism for cattle to recognise conspecifics in their herd, and finally the most recent cattle studies where vocalisations have been recorded in response to different farming situations, in both indoor and pasture-based systems are evaluated. These findings are then drawn together to show the ability to interpret specific temporal and spectral features of vocalisations to determine how animals are coping on farm, and the associated ability to use these features to improve welfare, alongside feed conversion efficiency and reproductive efficiency.

The evolution of cattle bioacoustics

While cattle bioacoustic studies have been conducted since the 20th century; there was a lack of accurate and efficient sound recording and analysing technology resulting in a paucity of reliable and interpretable research. Early reports of cattle vocalisations involved anecdotally describing the sounds produced by individuals, the contexts of the calls and the animals that expressed them (Schloeth, 1961; Kiley, 1972; Hall *et al.*, 1988). One of the first cattle studies recounted 11 different vocal signals in a herd of wild Camargue cattle (Schloeth, 1961); however, the calls were not recorded so could not be replayed for a further detailed analysis. It was only in 1972 that Kiley (1972) first recorded and spectrographically analysed the vocalisations of cattle, followed by Hall *et al.* (1988) who further incorporated statistical analyses to deduce the calls in a herd of semi-wild Chillingham cattle. Kiley (1972) suggested that in a herd of mixed breed beef and dairy cattle there were six distinct call types comprising different combinations of five syllables. Further, Hall *et al.* (1988) characterised bull vocalisations as 'lowing' and 'calling' and like Kiley (1972) who proposed that calls were made up of syllables, Hall *et al.* (1988)

suggested that these calls comprised a series of one or more 'hoots'. These vocalisations were classified based on their phonetic appearance and as different names were assigned to the calls in both studies, they are challenging to compare. For example, Hall *et al.* (1988) highlight the difficulty in matching Kiley's 'see-saw' vocalisation to their 'hoots' as the spectrogram was not clearly divided into its components. Further, Hall *et al.* (1988) weren't able to report any of Kiley's 'menen' type vocalisations in their test subjects. Kiley (1972) also broadly classified the vocal parameters resulting in the fundamental frequency, hereafter F0, of the syllables ranging from 50 to 800 Hz, amplitude arbitrarily categorised as low, medium or high and duration ranging from 0.1 to 2.8 s. Nevertheless, this research was the first to hypothesise that the vocalisations of cattle reflect their level of excitement, with increases in F0 relating to a more reactive or excited individual (Kiley, 1972).

As we will see in subsequent sections, the changes in vocal parameters are likely related to developmental growth and changes in affective state. Therefore, with further research, the analysis of vocalisations could assist in the management of cattle during feeding, improve detection rates during oestrus, and determine stress responses during calf separation, social isolation and painful husbandry procedures, all of which are situations where cattle are commonly vocal (Watts and Stookey, 2000). There has been recent interest in utilising sound analysis as a potential welfare monitor in dairy cows (Meen *et al.*, 2015), and some studies have already incorporated human-derived algorithms to analyse and then recognise specific cattle vocalisations (Jahns, 2008; Chung *et al.*, 2013). For future application in advanced dairy systems, a greater understanding of the cattle vocal repertoire is first necessary to determine the information that the calls encode, why particular animals are vocal and whether changes to vocal parameters are consistent across ages, different breeds and situations. In the following sections, we will see how adopting principles from biologically similar species can assist to reveal this information.

The source-filter theory: a human-adapted framework to understand vocal production

Our understanding of animal vocal production has increased due to the adoption of the source-filter theory. The source-filter theory was initially used to explain vocal production in humans (Fant, 1960; Titze, 1994) and since the vocal apparatus is similarly structured across mammalian species', this framework has now been generalised to a wide array of animals of different sizes. First, hypothesised by Fant (1960), the source-filter theory is a two stage process where the 'source' of the sound, produced by pulsations between the vocal folds, is passed through supralaryngeal vocal tract or 'filter' where it is modified before radiating out of the nose and mouth (Fant, 1960; Titze, 1994; Taylor and Reby, 2010). The source and filter are two independent production processes (Fant, 1960) with the 'source' of the sound first generated in the larynx. In mammals, the larynx consists of

thyroid cartilage, cricoid cartilage, arytenoid cartilage and vocal folds attached to both the posterior side of the arytenoid cartilage and anterior side of the thyroid cartilage (Bradbury and Vehrencamp, 1998; Taylor and Reby, 2010). The vocal folds are fleshy, lip-like mucous membranes comprised of three layers including muscle, a vocal ligament and epithelium, and in combination with the gaps between them, they form the glottis where the vocalisations are produced (Taylor and Reby, 2010). The rate of opening and closing of the glottis (source) contributes to the F₀, and the interaction of muscles, changes in airflow and sub-glottal pressure contributes to the amplitude, duration and tempo of the call (Reby and McComb, 2003; Taylor and Reby, 2010). These vocal parameters are all influenced by the anatomy of the larynx including the length, mass, thickness and tension of the vocal folds (Taylor and Reby, 2010; Briefer, 2012). The source parameters including F₀ and calling rate can therefore provide insight into the caller's arousal state mediated by changes in respiration or muscle tension in the vocal folds (Briefer, 2012). In general, higher vocalisation rates, higher frequencies and louder calls are associated with higher arousal, however, for specific details, refer to the review of Briefer (2012).

Following the 'source', the 'filter' or vocal tract allows the sound to be transported internally from the animal externally to the environment. The filter contains the oropharyngeal and nasopharyngeal cavities along with the oral and nasal cavities, all of which connect the glottis to the lip and nose (Titze, 1994; Briefer, 2012). This filter acts to selectively enhance or subdue specific ranges of frequencies from the source signal and this results in the production of a heterogeneous sound spectrum containing peaks of different formant frequencies (Fant, 1960; Taylor and Reby, 2010). In other words, the filter assists with the amplification of different frequencies, with formants constituting natural resonances of the vocal tract. As most mammals cannot alter the shape or dimensions of their vocal tract as it is physically constrained by skeletal structures including the skull (Taylor and Reby, 2010; Wyman *et al.*, 2012), the length of the vocal tract in cattle should significantly correlate with formant dispersion (Reby and McComb, 2003; Taylor and Reby, 2010; Wyman *et al.*, 2012), providing honest and indexical cues into the age, size and/or gender of the vocaliser (Briefer and McElligott, 2011; Padilla de la Torre *et al.*, 2015). Even for animals that can alter their vocal tract shape, for example, red deer that can retract their larynx, the minimum formant dispersion still correlates with age and body size (Reby and McComb, 2003). In beef calves formant frequencies decreased as calves aged, being a direct result of developmental growth (Padilla de la Torre *et al.*, 2015). Further, in bison although formant dispersion did not strongly associate with age, it correlated with mass, with heavier bulls having lower formant dispersion (Wyman *et al.*, 2012). These findings emphasise the idea that in mammals, longer vocal tracts should produce lower formant frequencies, and are directly related to animals larger in size (Taylor and Reby, 2010; Briefer and McElligott, 2011). Although radiographic analysis

has not confirmed this in cattle, the study of Padilla de la Torre *et al.* (2015) showed how maximum estimated vocal tract length, as determined from the formant frequencies of seven cattle test subjects were highly correlated to actual head length. Filter properties therefore contribute to the inter-individuality of animal vocalisations and in the farming context where individuals are not always visible, they could be used to provide an estimate of which animals in the herd are vocalising.

Affective state and vocal correlates of emotion

Most recently, a dimensional framework has been proposed for studying the emotions of animals. This framework examines arousal which is the excitation of the animal ranging from low to high, and valence which looks at positivity *v.* negativity of the situation (Mendl *et al.*, 2010). In line with this framework studies have begun examining the emotional information encoded in the vocalisations of livestock, in relation to specific source and filter parameters (Briefer, 2012). Although cattle vocal studies have traditionally analysed easily collectable measures such as vocalisation rate (Lidfors, 1996; Flower and Weary, 2001), classified animals as vocal or not to detect changes in welfare (Grandin, 1998 and 2001) and classified calls as either high-frequency open-mouth, or low-frequency closed-mouth to provide some meaning behind call production (Johnsen *et al.*, 2015), this framework could provide more detailed information about why vocal parameters differ, and thus deduce how animals are coping in response to various farming practices.

Vocalisation patterns have specifically been linked to arousal and valence in pigs, goats and horses (Linhart *et al.*, 2015; Briefer *et al.*, 2015a and 2015b; Leliveld *et al.*, 2016) with numerous studies relating stress to features of pig vocalisations (Weary *et al.*, 1998; Puppe *et al.*, 2005; Döpjan *et al.*, 2008). Contrarily there is limited research on the vocal correlates of emotion in cattle. There are consistencies in the vocal correlates of arousal within livestock species, mostly related to F₀ parameters and these seem to be in accordance with changes in behavioural and physiological parameters (Briefer *et al.*, 2015a and 2015b). In pigs, arousal was linked with intensity and central F₀ in calls (Linhart *et al.*, 2015); in horses arousal was highly correlated with F₀ max and F₀ start values and energy quartiles (Briefer *et al.*, 2015a) and further in goats, arousal was linked with F₀ mean and F₀ end values, as well as energy quartiles (Briefer *et al.*, 2015b). It is thus hypothesised that F₀ parameters would also increase due to increases in arousal in cattle.

Vocal correlates of valence on the other hand seem to be less conserved across species. For instance, in pigs positive valence was associated with a reduced vocal rate and negative valence was associated with calls of a longer duration (Leliveld *et al.*, 2016). In horses valence was correlated with duration and G₀ (second fundamental frequency) (Briefer *et al.*, 2015a), whereas in goats F₀ range and frequency modulation (FM) extent decreased from negative to positive valence (Briefer *et al.*, 2015b). Thus, the

specific acoustic parameters of valence in dairy cattle breeds need further exploration to rule out any species or breed effects. In addition, a comparison of the vocal correlates of arousal and valence is necessary between a multitude of farming contexts and since cattle have individually distinct voices (Padilla de la Torre *et al.*, 2015), farming contexts should be compared not only between animals, but also within individuals. So far, the vocalisations of a single cow subject to calf separation and hunger have been shown to differ in their formant frequencies (Ikeda and Ishii, 2008) and the vocalisations of cattle subject to feed anticipation and oestrus have been shown to differ in their sound intensity (Yeon *et al.*, 2006). Further and more accurate characterisation of cattle vocalisations is necessary to determine vocal correlates of valence in these putatively positive and negative situations.

The vocalisations of cattle during lying and ruminating also differ in mean maximum frequency to those produced during feeding, socialisation, stress or sexual receptivity (Meen *et al.*, 2015). Although these studies have begun to discern between the calls of different contexts, it is also necessary to consider call type and a more extensive range of vocal parameters. This is because in pigs the structure of the call type impacts the acoustical encoding of emotions (Linhart *et al.*, 2015). Although arousal led to an increase in central frequency and calling rate in the screams and grunts of pigs, increases in intensity linked with arousal were only apparent in screams (Linhart *et al.*, 2015). Considering that cattle produce nasal and open-mouth call types with different communicative purposes (Kiley, 1972; Padilla de la Torre *et al.*, 2015), further work is needed to determine how the acoustic features of these call types differ with changes in arousal and valence. Together with recording a greater number of contexts, a more extensive vocal repertoire could be mapped out for cattle, and we could deduce which farming practices cattle perceive as the most compromising, which may influence how we farm in advanced dairy systems.

The vocalisations of cattle within the herd and use in advanced dairy systems

The individuality of vocalisations

Not only is there high variability in the propensity of cattle to express calls (Watts and Stookey, 2001), but numerous studies have also reported high inter-cow variability in the acoustic characteristics of vocalisations (Barfield *et al.*, 1994; Yajuvendra *et al.*, 2013; Padilla de la Torre *et al.*, 2016). This variability between cattle surpasses any variability within cattle and contributes to the individual distinctiveness of the calls (Kiley, 1972). The uniqueness of each voice allows animals to recognise certain conspecifics in their herd and may be the result of a combined genetic and environmental effect (Padilla de la Torre *et al.*, 2016). This is particularly important for facilitating social interactions in the herd and in maintaining contact between mother and offspring in free-ranging environments where visual or olfactory cues may be absent (Padilla de la Torre *et al.*, 2016).

Vocalisations of cattle are typically harmonic in nature and generally range between 1.3 and 1.5 s in duration (Kiley, 1972; Padilla de la Torre *et al.*, 2015). A multitude of their acoustic parameters show individual distinctiveness, the most significant ones being the mean F0 and its range, formant frequencies, jitter and shimmer, noise-to-harmonic ratio, number of pulses and degree of voice break (Yajuvendra *et al.*, 2013). These relate to the source and filter parameters as previously explained. Individual distinctiveness in vocalisations is also most apparent in low frequency calls and older animals, suggesting that this feature develops with growth and age (Padilla de la Torre *et al.*, 2015). Considering that there are conspicuous qualitative and quantitative differences in the vocalisations of adult cattle, vocalisations could be used as a means of detecting certain individuals within large herds without interfering with their natural behaviours. For this to be integrated into advanced dairy systems, it is also necessary to determine who in the herd is most vocal and why.

Vocal recognition

Some playback experiments have been conducted in cattle to confirm the biological relevance of vocalisations to receivers, more specifically in the social context of mother and offspring. The ability of cattle to recognise their conspecifics as well as heterospecifics is first attributed to their acute sense of hearing, related to their large pinnae and head. Cattle hearing ability ranges from 23 Hz to 37 kHz in which their vocalisations lie, with frequency of best hearing at 8 kHz (Heffner, 1998). The ability of calves to recognise their mother's calls seems to be more prominent than calf recognition by cows, and may relate to its biological importance for calf survival, where in the wild calves are generally hidden (Watts and Stookey, 2000). This behaviour is apparent after just 48 h of birth (Marchant-Forde *et al.*, 2002), as well as at the ages of 3, 4 and 5 weeks in dairy calves, and older in beef calves (Barfield *et al.*, 1994; Padilla de la Torre *et al.*, 2016). Calves spent more time near a speaker in response to their mother's call than that of another conspecific or white noise (Barfield *et al.*, 1994; Marchant-Forde *et al.*, 2002; Padilla de la Torre *et al.*, 2016). These findings suggest that vocal recognition of specific individuals is acquired early in development and can be used in the absence of other cues to locate the mother. It may explain why Lidfors (1996) found that cows were considerably more vocal when kept with their calves during the first 24 h *postpartum*, as a mechanism of enabling their calves to learn their call. Further, the ability of calves to recognise their mothers is maintained with age suggesting that maternal attachment in calves is strong (Padilla de la Torre *et al.*, 2016). In contrast to calves, Marchant-Forde *et al.* (2002) showed how dairy cattle had a limited ability to distinguish between their calf and a conspecific when calves were separated for 24 h after parturition. This may reflect how early farming intervention can influence the development of natural cattle behaviours. By contrast, in free-ranging beef cattle that were not exposed to early separation, cows were more likely to respond to

playbacks if their offspring was younger, indicating an ability to recognise their young (Padilla de la Torre *et al.*, 2016). Nonetheless beef calf calls in this situation were only classified to the correct individual on 24% of occasions suggesting that calf call individuality is relatively low (Padilla de la Torre *et al.*, 2016). Although much of the research has targeted recognition in mother–offspring dyads, research should also be conducted in a herd of adult cattle and further, between beef, dairy and wild type breeds to determine if evolution and recent domestication has impacted the ability of cattle to respond to their conspecifics.

Calf separation

Cattle bioacoustic studies have focussed on vocalisations in response to separation and weaning, especially in commercial dairy conditions. The intent being to determine the association between age of separation and behavioural impacts from separating the calf from the mother immediately (Lidfors, 1996; Flower and Weary, 2001), 6 h *postpartum* (Weary and Chua, 2000), 1 day *postpartum* (Weary and Chua, 2000; Stěhulová *et al.*, 2008), 4 days *postpartum* (Lidfors, 1996; Flower and Weary, 2001; Stěhulová *et al.*, 2008), 1 week *postpartum* (Stěhulová *et al.*, 2008), 2 weeks *postpartum* (Flower and Weary, 2001) and finally 5 weeks *postpartum* (Thomas *et al.*, 2001). In addition, the latest studies have involved spectrographically examining cow–calf contact calls in a herd of free ranging, mixed-age beef cattle upon temporary separation (Padilla de la Torre *et al.*, 2015) as well as comparing fence-line and solid-wall separation in dairy cattle (Johnsen *et al.*, 2015).

Separation in these studies induced acute stress in calves, evident through their high vocal rate, licking behaviour, increased activity including placing their head out of the fence, longer standing periods and immediate rise in heart rate (Lidfors, 1996; Flower and Weary, 2001, Stěhulová *et al.*, 2008). The propensity of a calf to vocalise and vocal parameters of the call were impacted by its age (Padilla de la Torre *et al.*, 2015) and also time of separation from its mother (Lidfors, 1996; Stěhulová *et al.*, 2008). Although younger calves were more vocal before separation, older calves were more vocal afterwards (Lidfors, 1996; Weary and Chua, 2000). Further, later separation was associated with a greater number of vocalisations (Lidfors, 1996). The vocalisations produced by calves in response to separation had a higher F0, higher amplitude of up to 30 dB more and an emphasised harmonic compared with those produced before and this may indicate high arousal and reactivity in the caller (Weary and Chua, 2000; Briefer, 2012). Vocalisations have also been reported at peaks of 18 and 24 h post-separation (Flower and Weary, 2001) and this may reflect their ever increasing desire for milk. In accordance, Thomas *et al.* (2001) demonstrated how vocalisations are produced more regularly in calves deprived of milk compared with those fed *ad-libitum*. The vocalisations of beef calves can be further described as having an average duration of 1.4 s, an average F0 of 143 Hz and average formant frequencies (1 to 8)

ranging from 392 to 5813 Hz (Padilla de la Torre *et al.*, 2015). As these call parameters were collected by beef calves in relatively undisturbed conditions, it would be interesting to see how they compare to the calls of dairy calves in intensive production systems. As vocal parameters depend on the breed, size and age of the animal, it is likely that they would differ. For this to be discerned, the source–filter approach should be adopted by future studies.

Cattle also exhibit a greater vocal rate during the time of separation from their calves compared with any other time during the cow–calf interaction (Hopster *et al.*, 1995; Lidfors, 1996), with up to 286 vocalisations reported by Ikeda and Ishii (2008). This vocal behaviour is impacted by the time of separation (Weary and Chua, 2000; Flower and Weary, 2001; Stěhulová *et al.*, 2008), age of the calf (Lidfors, 1996) and also degree of separation, with cattle displaying greater vocal rates upon later separation after attachment has formed (Weary and Chua, 2000; Flower and Weary, 2001; Stěhulová *et al.*, 2008), alongside when visual and auditory contact is maintained (Stěhulová *et al.*, 2008). Some research has shown how displays of maternal behaviour are short lived, with cattle reducing their vocal responses after about 20 min of separation, however, this is highly dependent on the individual (Lidfors, 1996). Research has also demonstrated a parity interaction (Lidfors, 1996) with a greater number of calls from multiparous cattle compared with their primiparous conspecifics, however, this finding is not consistent across all studies (Flower and Weary, 2001). Differences in calling rate may be due to a variety of cattle breeds being tested with the former study using a mix of Swedish red, white and Friesians and the latter using purely Holstein-Friesians.

A variety of call types have been reported in both dairy cattle and calves in response to separation, including those with a high F0 and amplitude (Weary and Chua, 2000; Johnsen *et al.*, 2015) and those with a short duration, low amplitude and F0 (Hopster *et al.*, 1995; Johnsen *et al.*, 2015). This may relate to calls being produced on a graded continuum of low to high frequency (Kiley, 1972). In free-ranging beef cattle and calves both high- and low-frequency calls with the purpose of regaining contact have been described thoroughly (Padilla de la Torre *et al.*, 2015 and 2016). The high-frequency calls played the biological role of long-distance communication and indicated distress, whereas the low-frequency calls were mainly for close contact communication (Padilla de la Torre *et al.*, 2015). The characteristics of these calls could be used as a reference to which the calls of cattle in stressful conditions could be compared. In the study of Padilla de la Torre *et al.* (2015) the high-frequency calls of beef cattle were described as having a mean F0 of 153 Hz, formant frequencies (1 to 8) ranging from 228 to 3181 Hz, an average duration of 1.2 s, and being produced with the mouth fully open for at least part of the call (Padilla de la Torre *et al.*, 2015). In contrast, the low-frequency calls of beef cattle were characterised by having a mean F0 of 81 Hz, formant frequencies (2 to 8) ranging from 634 to 3224 Hz, an average duration of 1.3 s, and being produced

with the mouth closed (Padilla de la Torre *et al.*, 2015). These call types draw similarities to the calls described by Hall *et al.* (1988) including the high-frequency 'hoots' and low-frequency 'lows'. In dairy cattle it has been further shown that calves subject to solid-wall separation with mere auditory contact, produced significantly more high-frequency vocalisations to low-frequency vocalisations than that of their fence-line separated conspecifics (Johnsen *et al.*, 2015). These calls were not spectrographically analysed emphasising how further research is needed to characterise the vocalisations in the context of dairy calf separation using the source-filter approach. Knowledge of these call types should be applied in future cow-calf separation studies, to determine how age and method of separation affects calling features including the acoustical encoding of emotions. If research is conducted to examine the vocal correlates of emotion in cattle-calf separation calls, this could assist with developing management strategies for housing and rearing animals on farm.

Social isolation

Before recent domestication, cattle evolved in a herd environment (Kiley, 1972) which enabled the development of long-lasting social bonds (Færevik *et al.*, 2006) and facilitated collective predator detection (Padilla de la Torre *et al.*, 2016). With the exception of calving, where cattle prefer to be isolated from conspecifics, cattle are highly gregarious, meaning that isolation from their conspecifics on farm can be detrimental to their welfare and overall fitness. On dairy farms it is often necessary for animals to be separated from their conspecifics for medical or scientific procedures. For example, the accepted routine for sick or injured animals is to separate them in order to prevent further transmission of disease and to facilitate the animal's recovery. As a consequence of this isolation, cattle exhibit marked physiological changes including increased heart rate, salivary cortisol, urination and defecation rates (Mueller and Schrader, 2005) alongside changes in their locomotory activity (Mueller and Schrader, 2005; Færevik *et al.*, 2006). As per cow-calf separation, cattle isolated from their familiar conspecifics additionally exhibit increased vocal responses (Mueller and Schrader, 2005; Færevik *et al.*, 2006) with the communicative purpose of regaining contact with their herd or expressing their level of distress.

While little is known about the acoustic characteristics of these social isolation calls, work has been undertaken to deduce which intrinsic characteristics of the animal make them vocal. It was shown that individuals vary in their coping strategies to deal with fear with the highly social cattle exhibiting a larger number of vocal responses to isolation (Mueller and Schrader, 2005). Again, there is high inter-animal variability in the propensity to vocalise, with one study having <40% of their test subjects vocalising in response to visual isolation (Watts and Stookey, 2001). Cattle are also more vocal in the presence of unfamiliar versus familiar conspecifics (Færevik *et al.*, 2006) and further, the behavioural responses to isolation are highly repeatable

suggesting that they are ingrained into the personality of the individual (Watts and Stookey, 2001; Mueller and Schrader, 2005). These vocal responses fail to diminish across experiments emphasising how cattle have a low level of habituation to isolation which is similar to that found in goats (Mueller and Schrader, 2005; Siebert *et al.*, 2011). It is also evident how the genotype and phenotype of an individual can influence their propensity to vocalise and features of their vocalisation (Watts and Stookey, 2001; Watts *et al.*, 2001). The sire and parental lineage contribute to variability in beef calf responses in terms of number of vocalisations, F0, call duration, amplitude and latency to call (Watts *et al.*, 2001). In addition, older, heavier animals are more vocal producing higher frequency calls, with calves aged 11 to 15 months producing calls with an average F0 of 99 Hz, and calves aged 8 to 12 months producing calls with an average F0 of 96 Hz in response to 1-min physical isolation (Watts and Stookey, 2001). This again emphasises how vocal parameters change with breed, size and age of the animal.

Although there is a lack of cattle isolation call acoustic analysis, in other gregarious livestock species, it has been suggested that during isolation, animals exhibit an active then passive coping response, where there is an initial increased incidence of high-frequency, open-mouth vocalisations followed by a period of decreased activity and low-frequency mouth-closed vocalisations irrespective of the degree of isolation (Siebert *et al.*, 2011). In dwarf goats the high-frequency calls have been described as an 'honest' signal of their desire to restore connection with conspecifics and the low-frequency calls have been described as a form of auto-communication, or mechanism to calm themselves (Siebert *et al.*, 2011). This hypothesis may explain why during partial isolation, more high-frequency calls were produced compared with full isolation, as permanent sensory feedback from peers induces active responses (Siebert *et al.*, 2011). Considering cattle produce both high- and low-frequency vocalisations in response to maternal or calf separation and they are also highly social (Padilla de la Torre *et al.*, 2015), it is likely that they too produce these contact calls in response to social isolation from their herd and this requires more scientific exploration. Work to date in cattle has either involved individuals being separated for a 1-min duration (Watts and Stookey, 1999; Watts *et al.*, 2001) or has failed to measure acoustic parameters other than vocal rate (Mueller and Schrader, 2005; Færevik *et al.*, 2006). Thus, longer isolation periods should be implemented to determine if, like in goats, stress responses turn from active to passive in cattle and whether this is evident through spectrographic features of their calls. Further, in line with the study on goats, different degrees of isolation including complete (social, visual, acoustic and olfactory) and partial should be explored to determine whether vocal parameters significantly differ in these circumstances.

Oestrus

Though infrequent and relatively under studied, cattle have also been shown to vocalise in expression of their sexual

receptivity and oestrous condition (Yeon *et al.*, 2006; Meen *et al.*, 2015). Meen *et al.* (2015) reported that 8 out of 540 heifer calls and a further 4 out of 307 cow calls in a barn setting were attributed to sexual behaviour. Moreover, bulls guarding cows in oestrus make very low-intensity, low-frequency mouth-closed calls (Hall *et al.*, 1988). Cattle increase their vocal rate the day before oestrus, which coincides with the time they start to display visual changes of sexual receptivity including redness and swelling of the vulva (Schön *et al.*, 2007). In addition, the non-harmonic or noisy structure of the vocalisation increases as the oestrus climax approaches (Schön *et al.*, 2007). In Korean Native Cattle, the vocalisations of oestrus can be distinguished from those produced during other highly arousing states, such as food anticipation by having an average sound intensity of 69 dB (Yeon *et al.*, 2006). These calls have further been described as having a harsh energy distribution, similar to a roaring sound; however, they cannot, be discerned from calls produced during stress-, social- or feeding-related situations based on their F0-related features alone (Yeon *et al.*, 2006; Meen *et al.*, 2015). Meen *et al.* (2015) showed the mean maximum frequencies of calls produced by Holstein-Friesian's during feeding, social interactions, sexual interactions or stress-related situations to be similar. In addition, Yeon *et al.* (2006) showed no significant differences in duration or F0 of calls produced by cattle in oestrus and a food-anticipatory state. All of these contexts likely induce similar arousal levels in cattle, which would explain the lack of differences in the F0-related parameters. Although it has previously been suggested that vocalisations could be monitored to assist farmers in selecting an appropriate joining and insemination period (Schön *et al.*, 2007), the low incidence of these calls and similarities to vocalisations under other contexts emphasises how they should not be solely relied upon at this stage. Classifying an animal as in-oestrus based on vocalisations alone is not accurate, considering that non-oestrus cattle also vocalise and the number of calls produced per animal is highly variable (Yeon *et al.*, 2006; Schön *et al.*, 2007). For this technology to be implemented, research is necessary to extract the specific source and filter characteristics related to these calls and determine if like in red deer (Reby and McComb, 2003) and bison (Wyman *et al.*, 2012), there are reliable cues of reproductive fitness encoded in these vocalisations.

Feeding

As a result of routine feeding management on dairy farms, cattle may vocalise in anticipation of food (Yeon *et al.*, 2006; Ikeda and Ishii, 2008; Schütz *et al.*, 2013) and this is commonly linked with increased activity including short, abrupt, quick changing movements (Boissy *et al.*, 2007; Briefer *et al.*, 2015b). Up until a certain point, anticipation of food is associated with a behavioural outcome that the animal will find pleasurable and fitness enhancing, and this is associated with a positive valence (Boissy *et al.*, 2007; Briefer *et al.*, 2015b). As good welfare involves not only the absence of negative events but also the presence of positive experiences

such as pleasure (Boissy *et al.*, 2007), research into these calls is warranted. It allows us to see whether certain vocal parameters can be interpreted as a proxy of good welfare in addition to signs of distress.

Further to anticipation, anecdotal reports have suggested that cattle may vocalise as an indicator of frustration. Frustration is described as 'an aversive state that results from non-reward, reduced reward or delayed reward' (Amsel, 1992) and in the context of feeding, frustration could occur due to prolonged anticipation of a food reward or inability to access food from competition at the food source or viewing their conspecifics eating when they cannot eat. The omission of the food reward is perceived as a negative event, as in the wild it would compromise their fitness due to lack of intake and energy, therefore it is associated with a negative valence (Briefer *et al.*, 2015b).

Although there is limited research on the acoustic components of cattle vocalisations associated with feeding, vocalisation rate has commonly been monitored as a behavioural indicator of feeding-related changes. Studies have shown how through a greater restriction of food quantity, vocalisation rate increases amongst dairy cattle regardless of body condition score and this is often in response to seeing the herdsman, to whom they have previously associated feeding (Valizahed *et al.*, 2008; Schütz *et al.*, 2013). It is also apparent how quality of food can impact the vocalisation rate, with dairy cattle being more vocal when provided with oat hay as opposed to grass hay during periods of drying off (Valizahed *et al.*, 2008). These calls have been associated with frustration and distress as during the cessation of milking cattle are often hungry (Valizahed *et al.*, 2008).

To our knowledge, only three studies have specifically examined the temporal and spectral features of cattle vocalisations in response to feeding-related situations (Kiley, 1972; Yeon *et al.*, 2006; Ikeda and Ishii, 2008) and a further one to deduce these impacts on calf vocalisations (Thomas *et al.*, 2001). However, to deduce any differences between anticipatory and frustratory vocal responses, further acoustic characterisation is needed. In the study of Kiley (1972) through a classical conditioning paradigm, cattle learnt to associate feeding time with the rattling of bucket, appearance of handler or running water. As they anticipated their food they began to produce regular 'mm' calls of low amplitude and frequency to indicate their desire to eat. This was then followed by repeated 'men', 'menh' or 'menenh' calls, which increased in amplitude and duration upon sighting the handler especially if the cows were not rewarded with food and were therefore frustrated (Kiley, 1972). It can be deduced that these vocalisations are the cattle's way of communicating their motivation for the food. Ikeda and Ishii (2008) provoked feeding calls by delaying feeding time by 1 h and Yeon *et al.* (2006) recorded the anticipatory vocalisations at feeding time at 1600 h. In the studies of Yeon *et al.* (2006) and Ikeda and Ishii (2008) the average food-anticipation call had an F0 of 214 and 330 Hz and an average duration of 1.85 and 1.8 s, respectively. Given that vocal parameters depend on factors such as age and size of the

individual, this may explain the between-individual differences in the same context. Yeon *et al.* (2006) found that in the 26 Korean Native Cows tested, the average intensity of the call was 71 dB with high individual variability in all of the call parameters tested. To further explain this individual variability, a more rigorous analysis should be undertaken to accurately relate the formants to the length of the vocal tract and since the study of Ikeda and Ishii (2008) only examined a single cow, caution should be taken when applying these findings to the cattle population level. Ikeda and Ishii (2008) found that the first six formant values of a single Korean Native Cow were 309, 623, 940, 1283, 1606 and 1907 Hz, respectively. Whether there are differences in formant values associated with the feeding routine needs clarification using a greater number of animals.

In goats, a comparison of food-anticipation and food-frustration calls has been completed to determine how call parameters change when situations are both positively and negatively valenced (Briefer *et al.*, 2015b). In the positive feeding situation, vocalisations were characterised by a lower F0 range and smaller frequency modulations (Briefer *et al.*, 2015b) suggesting these parameters are more influenced by valence. If a similar experiment were to be completed in dairy cattle, there is potential to determine which cattle in the milking herd perceive supplementary feeding at the milking unit as positive and negative, as well as why. Further, different food types (both pasture and mixed ration) could be used to determine which ones the cattle find most desirable and motivating, which could assist in enticing cows in voluntary cow traffic systems. In the study on goats a classical conditioning paradigm was adopted, in which goats were enticed with vision of a food bucket (the conditioned stimulus). To collect anticipatory calls, they viewed the food for 1 min, and to measure calls of frustrative non-reward only one of the two goats received the food during the proceeding 4 min. Alternative measures of frustration could involve fully preventing reward access to all of the test subjects for the given trial, or further increasing the anticipatory period. As cattle are highly gregarious, it is recommended that they instead be tested in a group setting so calls of frustration are not confounded with calls of contact. Similar to Valizadeh *et al.* (2008) a variety of food types could be implemented to determine which feeding method is the least frustrating and stressful to cattle during drying off, as apparent in their vocal features. Physiological parameters such as heart rate and behavioural parameters such as movement and activity levels should also be measured to confirm how arousing these feeding situations are.

Painful husbandry procedures

Vocalisations are one of the most apparent behavioural changes caused by nociception or discomfort in cattle and in previous studies they have been quantified as a method of assessing how cattle react to different routine husbandry procedures (Watts and Stookey, 1999; Grandin, 2001). Vocalisation rate and/or the proportion of vocalisers in a herd have been reported in calves subject to dehorning, with and

without non-steroidal anti-inflammatory drugs (NSAIDs) (Stilwell *et al.*, 2008), calves experiencing hot iron disbudding with and without sedation and with NSAIDs (Caray *et al.*, 2015), calves exposed to restraint and hot iron branding (Watts and Stookey, 1999), bulls subject to electro-ejaculation (Whitlock *et al.*, 2012) and adult bulls, steers or cows before slaughter (Grandin, 1998 and 2001). In general, these studies have indicated that higher vocal rates and a greater number of animals vocalising relate to a more stressful or painful farming procedure.

There is high inter-cow variability in the propensity to vocalise in response to pain and acute stress, with Whitlock *et al.* (2012) showing how 56% of bulls vocalised in response to electro-ejaculation compared with none vocalising during a control period. Further, Watts and Stookey (1999) showed how only 34% of calves vocalised in response to hot iron branding, and Grandin (1998) showed how only 10% of cattle vocalised in the abattoir setting even after observable aversive events including electric prodding, being placed on the stunning box floor, during missed captive bolt stunning, or during excessive restraint. In addition, Grandin (2001) showed how at 42% of abattoirs tested, only 0% to 1% of cattle vocalised during handling and stunning. Although the studies of Stilwell *et al.* (2008) and Caray *et al.* (2015) both show elevated cortisol levels post dehorning and disbudding, respectively, indicating that the procedures were indeed stressful and painful, Stilwell *et al.* (2008) reported no vocalisations from any of the male or female calves tested. In contrast, Caray *et al.* (2015) showed how during the disbudding procedure and the following 15 min, even calves with NSAID's were significantly more vocal than those sham-disbudded, vocalising up to 7 h post treatment, suggesting that the pain is long lasting. These differences in findings again reflect the high inter-animal variability in vocal behaviour indicating how in addition, behavioural and physiological parameters such as activity levels, heart rate and IR thermography should be taken for a reliable measure of pain, in particular, that related to the sympatho-adrenomedullary response. It further highlights how additional research should be conducted to determine the specific characteristics of the vocal animals such as age, breed, sex, weight and social dominance to give reason for the variability in the propensity to vocalise in response to pain. Already significant breed effects have been found with Charolais calves more vocal than their Holstein-Friesian conspecifics (Caray *et al.*, 2015).

Vocalisations are salient and easy to collect. Although the occurrence of vocal animals in a herd may be low, any form of vocalisation may be representative of the level of pain or fear-induced stress that a procedure can cause to the herd. As prey animals, cattle tend to mask signs of pain or weakness to avoid detection by predators. Thus, the relative infrequency of cattle vocalisations may emphasise how when they are produced, they are indeed biologically important. This has been suggested by Grandin (2001) who concluded that the occurrence of >5% of the animals vocalising in any herd is indicative of handling and

equipment problems in abattoirs. Thus, understanding of this vocal behaviour may become useful in examining the welfare of cattle herds at the large scale. For this to be possible, extensive research should also be conducted to analyse the temporal and spectral features of these pain-induced vocalisations. Already in piglets vocalisations have been used to evaluate pain levels during the different phases of castration (Weary *et al.*, 1998; Puppe *et al.*, 2005). To our knowledge, only Watts and Stookey (1999) have examined the spectral components of calls produced by cattle in painful situations. Beef calves subject to branding produced calls of a higher maximum frequency, a greater frequency range and higher relative intensity compared with those unbranded (Watts and Stookey, 1999), which is in alignment with arousal-mediated changes to source parameters as previously highlighted. Vocalisations are advantageous in that they may reveal multi-dimensional information about an animal's arousal and valence (Briefer, 2012). So, if the vocal correlates of emotion in cattle are mapped out, the vocalisations in response to different husbandry procedures could be compared, to determine which most require pain alleviation or farming intervention. In addition, vocalisations do not rely on a degree of restraint and invasiveness which traditional pain measures such as heart rate or cortisol encounter suggesting that they could be more applicable to the farming context.

Conclusions

This review provides the current knowledge in the field of cattle bioacoustics, with a focus on dairy cattle, including the contexts of calf separation and weaning, social isolation, oestrus, feeding and during painful husbandry procedures. Further, we have highlighted knowledge gaps and opportunities that exist in this area for additional research to enable improved animal welfare and production efficiency. A number of conclusions can be drawn from the literature presented on this topic. It has been shown that vocalisations can encode information about the age, reproductive, physiological and emotional state of the caller, evidenced by source and filter parameters. It has also been shown that cattle have high inter-animal variability in their vocal features suggesting that vocalisations contribute to individual identity within large herds. In this regard, there is potential for vocalisations to be interpreted to assess how cattle are coping with their farming environment. Further research should seek to fill key gaps in knowledge identified from this review including the temporal and spectral characterisation of calls in specific farming contexts, and with reference to the source-filter theory map out the vocal correlates associated with arousal and valence in dairy cattle breeds. Multiple farming situations should be observed to determine the extent to which vocal correlates of arousal and valence can be used across contexts and both low- and high-frequency calls should be studied to distinguish how the information encoded differs. Finally, playback studies should be undertaken to determine herd responses to certain calls and the biological relevance of vocal behaviour in the domestic setting.

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