Mother--Offspring Recognition via Contact Calls in Cattle, Bos taurus

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Recommended Citation

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KEYWORDS

ABSTRACT

Individual recognition in gregarious species is fundamental in order to avoid misdirected parental investment. In ungulates, two very different parental care strategies have been identified: 'hider' offspring usually lie concealed in vegetation whereas offspring of 'follower' species remain with their mothers while they forage. These two strategies have been suggested to impact on mother-offspring vocal recognition, with unidirectional recognition of the mother by offspring occurring in hiders and bidirectional recognition in followers. In domestic cattle, *Bos taurus*, a facultative hider species, vocal communication and recognition have not been studied in detail under free-ranging conditions, where cows and calves can graze freely and where hiding behaviour can occur. We hypothesized that, as a hider species, cattle under these circumstances would display unidirectional vocal recognition. To test this hypothesis, we conducted playback experiments using mother-offspring contact calls. We found that cows were more likely to respond, by moving their ears and/or looking, turning or walking towards the loudspeaker, to calls of their own calves than to calls from other calves. Similarly, calves responded more rapidly, and were more likely to move their ears and/or look, turn or walk towards the loudspeaker, and to call back and/or meet their mothers, in response to calls from their own mothers than to calls from other females. Contrary to our predictions, our results suggest that mother-offspring vocal individual recognition is bidirectional in cattle. Additionally, mothers of younger calves tended to respond more strongly to playbacks than mothers of older calves. Therefore, mother responses to calf vocalizations are at least partially influenced by calf age.

Recognition plays an important role in the social lives of many mammals, allowing them to identify the species, sex, individuality and social status of other individuals (Tibbetts & Dale, 2007). It is crucial, in particular, for the survival of dependent offspring. Mothers that live and breed in large, high-density colonies, where the risk of misdirected parental care is high, need selective strategies in order to restrict care exclusively to their own offspring and hence maximize their developmental rate and chances of survival (Nowak, Porter, Lévy, Orgeur, & Schaal, 2000; Trivers, 1972). Sophisticated recognition strategies are seen in many social mammals where, for example, mother and offspring are able to use a refined parent-offspring vocal recognition process to find each other even after long periods of time out of sight (e.g. fallow deer, *Dama dama*: Torriani, Vannoni, & McElligott, 2006; walrus, *Odobenus rosmasus rosmasus*: Charrier, Aubin, & Mathevon, 2010; Australian sea lion, *Neophoca cinerea*: Pitcher, Harcourt, & Charrier, 2010; goats, *Capra hircus*: Briefer & McElligott, 2011).

In gregarious species, the recognition process among familiar and unfamiliar conspecifics, and in particular between mother and offspring, involves vision (Alexander, 1977; Coulon, Deputte, Heyman, & Baudoin, 2009; Coulon, Deputte, Heyman, Richard, & Delatouch, 2007), olfaction (Alexander, 1977, 1978) and audition (Alexander & Shilito, 1977). While vision is only useful in open habitats, and olfactory cues only permit identification at short range (<1m; Alexander & Shilito, 1977; Lickliter & Heron, 1984; Lingle, Rendall, & Pellis, 2007), vocalizations are potentially useful over both short (sheep, *Ovis aries*: Sèbe, Nowak, Poindron, & Aubin, 2007) and long distances, and in both open (Atlantic walrus: Charrier et al., 2010) and densely vegetated habitats (fallow deer: Torriani et al., 2006). Therefore, vocal communication appears to be a key factor for long-distance mother-offspring recognition in gregarious species.

Ungulates give birth to precocial offspring that are morphologically well developed, and potentially able to follow their mother shortly after birth (Broad, Curley, & Kaverne, 2006). Newborns show rapid development of interindividual recognition, and mothers usually care exclusively for their own young (Nowak et al., 2000). Two main strategies for avoiding predators in the first few weeks of life have been observed in ungulate newborns: 'hiding' and 'following' (Fisher, Blomberg, & Owens, 2002; Lent, 1974). Hider offspring do not follow their mothers and spend most of their time hidden and silent in vegetation in order to avoid potential predators. Mothers usually forage at least 100 m away from their offspring's hiding place and return intermittently to nurse the offspring. Because hider offspring have sedentary habits and mothers bring milk to their offspring, energetic expenditure for them is minimal and they grow quickly (Fisher et al., 2002). By contrast, follower offspring are able to follow their mothers and therefore they rely on maternal and group defence to avoid predators. Follower offspring are potentially able to suckle more often because they spend most of the time near their mothers (Fisher et al., 2002; Jensen, 2001; Lent, 1974).

It is possible that the hiding and following strategies may have affected the vocal recognition process between mothers and offspring, because of the large differences in the way that they interact (rate and duration of interactions), as well as in the way they initiate interactions during the first weeks of life. To initiate nursing bouts, females of hider species remember the approximate locations of their hidden offspring (Lent, 1974; Torriani et al., 2006), and we might therefore expect that there is little selection pressure on offspring to produce individualized calls or on the mother to identify her offspring's calls. Additionally, offspring mainly stay silent to avoid detection by predators. However, to nurse, offspring should be able to identify their own mother by her calls in order to avoid leaving their hiding place, and unnecessarily exposing themselves to predation risk, in response to calls from adult females other than their mother. Therefore, hider species are expected to display low vocal individuality in newborn offspring and strong individuality in mother calls, as well as a unidirectional recognition process of mothers by offspring, at least in the early stages of the offspring's life (while they hide; Torriani et al., 2006). By contrast, follower species live surrounded by many conspecifics (Fisher et al., 2002; Jensen, 2001; Lent, 1974). Consequently, development of strong vocal individuality in both mothers and offspring is predicted, in order to avoid misdirected maternal care (e.g. sheep; Sèbe et al., 2007; reindeer, *Rangifer tarandus*: Espmark, 1971).

Cattle are a facultative hider species; when calves are artificially provided with high vegetation, they spend time using it for concealment, suggesting that the absence of hiding behaviour in domesticated cattle may largely be a result of the lack of cover (Bouissou, Boissy, Le Neindre, & Veissier, 2001; Jensen, 2001; von Keyserlingk & Weary, 2007; Langbein & Raasch, 2000; Watts & Stookey, 2000). Isolation to give birth is an important preliminary step in the formation of the mothereoffspring bond, because it protects the dyad from disturbances by other cows and predators, and facilitates early interactions without interference (Tucker, 2009). The modern artificial environment in farms is likely to suppress or alter much maternal behaviour in domestic cattle. Despite this, a preference for isolation and a semblance of territoriality for a small area are still evident (Arave & Albright, 1981).

Playback studies in cattle have shown that calves are able to identify their own mother's vocalizations (Barfield, Tang-Martinez, & Trainer, 1994; Marchant-Forde, Marchant-Forde, & Weary, 2002). However, there has been no definitive test of maternal recognition of calf vocalizations. One study reported that dairy cows display a poor ability to respond preferentially to their own calves' calls (Marchant-Forde et al., 2002), but this evidence comes from experiments conducted in the artificial conditions of a dairy farm. In Marchant-Forde et al.'s (2002) study, mothers were separated from their calves within 24 h of birth, and playbacks were performed indoors. It therefore remains unknown whether parent-offspring recognition in this species under more natural conditions is uni- or bi-directional.

In this study, we present the first experimental test of bidirectional individual recognition in free-range cattle, where cows and calves graze freely in a large area, where hiding behaviour can occur and mothers and offspring interact

over a prolonged period of months. We investigated the ability of cattle to use vocal cues of individuality present in contact calls (Padilla de la Torre, Briefer, Reader, & McElligott, 2015) in order to distinguish their own calf/ mother from other members of the herd. We recorded and played back high-frequency contact calls (HFCs, produced with the mouth fully opened and characterized by high fundamental frequencies) from cows and calves in free-ranging conditions, without artificial manipulation or isolation, and observed behavioural responses by kin and familiar nonkin.

METHODS

Study Site and Subjects

The study was carried out with two crossbred beef cattle herds situated in two separate fields (herd 1: N = 21 adult multiparous females; herd 2: N = 23 adult multiparous females) on a farm in Radcliffe on Trent (52°93′72″N, 1°06′09″W), Nottinghamshire, U.K., from February to August 2010. The two fenced fields were approximately 52 ha (herd 1) and 23 ha (herd 2), and were separated by a road (3 m wide). Recordings and playbacks were carried out in each field independently. For the playback experiments, vocalizations of 42 individuals (cows: N = 20, 100 vocalizations; calves: N = 22, 66 vocalizations) were tested. Playbacks of calf calls to cows were all carried out between 5 and 10 days after the calf recordings were made. All individuals included in this study were free to roam in the fields with fresh grass and water ad libitum. Calves included in this study were all born between February and August 2010, and all were sired by the same bull. The two herds were kept separately in their fields without interchange of animals, except for two cows, not used in the experiment, which were transferred from one field to the other between the time we made the recordings and playbacks. All the calves included in the study were kept all year long in the same fielFd with their mothers.

Sound Recording

Recordings of individual cow and calf contact calls were made opportunistically (i.e. when cattle spontaneously vocalized) between 0800 and 1700 hours from February to August 2010. Vocalizations were produced when the mother was in another part of the field and were followed by reunion with the calf and nursing. Similarly, calf calls were always produced when their mothers were in another part of the field and were followed by reunion with the mother and suckling. Calls were recorded at distances of 10-30 m from the vocalizing animal with a Sennheiser MKH70 directional microphone, connected to a Maranzt PMD660 digital recorder (sampling rate 44.1 kHz). Accurate, individual identification was done from specific ID tags placed in the animals' ears by the farmer and by visual recognition of coat markings. Because of the farm records, the exact ages of the calves at the moment when calls were recorded were known. Playbacks were never conducted more than 10 days after the recordings were carried out, in order to minimize age-related differences between the calls played back and the actual calls of the calf at the time of the playbacks.

Playback Sequences

Vocalizations were uploaded to a computer at a sampling rate of 44.1 kHz and saved in a WAV format at 16-bit amplitude resolution. We used the Praat v.5.1.44 DSP Package (Boersma & Weenink, 2009) to build the sequences for the playback experiments. Calls were individually visualized using spectrograms in Praat (FFT method, window length = 0.1 s, time steps = 100, frequency steps = 250, Gaussian window shape, dynamic range = 40 dB). For both cows and calves, only HFCs (as opposed to low-frequency calls (LFC) produced with the mouth closed or only partially opened; Padilla de la Torre et al., 2015), with low levels of background noise, were considered for the playback experiments. HFCs were used instead of LFCs to ensure audibility, because LFCs are lower in amplitude than HFC, and the trials were carried out in an open field at relatively long distances (10-30 m).

Because cows and calves sometimes produced single calls (not in sequence), it was not always possible to acquire natural sequences for all individuals tested. Furthermore, because our aim was to test whether mother and offspring recognize each other individually using the acoustic structure of calls (as opposed to other parameters such as call rate or intercall intervals), we prepared standardized sequences for cows and calves composed of the same number of calls and silence intervals (e.g. Briefer & McElligott, 2011). Call sequences prepared for the playback experiments were designed to reflect natural sequences. To this end, the average silence interval between each call and the total number of mother-offspring contact calls present in natural sequences were first calculated using 31 sequences from

20 cows and 19 sequences from 12 calves (age range 10-184 days old) from the study population. The natural number of calls per sequence observed in the field was 5.32 ± 0.42 (mean ± SEM; range 1-12 calls) for cow calls and 2.89 ± 0.93 (range 1-4 calls) for calf calls. The natural silence interval was 2.71 ± 2.55 s between cow calls and 2.83 ± 2.40 s between calf calls. To match these averages, sequences of five cow calls interspersed with 2.7 s of silence intervals were created for the playbacks to calves (see audio file S1 in the Supplementary material for an example), while sequences of three calf calls interspersed with 2.8 s of silence intervals were created for playbacks to cows (see audio file S2 in the Supplementary material for an example). To avoid pseudoreplication, all playback sequences included different HFC calls from each cow and calf (McGregor, 1992). They were preceded by 5 min of silence to allow the experimenter to start the playback and move away from the loudspeaker. Using Goldwave (version 5.11; Craig, 2000), we rescaled each recorded vocalization to match the root mean square (RMS) amplitude of the different vocalizations included in the sequences at the same output level. The prepared sequences were stored as mp3 files on a CD at a sampling rate of 44.1 KHz and a bit rate of 224 kbps. To verify that the acoustic structure of the sequences played back were not affected by the audio file format change (from wav to mp3), each sequence was inspected visually (spectrum and spectrogram) and by ear in both file formats (wav and mp3 files) using Praat.

Playback Procedure

All playback trials were performed opportunistically in the field (i.e. when mothers and their calves were separated by at least 30 m from each other, not in direct line of sight, and cover for experimenters and equipment was available). All playback experiments were carried out without any artificial isolation or manipulation of the animals, in order to cause the least disturbance possible. A total of 42 playback trials were carried out, with a maximum of two playback trials per day (always one cow and one calf), and at least 3-4 h between trials allowing the animals to return to their normal activities. During each playback trial, the behavioural responses of three individuals were filmed simultaneously. The 'Own' individual was the mother or offspring of the individual whose calls were being played in that particular trial. The 'Others' were the two nearest individuals in the field that were not the mother or offspring of the calf or cow whose calls were being played. Each Own individual (cows, $N = 22$; calves, $N = 20$) was tested once with Own calls. The responses of Other cows and calves were opportunistically scored (cows, $N = 44$; calves, $N = 40$), depending on their proximity to the animal receiving the Own call (5-10 m on average). On average, each cow was included as the Other individual 1.40 ± 0.95 times (mean ± SD; range 0-3 times), and each calf 1.31 ± 1.12 times (mean ± SD; range 0-2 times). Calls of calves played back to Own mothers were from animals that were on average 70.56 ± 8.53 days old, and those played back to Other cows were from calves that were 69.51 ± 6.56 days old. Similarly, calves tested with Own mother calls were on average 64.10 ± 7.62 days old, whereas those tested with Other cow calls were on average 69.77 ± 6.69 days old.

We played back call sequences using a Skytronic TEC076 portable speaker system (frequency response 50-20 kHz ± 3 dB). Because the fields were large (52 ha and 23 ha), individuals were usually widely separated. This allowed us to test cows and calves when their own offspring or mothers were at least 30 m away and not in direct line of sight, to avoid auditory and visual contact as much as possible. The loudspeaker was hidden with a camouflage tent or in the bushes at the edge of the field, 10-30 m from the subject. The sequences were played at an intensity estimated to be normal for cattle (mean ± SD: cows, 93.79 ± 0.47 dB; calves, 93.95 ± 0.41 dB; measured at 1 m using a sound level meter, *C* weighting; SoundTest-Master, Laserliner, Warwick, U.K.). All playback trials were initiated when the individuals (Own and Other) were involved in normal activities (i.e. grazing, standing or lying down) and looking away from the speaker.

Each trial was filmed by two experimenters with digital video cameras (Sony DCR-SR58 and Panasonic SDH-H80), hidden 5-20 m from the subjects. One experimenter recorded the behavioural response of Own individuals. The second experimenter first selected the sequences to play and then moved away from the loudspeaker during the 5 min preplayback silence, in order to position herself next to the second video camera and to record the response of the two nearest Other individuals. Playback trials were conducted when no people (farmers/walkers) or food (other than grass) were present near the loudspeaker.

Behavioural Responses

The behavioural responses of cows and calves were assessed from videos of the playbacks. For each tested individual, we measured the presence (yes or no) of each of the four following behavioural measures (in order of

response strength): (1) ear movements and/or looking towards loudspeaker; (2) standing up (when the subject was lying down at the beginning of the playback) or turned towards loudspeaker (when the subject was standing at the beginning of the playback); (3) walking towards loudspeaker; (4) calling back and/or meeting Own mother/calf. Behavioural responses were clustered in some cases (1, 2 and 4) because they often occurred simultaneously. Additionally, the latency for the first behavioural response to occur was recorded as the time between the beginning of the first call in the playback sequence and the first behavioural response (i.e. one of the four above-mentioned behavioural measures). All behavioural responses were scored by an observer who was blind as to which subject was Own and which was Other.

Statistical Analysis

Differences in each behavioural response (behavioural measures 1-4) between treatments (Own versus Other) were examined using binomial generalized linear mixed models (binomial GLMMs; logit link function; one model per behavioural response) for both cows and calves. When analysing responses to playbacks of calf calls to cows, the ages (number of days from birth until the moment of the trial) of the calf providing the playback and of the calf of the mother whose response was being recorded were included as covariates in the models, together with the date of the playback. With binomial data, and relatively small sample sizes, it was not possible to test all possible interaction terms (parameter estimates would not converge). Thus, we tested only the main effects, plus the interaction between treatment and the age of the calf of the mother whose response was being recorded. When calves were receiving the playback, their own age was included, as well as the date of the playback. All models included trial as a random effect. GLMMs were analysed using R v 2.13.0 (R Development Core Team, 2009). For each model, we assessed the statistical significance of the factors by comparing the model with and without the factor included using likelihood-ratio tests (LRT). The LRT statistics follow a chi-square distribution with degrees of freedom equal to the difference in the number of parameters. Additionally, differences between the latency to react to Other and Own playbacks were analysed using a Wilcoxon signed-rank test. This analysis was carried out using SPSS v 20 (SPSS Inc, Armonk, NY, U.S.A.). All results are presented as means ± SEM.

Ethical Note

Animal care and all experimental procedures were carried out in accordance with the ASAB/ABS (2012) guidelines. Cattle included in this study were habituated to the presence of farmers and the researchers. The habituation to people allows for approaches close enough to conduct playback experiments (Pitcher, Briefer, & McElligott, 2015). During the recordings, mothers and calves were never manipulated or isolated. Likewise, playbacks were carried out opportunistically when mothers and calves were spontaneously separated (in different parts of the field). All mothers accepted their calves for nursing after the playbacks.

RESULTS

Cow Behavioural Responses to Playbacks

For three of the four types of behavioural response measured, mothers were significantly more likely to respond to calls from their own calves (Own) than to calls from calves belonging to other cows (Other; Fig. 1, Table 1).

There was an effect of the age of the calf belonging to the cow, on three of the four behavioural responses, with cows overall being more likely to respond to playbacks (Own and Other) if their own calves were younger (Table 1, Fig. 2). There was also an interaction between the age of a cow's calf and the playback treatment for three of the behavioural responses (Table 1). There was no significant effect of the age of the calf whose calls were used for the playback, or of the date when the playbacks were carried out, on any of the behavioural responses (Table 1).

Calf Behavioural Responses to Playbacks

In the four types of behavioural response measured, calves were significantly more likely to respond to calls from their own mothers than to calls from other cows (Other; Fig. 3, Table 2).

There was no significant effect of calf age on the probability that it would show any of the observed behaviours in response to the playbacks, nor was there an interaction between the playback treatment (Own or Other) and age. Similarly, there was no significant effect of the date when the playbacks were carried out (Table 2).

Latency of Behavioural Responses to Playbacks

Calves reacted faster to playbacks of their own mothers (Own) than to other cows (Other; Fig. 4; Wilcoxon signed-rank test: $Z = -2.93$, $N = 13$, $P = 0.003$). By contrast, in cows, there was no difference in the latency to react in response to playbacks of calls from Own and Other calves (Wilcoxon signed-rank test: $Z = -1.858$, $N = 15$, $P = 0.063$).

DISCUSSION

We investigated whether mother-offspring individual vocal recognition occurs in cattle using playback experiments. The ability of mother and offspring to identify each other is thought to be linked to parental care and predator avoidance strategies in ungulates (Torriani et al., 2006). The general consensus is that cattle are a hider species (Bouissou et al., 2001; von Keyserlingk &Weary, 2007; Tucker, 2009; Watts & Stookey, 2000), and we accordingly predicted (Lent, 1974; Torriani et al., 2006) that unidirectional vocal recognition of mothers by calves would be evident. Our results support previous studies (Barfield et al., 1994; Marchant-Forde et al., 2002), which suggested that calves can distinguish the calls of their own mothers from those of other cows. Our results also reveal for the first time that cows are also able to recognize the calls of their own calves. Contrary to our initial prediction, we thus found bidirectional and not unidirectional mother-offspring recognition in cattle, which is more similar to the recognition process observed in follower species (Espmark, 1971; Sèbe et al., 2007) than in other hider species (e.g. fallow deer: Torriani et al., 2006). Additionally, our findings suggest that responses to vocalizations are partially influenced by own calf age, with cows overall being more likely to respond to playbacks of their own calf when they were younger. Overall, our findings show that there is bidirectional individual recognition by vocal cues between mothers and offspring in domestic cattle. Our study highlights the need for more comparative studies using domestic and closely related wild species since they may yield important insights into the evolution of vocal communication, and into the genetic and environmental changes that have occurred throughout domestication (Price, 1984; Bradley & Magee, 2006; Zeder, 2012).

Individual bidirectional vocal recognition displayed by cows and calves could reflect the fact that hiding behaviour in domestic cattle is relatively weak (Bouissou et al., 2001; Vitale, Tenucci, Papini, & Lovari, 1986). Indeed, the period of hiding (or isolation if hiding is not possible) appears to be rather short: 3 weeks after birth, calves spend most of their time in small groups with other offspring of similar ages (Bouissou et al., 2001; Vitale et al., 1986). The classification of species as hiders or followers in domestic settings is not clear cut, because their normal social behaviours may be markedly constrained. Domestic cattle have commonly been classified as a hider species because, although cattle in modern farming environments often do not have the opportunity to hide their young, when cover is provided, hiding behaviour has been observed (Langbein & Raasch, 2000). Similarly, domestic goats, in which bidirectional vocal recognition has also been observed (Briefer & McElligott, 2011), are classified as a hider species, despite the fact that some researchers have reported that they do not display hiding behaviour under some domestic settings (Rudge, 1970; Tennessen & Hudson, 1981). We hypothesize that early social integration with other conspecifics observed in both cattle and goats has favoured bidirectional recognition in these species.

The wild ancestors of domestic cattle are extinct (Bradley & Magee, 2006). However, feral populations of ancient cattle breeds and other closely related bovid species might provide evidence of the antipredator strategy that existed before this species was domesticated. For example, Chillingham cattle offspring are reported to hide (Hall, 1986), and Maremma cattle have been observed displaying both hider and follower strategies in the early weeks of life, depending on the availability of cover (Vitale et al., 1986). It may be more generally true that attempts to divide ungulates into hiders and followers, and to make predictions about mother-offspring recognition based on this dichotomy without considering intermediate behavioural patterns (Ralls, Kranz, & Lundrigan, 1986), are flawed. Extensive research about maternal behaviour in captive ungulates (Ralls et al., 1986; Ralls, Kranz, & Lundrigan, 1987) has led to the conclusion that the hider-follower dichotomy is an overly simplistic characterization of the mother-offspring predator-avoiding strategy, which is not effective in describing the whole range of behavioural patterns adopted by ungulates.

Figure 1. Proportion of cows responding to playbacks of their Own or a different (Other) calf. Four different behavioural responses were recorded, and these are presented in order of the strength of the response (i.e. from ear movement/look towards the speaker to calling back/meeting calf), with the strongest response on the right (binomial GLMM: *$P < 0.05$; *** $P < 0.001$). Error bars are 95% confidence intervals from the binomial distribution.
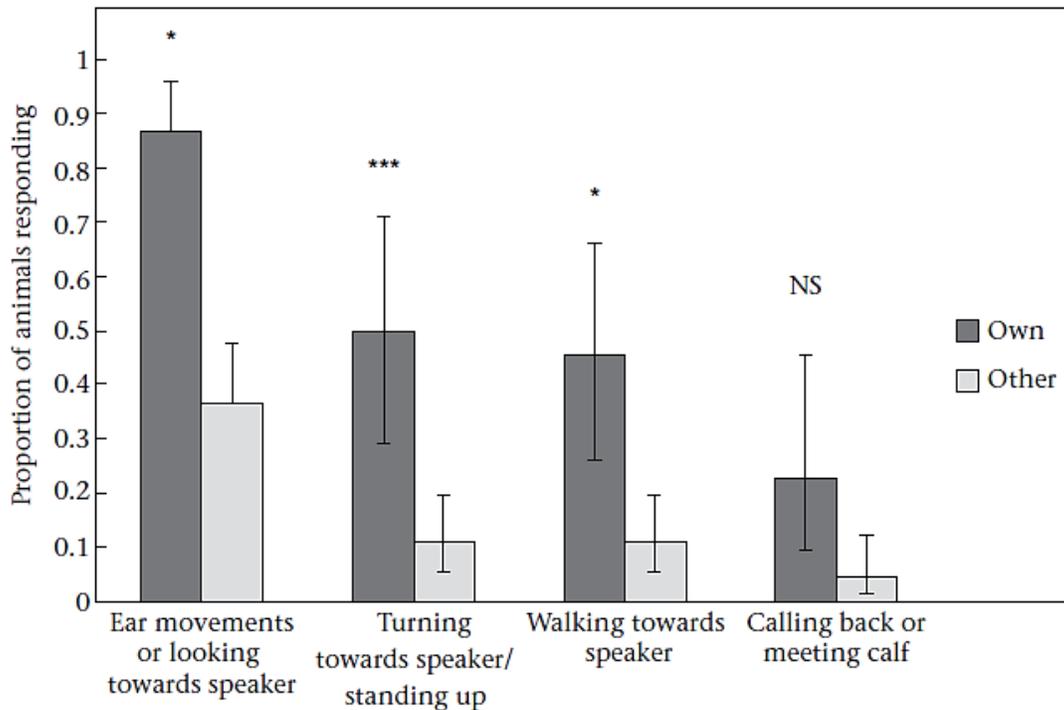

Table 1. Results of binomial generalized linear mixed models testing the effect of the playback treatment (Own or Other), the age of the calf providing the playback call and the interaction between the two on the probability that cows would respond (four behavioural responses)

Effect	Ear movements or looking towards speaker	Turning towards speaker/standing up	Walking towards speaker	Calling back or meeting calf
Playback treatment (Own vs Other cows)	$X^2_1 = 5.95$	$X^2_1 = 7.43$	$X^2_1 = 5.85$	$X^2_1 = 2.69$
	$P = 0.014$	$P < 0.001$	$P = 0.015$	$P = 0.100$
Age of calf belonging to cow	$X^2_1 = 1.26$	$X^2_1 = 12.39$	$X^2_1 = 13.71$	$X^2_1 = 5.69$
	$P = 0.260$	$P < 0.001$	$P < 0.001$	$P = 0.017$
Age of calf providing playback	$X^2_1 = 0.02$	$X^2_1 = 0.17$	$X^2_1 = 0.09$	$X^2_1 = 1.75$
	$P = 0.883$	$P = 0.677$	$P = 0.755$	$P = 0.185$
Playback treatment * Age of calf belonging to cow	$X^2_1 = 6.09$	$X^2_1 = 10.34$	$X^2_1 = 9.39$	$X^2_1 = 1.81$
	$P = 0.013$	$P = 0.001$	$P = 0.002$	$P = 0.177$
Date of playback	$X^2_1 = 2.26$	$X^2_1 = 0.43$	$X^2_1 = 1.46$	$X^2_1 = 0.26$
	$P = 0.131$	$P = 0.511$	$P = 0.226$	$P = 0.604$

The age of the calf belonging to the Own or Other cow and the date of the playback trial were tested as covariates. Because Own and Other animals were tested with playbacks simultaneously, the playback trial was fitted as a random effect.

Figure 2. The effect of the age of a cow's calf on the likelihood that she would respond to playbacks of calls from Own and Other calves. Data shown are the mean age ± SEM of the calves belonging to tested cows, which either did or did not respond to playbacks, for the four behavioural measures. The behavioural responses are presented in order of strength. (a) Ear movements or looking towards speaker. (b) Turning towards speaker or standing up. (c) Walking towards speaker. (d) Calling back or meeting their own calf (binomial GLMM).
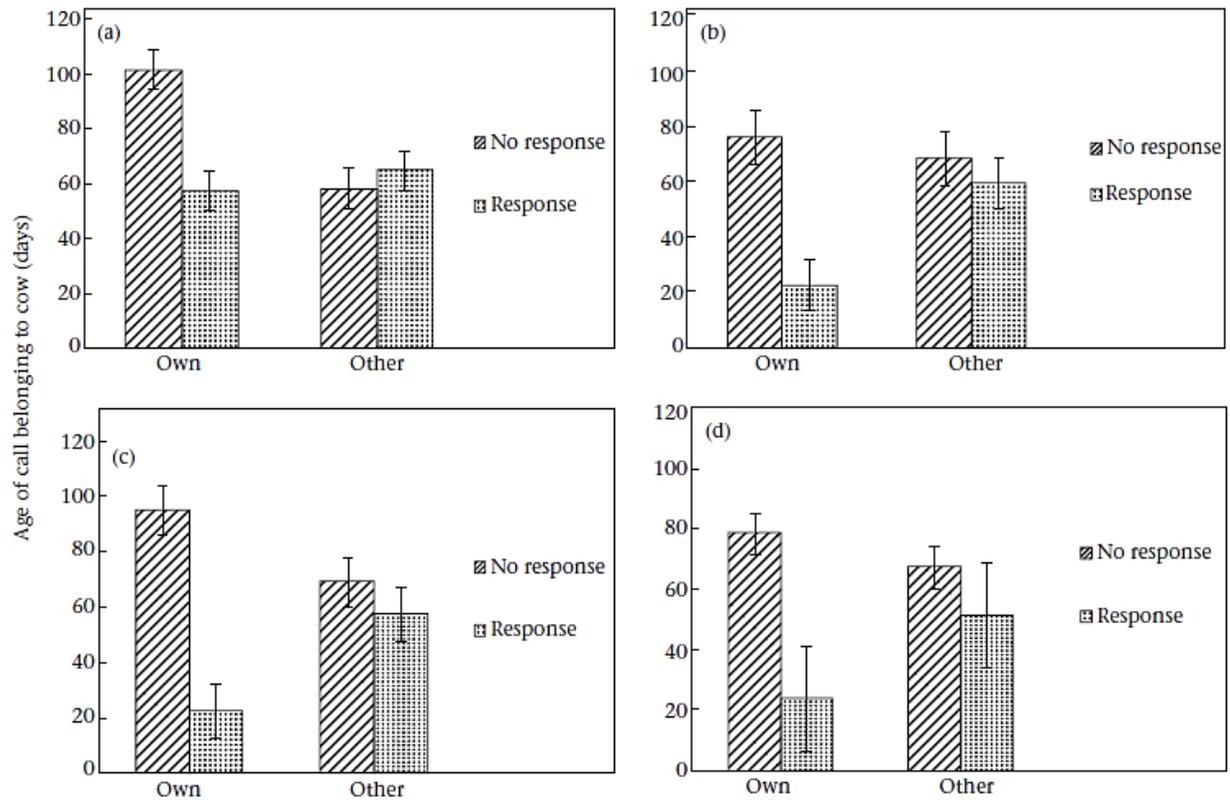

Irrespective of the hider-follower dichotomy, when considering the relationship between the extent of vocal individuality observed in a species and the behavioural strategies exhibited by that species in its evolutionary past, it is important to remember that detectable individuality does not necessarily need to 'evolve' as an adaptive trait. Some degree of individuality must exist in all species that vocalize, as a necessary consequence of the unique combination of genotype and environment experienced by each individual. These combinations will generate differences between individuals in vocal-tract morphology, and hence in the acoustic properties of vocalizations. Similarly, the ability to detect individuality in conspecifics may arise as an inevitable consequence of selection on sensory and cognitive capabilities caused by the benefits of being able to interpret other subtle differences in sounds present in the environment. Hence, it may be the case that individuality in mother-offspring cattle contact vocalizations (Padilla de la Torre et al., 2015), and bidirectional recognition, has not been shaped by any selective pressures associated with the behavioural strategy employed by mothers and offspring in the ancestors of modern cattle.

Our results show that the age of the calf is an important factor in determining a cow's response to playbacks. Mothers of younger calves tended to respond more strongly than mothers of older calves to playbacks in general. The mother-offspring relationship weakens over time as the calf grows and becomes more independent, in modern domestic cattle (von Keyserlingk & Weary, 2007; Thomas, Weary, & Appleby, 2001), in ancient breeds (Maremma cattle; Vitale et al., 1986) and in other ungulates such as American bison, *Bison bison* (Green, 1992). By contrast, even though a decrease in responsiveness in older calves might be expected as they become more independent from their mother with regard to feeding (i.e. weaning period) and less vulnerable to predators (Estes & Estes, 1979; Green, 1992; von

Keyserlingk & Weary, 2007; Thomas et al., 2001; Vitale et al., 1986), there was no reciprocal tendency in this study for older calves to pay less attention to playbacks of their mother's calls. This is probably linked to the strength of the attachment of calves to their mothers, which does not seem to decrease with age even after weaning (Veissier & Le Neindre, 1989).

Figure 3. Proportion of calves responding to playbacks from Own and Other cows. Four different behavioural responses are presented in order of the strength of the response of the observed reaction to the playback trial, from left to right (binomial GLMM: *$P < 0.05$; ***$P < 0.001$). Error bars are 95% confidence intervals from the binomial distribution.
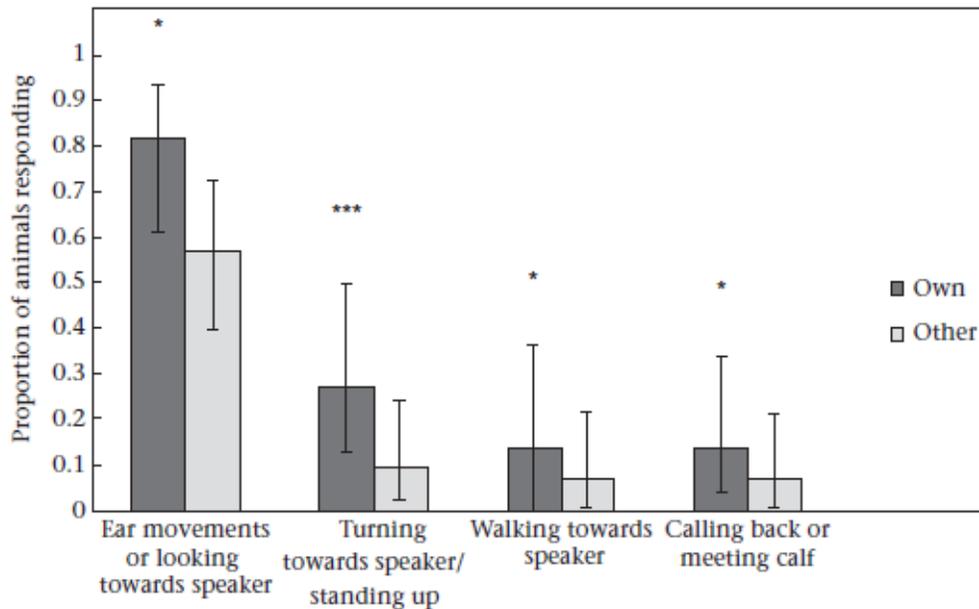

Table 2. Results of binomial generalized linear mixed models testing the effect of the playback treatment (Own or Other cow), the age of the calf, the interaction between the two and the date of the playback trial on the probability that calves would respond (four behavioural responses)

Effect	Ear movements or looking towards speaker	Turning towards speaker/standing up	Walking towards speaker	Calling back or meeting calf
Playback treatment (Own vs Other cows)	$X^2_1 = 4.17$	$X^2_1 = 12.0$	$X^2_1 = 5.98$	$X^2_1 = 5.98$
	$P = 0.041$	$P < 0.001$	$P = 0.014$	$P = 0.014$
Age of calf providing playback	$X^2_1 = 0.05$	$X^2_1 = 0.00$	$X^2_1 = 0.56$	$X^2_1 = 0.56$
	$P = 0.816$	$P = 0.999$	$P = 0.452$	$P = 0.452$
Playback treatment ∗ Age of calf	$X^2_1 = 0.04$	$X^2_1 = 0.09$	$X^2_1 = 0.16$	$X^2_1 = 0.16$
	$P = 0.834$	$P = 0.755$	$P = 0.688$	$P = 0.688$
Date of playback	$X^2_1 = 0.07$	$X^2_1 = 0.06$	$X^2_1 = 0.78$	$X^2_1 = 0.78$
	$P = 0.789$	$P = 0.803$	$P = 0.376$	$P = 0.376$

Because Own and Other animals were exposed to playback simultaneously, playback trial was fitted as a random effect.

Figure 4. Average ± SEM latency to respond in one of four ways (ear movements and/or looking towards speaker; turning towards speaker or standing up; walking towards speaker; calling back and/or meeting their own calf or mother) to playbacks of calls from Own and Other animals in cows and calves (Wilcoxon signed-rank test: **$P < 0.01$).
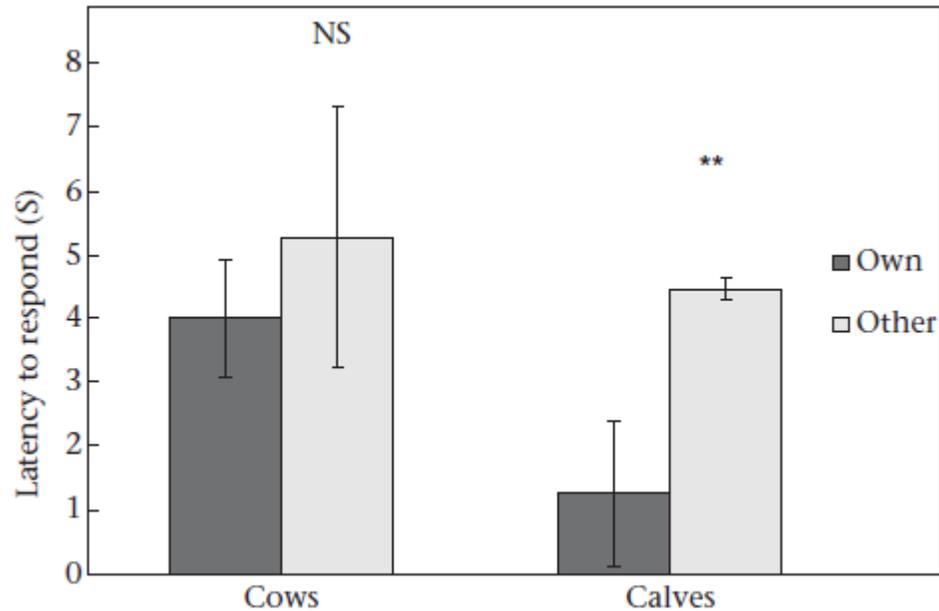
Conclusion

Unlike previous studies aimed at testing cattle mother-offspring recognition (e.g. Barfield et al., 1994; Marchant-Forde et al., 2002), our study was carried out on free-range animals, which were allowed to graze undisturbed outdoors in relatively large fields. Our findings strongly suggest that, under these conditions, individual vocal recognition between domestic cows and calves is bidirectional, and that the response of mothers is at least partly influenced by their own calf's age. Despite cattle being classified as a hider species, the recognition process thus seems more similar to what has been observed in follower species (Espmark, 1971; Sèbe et al., 2007) than in other hider species (Torriani et al., 2006). To understand how and why this pattern exists in a domestic setting, we need a greater understanding of the conditions under which individual recognition has evolved. Detailed comparative behavioural studies of domestic, feral and wild ungulates are needed to determine the differences in parent-offspring interactions within and between species (Ralls et al., 1986, 1987), beyond the simple classification of species as 'hiders' or 'followers' (Fisher et al., 2002; Ralls et al., 1986).

Acknowledgments

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.02.004.

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