



Padilla de la Torre, Monica and Briefer, Elodie F. and Ochocki, Brad M. and McElligott, Alan G. and Reader, Tom (2016) Mother-offspring recognition via contact calls in cattle, *Bos taurus*. *Animal Behaviour*, 114 . pp. 147-154. ISSN 0003-3472

Access from the University of Nottingham repository:

<http://eprints.nottingham.ac.uk/34713/1/Padilla%20et%20al-%20ANBEH-D-15-00825R1complete%20ms.pdf>

Copyright and reuse:

The Nottingham ePrints service makes this work by researchers of the University of Nottingham available open access under the following conditions.

This article is made available under the Creative Commons Attribution Non-commercial No Derivatives licence and may be reused according to the conditions of the licence. For more details see: <http://creativecommons.org/licenses/by-nc-nd/2.5/>

A note on versions:

The version presented here may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the repository url above for details on accessing the published version and note that access may require a subscription.

For more information, please contact eprints@nottingham.ac.uk

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Mother-offspring recognition via contact calls in cattle (*Bos taurus*)

**Mónica Padilla de la Torre^{a,c}, Elodie F. Briefer^{b,c}, Brad M. Ochocki^{a,d}, Alan G. McElligott^b, Tom
Reader^a**

^aSchool of Life Sciences, University of Nottingham, University Park, Nottingham NG7 2RD, UK

^bQueen Mary University of London, Biological and Experimental Psychology, School of Biological and
Chemical Sciences, London, UK

^c*Present Address:* Institute of Agricultural Sciences, ETH Zürich, Universitätstrasse 2, 8092 Zürich,
Switzerland

^d*Present Address:* Department of BioSciences , 6100 Main Street, MS 170, Rice University, Houston,
TX 77005-1827, USA

Corresponding authors:

MPdIT: mopat76@gmail.com

Tel. + 41 44 632 05 85

Fax + 41 44 632 11 28

AGM: a.g.mcelligott@qmul.ac.uk

Tel. + 44 20 7882 3298

Fax + 44 20 8983 0973

TR: tom.reader@nottingham.ac.uk

Tel. + 44 0115 951 3213

Fax + 44 0115 951 3251

24 Individual recognition in gregarious species is fundamental in order to avoid misdirected parental
25 investment. In ungulates, two very different parental care strategies have been identified: “hider”
26 offspring usually lie concealed in vegetation whereas offspring of “follower” species remain with
27 their mothers while they forage. These two strategies have been suggested to impact on mother-
28 offspring vocal recognition, with unidirectional recognition of the mother by offspring occurring in
29 hiders and bidirectional recognition occurring in followers. In domestic cattle (*Bos taurus*), a
30 facultative hider species, vocal communication and recognition has not been studied in detail under
31 free-ranging conditions, where cows and calves can graze freely and where hiding behaviour can
32 occur. We hypothesised that, as a hider species, cattle under these circumstances would display
33 unidirectional vocal recognition. In order to test this hypothesis, we conducted playback experiments
34 using mother-offspring contact calls. We found that cows were more likely to respond, by moving
35 their ears and/or looking towards the speaker and directing their body or walking towards the
36 loudspeaker, to calls of their own calves than to calls from other calves. Similarly, calves responded
37 more rapidly, and were more likely to move their ears and/or look towards the speaker, direct their
38 body or walk towards the loudspeaker, and to call back and/or meet their mothers, in response to
39 calls from their own mothers than to calls from other females. Contrary to our predictions, our
40 results suggest that mother-offspring vocal individual recognition is bidirectional in cattle.
41 Additionally, mothers of younger calves tended to respond more strongly to playbacks than mothers
42 of older calves. Therefore, mother responses to calf vocalisations are at least partially influenced by
43 calf age.

44

45 **Keywords:**

46 Bidirectional individual recognition, Bioacoustics, free-ranging cattle, playbacks, vocalisations

47

48 Recognition plays an important role in the social lives of many mammals, allowing them to identify
49 the species, sex, individuality, and social status of other individuals (Tibbetts & Dale, 2007).
50 Recognition is achieved through several sensory modalities and is crucial in particular for the survival
51 of dependent offspring. Mothers that live and breed in large, high-density colonies, where the risk of
52 misdirected parental care is high, need selective strategies in order to restrict lactation exclusively to
53 their own offspring and hence maximise their developmental rate and chances of survival (Trivers,
54 1972; Nowak, Porter, Lévy, Orgeur, & Schaal, 2000). Sophisticated recognition strategies are seen in
55 many social mammals where, for example, mother and offspring are able to use a refined parent-
56 offspring vocal recognition process to find each other even after long periods of time out of sight
57 (e.g. fallow deer: *Dama dama*, Torriani, Vannoni, & McElligott, 2006; walrus: *Odobenus rosmarus*
58 *rosmarus*, Charrier, Aubin, & Mathevon, 2010; Australian sea lion: *Neophoca cinerea*, Pitcher,
59 Harcourt, & Charrier, 2010; goats: *Capra hircus*, Briefer & McElligott, 2011).

60

61 In gregarious species, the recognition process among familiar and unfamiliar conspecifics, and in
62 particular between mother and offspring, involves vision (Alexander, 1977; Coulon, Deputte,
63 Heyman, Richard, & Delatouch, 2007; Coulon, Deputte, Heyman, & Baudoin, 2009), olfaction
64 (Alexander, 1977, 1978) and audition (Alexander & Shillito, 1977). While vision is only useful in open
65 habitats, and olfactory cues only permit identification at short range (< 1 m; Alexander & Shillito,
66 1977; Lickliter & Heron, 1984; Lingle, Rendall, & Pellis, 2007), vocalisations are potentially useful over
67 both short (sheep, *Ovis aries*; Sèbe, Nowak, Poindron, & Aubin, 2007) and long distances, and in both
68 open (Atlantic walrus; Charrier et al., 2010) and densely-vegetated habitats (fallow deer; Torriani et
69 al., 2006). Therefore, vocal communication appears to be a key factor for long-distance mother-
70 offspring recognition in gregarious species.

71

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

85

86 It is possible that the hiding and following strategies may have affected the vocal recognition process
87 between mothers and offspring, because of the large differences in the way that they interact (rate
88 and duration of interactions), as well as in the way they initiate interactions during the first weeks of
89 life. In order to initiate nursing bouts, females of hider species remember the approximate locations
90 of their hidden offspring (Lent, 1974; Torriani et al., 2006), and we might therefore expect that there
91 is little selection pressure on offspring to produce individualised calls or on the mother to identify her
92 offspring's calls. Additionally, offspring mainly stay silent to avoid detection by predators. However,
93 to nurse, offspring should be able to identify their own mother by their calls in order to avoid leaving
94 their hiding place, and unnecessarily exposing themselves to predation risk, in response to calls from
95 adult females other than their mother. Therefore, hider species are expected to display low vocal
96 individuality in newborn offspring and strong individuality in mother calls, as well as a unidirectional

97 recognition process of mothers by offspring, at least in early stages of the offspring's life (while they
98 hide; Torriani et al., 2006). By contrast, follower species live surrounded by many conspecifics (Fisher
99 et al., 2002; Jensen 2001; Lent 1974). Consequently, development of strong vocal individuality in
100 both mothers and offspring is predicted, in order to avoid misdirected maternal care (e.g. sheep;
101 Sèbe et al., 2007; and reindeer, *Rangifer tarandus*; Espmark, 1971).

102
103 Cattle are a facultative hider species; when calves are artificially provided by with high vegetation,
104 they spend time using it for concealment, suggesting that the absence of hiding behaviour in
105 domesticated cattle may largely be a result of the lack of cover (Bouissou, Boissy, Le Neindre, &
106 Veissier, 2001; Jensen 2001; Langbein & Raasch (2000); von Keyserlingk & Weary, 2007; Watts &
107 Stookey, 2000). Isolation to give birth is an important preliminary step in the formation of the
108 mother-offspring bond, because it protects the dyad from disturbances by other cows and predators,
109 and facilitates early interactions without interference (Tucker, 2009). The modern artificial
110 environment in farms is likely to suppress or alter much maternal behaviour in domestic cattle.
111 Despite this, a preference for isolation and a semblance of territoriality for a small area are still
112 evident (Arave & Albright, 1981).

113
114 Playback studies in cattle have shown that calves are able to identify their own mother's
115 vocalisations (Barfield, Tang-Martinez, & Trainer, 1994; Marchant-Forde, Marchant-Forde, & Weary,
116 2002). However, there has been no definitive test of maternal recognition of calf vocalisations. One
117 study reported that dairy cows display a poor ability to respond preferentially to their own calves'
118 calls (Marchant-Forde et al., 2002), but this evidence comes from experiments conducted in the
119 artificial conditions of a dairy farm. In Marchant-Forde et al. (2002), mothers were separated from
120 their calves within 24 hours of birth, and playbacks were performed indoors. It therefore remains

121 unknown whether parent-offspring recognition in this species under more natural conditions is uni-
122 or bidirectional.

123

124 In this study, we present the first experimental test of bi-directional individual recognition in free-
125 range cattle, where cows and calves graze freely in a large area, where hiding behaviour can occur
126 and mothers and offspring interact over a prolonged period of months. We investigated the ability of
127 cattle to use vocal cues of individuality present in contact calls (Padilla de la Torre, Briefer, Reader, &
128 McElligott, 2015) in order to distinguish their own calf/mother from other members of the herd. We
129 recorded and played back high-frequency contact calls (HFCs, produced with the mouth fully opened
130 and characterised by high fundamental frequencies) from cows and calves in free ranging conditions,
131 without artificial manipulation or isolation, and observed behavioural responses by kin and familiar
132 non-kin.

133

134 Methods

135 *Study site and subjects*

136 The study was carried out with two crossbred beef cattle herds situated in two separate fields (Herd
137 1: $N = 21$ adult multiparous females; Herd 2: $n = 23$ adult multiparous females) on a farm in Radcliffe
138 on Trent ($52^{\circ} 93' 72''$, $1^{\circ} 06' 09''$ W), Nottinghamshire, UK, from February of 2010 to August 2010.
139 The two fenced fields were approximately 52 ha (herd 1) and 23 ha (herd 2), and were separated by a
140 road (3 m wide). Recordings and playbacks were carried out in each field independently. For the
141 playback experiments, vocalisations of 42 individuals (cows: $N = 20$, 100 vocalisations; calves: $N = 22$,
142 66 vocalisations) were tested. Playbacks of calf calls to cows were all carried out between 5 to 10
143 days after the calf recordings were made. All individuals included in this study were free to roam in
144 the fields with fresh grass and water *ad libitum*. Calves included in this study were all born between
145 February and August 2010, and all were sired by the same bull. The two herds were kept separately
146 in their fields without interchange of animals, except for two cows, not used in the experiment,
147 which were transferred from one field to the other between the time we made the recordings and
148 playbacks. All the calves included in the study were kept all year long in the same field with their
149 mothers.

150

151 *Sound recording*

152 Recordings of individual cow and calf contact calls were made opportunistically (i.e. when cattle
153 spontaneously produced vocalisations) between 8 am and 5 pm from February to August 2010.
154 Vocalisations were produced when the mother was in another part of the field and were followed by
155 reunion with the calf and nursing. Similarly, calf calls were always produced when their mothers
156 were in another part of the field and were followed by reunion with the mother and suckling. Calls
157 were recorded at distances of 10 - 30 m from the vocalizing animal with a Sennheiser MKH70

158 directional microphone, connected to a Marantz PMD660 digital recorder (sampling rate 44.1 kHz).
159 Accurate, individual identification was done from specific ID tags placed in the animals' ears by the
160 farmer and by visual recognition of coat markings. Because of the farm records, the exact ages of the
161 calves at the moment when calls were recorded were known. Playbacks were never conducted more
162 than 10 days after the recordings were carried out, in order to minimise age-related differences
163 between the calls played back and the actual calls of the calf at the time of the playbacks.

164

165 *Playback sequences*

166 Vocalisations were uploaded to a computer at a sampling rate of 44.1 kHz and saved in a WAV
167 format at 16-bit amplitude resolution. We used Praat v.5.1.44 DSP Package (Boersma & Weenink,
168 2009) to build the sequences for the playback experiments. Calls were individually visualised using
169 spectrograms in Praat (FFT method, window length = 0.1 s, time steps = 100, frequency steps = 250,
170 Gaussian window shape, dynamic range = 40 dB). For both cows and calves, only HFCs (as opposed to
171 low-frequency calls (LFC) produced with the mouth closed or only partially opened; Padilla de la
172 Torre et al. 2015), with low levels of background noise, were considered for the playback
173 experiments. HFCs were used instead of LFCs to ensure audibility, because LFCs are lower in
174 amplitude than HFC, and the trials were carried out in an open field at relatively (10 – 30 m) long
175 distances.

176

177 Because cows and calves sometimes produced single calls (not in sequence), it was not always
178 possible to acquire natural sequences for all individuals tested. Furthermore, because our aim was to
179 test if mother and offspring recognise each other individually using the acoustic structure of calls (as
180 opposed to other parameters such as call rate or inter-call intervals), we prepared standardised
181 sequences for cows and calves composed of the same number of calls and silence intervals (e.g.

182 Briefer & McElligott, 2011). Call sequences prepared for the playback experiments were designed to
183 reflect natural sequences. To this end, the average silence interval between each call, and the total
184 number of mother-offspring contact calls present in natural sequences was first calculated using 31
185 sequences from 20 cows, and 19 sequences from 12 calves (age range: 10 -184 days old) from the
186 study population. The natural number of calls per sequence observed in the field was 5.32 ± 0.42
187 (mean \pm SEM; range = 1 - 12 calls) for cow calls and 2.89 ± 0.93 (range = 1 - 4 calls) for calf calls. The
188 natural silence interval was 2.71 ± 2.55 s between cow calls, and 2.83 ± 2.40 s between calf calls. To
189 match these averages, sequences of 5 cow calls interspersed with 2.7 s of silence intervals were
190 created for the playbacks to calves (See supplementary material 1 for an example; SM1), while
191 sequences of 3 calf calls interspersed with 2.8 s of silence intervals were created for playbacks to
192 cows (See supplementary material 2 for an example; SM2). In order to avoid pseudoreplication, all
193 playback sequences included different HFC calls from each cow and calf (McGregor et al., 1992). They
194 were preceded by 5 minutes silence to allow the experimenter to start the playback and move away
195 from the loudspeaker. Using Goldwave (version 5.11; Craig, 2000), we rescaled each recorded
196 vocalisation to match the root mean square (RMS) amplitude of the different vocalisations included
197 in the sequences at the same output level. The prepared sequences were stored as mp3 files on a CD
198 at sampling rate of 44.1 KHz and a bit rate of 224 kbps. In order to verify that the acoustic structure
199 of the sequences played back were not affected by the audio file format change (from wav to mp3),
200 each sequence was inspected visually (spectrum and spectrogram) and by ear in both file formats
201 (wav and mp3 files) using Praat.

202

203 *Playback procedure*

204 All playback trials were performed opportunistically in the field (i.e. when mothers and their calves
205 were separated by at least 30 m from each other, not in direct line of sight, and cover for

206 experimenters and equipment was available). All playback experiments were carried out without any
207 artificial isolation or manipulation of the animals, in order to cause the least disturbance possible. A
208 total of 42 playback trials were carried out, with a maximum of two playback trials per day (always
209 one cow and one calf), and at least 3 - 4 hours between trials allowing the animals to return to their
210 normal activities. During each playback trial, the behavioural responses of three individuals were
211 filmed simultaneously: the "Own" individual was the mother or offspring of the individual whose calls
212 were being played in that particular trial. The "Others" were the two nearest individuals in the field
213 that were not the mother or offspring of the calf or cow whose calls were being played. Each Own
214 individual (cows, $N = 22$; calves, $N = 20$) was tested once with Own calls. The response of Other cows
215 and calves were opportunistically scored (cows, $N = 44$; calves, $N = 40$), depending on their proximity
216 to the animal receiving the Own call (5 - 10 m on average). On average, each cow was included as the
217 Other individual 1.40 ± 0.95 times (mean \pm SD; range = 0 - 3 times), and each calf 1.31 ± 1.12 times
218 (mean \pm SD; range = 0 - 2 times). Calls of calves played back to Own mothers were from animals
219 which were on average 70.56 ± 8.53 days old, and those played back to Other cows were from calves
220 which were 69.51 ± 6.56 days old. Similarly, calves tested with Own mother calls were on average
221 64.10 ± 7.62 days old, whereas those tested with Other cow calls were on average 69.77 ± 6.69 days
222 old.

223

224 We played back call sequences using a Skytronic TEC076 portable speaker system (frequency
225 response: 50 – 20 kHz \pm 3dB). Because the fields were large (52 ha and 23 ha), individuals were
226 usually widely separated. This allowed us to test cows and calves when their own offspring or
227 mothers were at least 30 m away and not in direct line of sight, to avoid auditory and visual contact
228 as much as possible. The loudspeaker was hidden with a camouflage tent or in the bushes at the
229 edge of the field, 10 – 30 m away from the subject. The sequences were played at an intensity
230 estimated to be normal for cattle (mean \pm SD: cows, 93.79 ± 0.47 dB; calves, 93.95 ± 0.41 measured

231 at 1 m using a sound level meter, C weighting; SoundTest-Master, Laserlinerer, UK). All playback trials
232 were initiated when the individuals (Own and Other) were involved in normal activities (i.e. grazing,
233 standing or lying down) and looking away from the speaker.

234

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

242

243 *Behavioural responses*

244 The behavioural responses of cows and calves were assessed from videos of the playbacks. For each
245 tested individual, we measured the presence (yes or no) of each of the four following behavioural
246 measures (in order of response strength): (1) ear movements and/or looking towards loudspeaker;
247 (2) standing up (when the subject was lying down at the beginning of the playback) or directing body
248 towards loudspeaker (when the subject was standing at the beginning of the playback); (3) walking
249 towards loudspeaker; (4) calling back and/or meeting Own mother/calf. Behavioural responses were
250 clustered in some cases (1, 2 and 4) because they often occurred simultaneously. Additionally, the
251 latency for the first behavioural response to occur was recorded as the time between the beginning
252 of the first call in the playback sequence and the first behavioural response (i.e. one of the four
253 above mentioned behavioural measures). All behavioural responses were scored by an observer who
254 was blind as to which subject was Own and which was Other.

255

256 *Statistical analysis*

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

274

275 *Ethical Note*

276 Animal care and all experimental procedures were carried out in accordance with the Guidelines for
277 the treatment of animals in behavioural research and teaching of the Association for the Study of
278 Animal Behaviour (ASAB, 2012). Cattle included in this study (farm in Radcliffe on Trent,

279 Nottinghamshire) were habituated to the presence of farmers and the researchers. The habituation
280 to people allows for approaches close enough to conduct playback experiments (Pitcher, Briefer,
281 McElligott, 2015). During the recordings, mothers and calves were never manipulated or isolated.
282 Likewise, playbacks experiments were carried out opportunistically when mothers and calves were
283 spontaneously separated (in different parts of the field). All mothers accepted their calves for nursing
284 after the playbacks.

285

286 Results

287 *Cow behavioural responses to playbacks*

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

291

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

298

299 *Calf behavioural responses to playbacks*

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

302

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

307

308 *Latency of behavioural responses to playbacks*

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

313

314

315 Discussion

316 We investigated if mother-offspring individual vocal recognition occurs in cattle using playback
317 experiments. The ability of mother and offspring to identify each other is thought to be linked to
318 parental care and predator avoidance strategies in ungulates (Torriani et al., 2006). The general
319 consensus is that cattle are a hider species (Bouissou et al., 2001; Tucker, 2009; von Keyserlingk &
320 Weary 2007; Watts & Stookey, 2000), and we accordingly predicted (Lent, 1974; Torriani et al., 2006)
321 that unidirectional vocal recognition of mothers by calves would be evident. Our results support
322 previous studies (Barfield et al., 1994; Marchant-Forde et al., 2002), which suggested that calves can
323 distinguish the calls of their own mothers from those of other cows. Our results also reveal for the
324 first time that cows are also able to recognise the calls of their own calves. Contrary to our initial
325 prediction, we thus found bidirectional and not unidirectional mother-offspring recognition in cattle,
326 which is more similar to the recognition process observed in follower species (Espmark, 1971; Sèbe
327 et al., 2007) than in other hider species (e.g. fallow deer, Torriani et al., 2006). Additionally, our
328 findings suggest that responses to vocalisations are partially influenced by own calf age, with cows
329 overall being more likely to respond to playbacks of their own calf when they were younger. Overall,
330 our findings show that there is bi-directional individual recognition by vocal cues between mothers
331 and offspring in domestic cattle. Comparative studies using domestic and closely related wild species
332 may yield important insights into the evolution of vocal communication, and into the genetic and
333 environmental changes that have occurred throughout domestication (Price, 1984; Bradley & Magee,
334 2006; Zeder, 2012).

335

336 Despite the classification of domestic cattle as a hider species (Langbein & Raasch, 2000; Flower &
337 Weary, 2003; von Keyserlingk & Weary, 2007), and the prediction that hider species would show
338 unidirectional recognition between offspring and mothers (Fisher et al., 2002; Sèbe et al., 2007;

339 Torriani et al., 2006), the results of our study reveal that cows and calves display bidirectional
340 individual vocal recognition. This important finding could reflect the fact that hiding behaviour in
341 domestic cattle is relatively weak (Bouissou et al., 2001; Vitale, Tenucci, Papini, & Lovari, 1986).
342 Indeed, the period of hiding (or isolation if hiding is not possible) appears to be rather short, and
343 three weeks after birth, calves spend most of their time in small groups with other offspring of
344 similar ages (Bouissou et al., 2001; Vitale et al., 1986). The classification of species as hiders or
345 followers in domestic settings is not clear cut, because their normal social behaviours may be
346 markedly constrained. Domestic cattle have commonly been classified as a hider species because,
347 although cattle in modern farming environments often do not have the opportunity to hide their
348 young, when cover is provided, hiding behaviour has been observed (Langbein & Raasch, 2000).
349 Similarly, domestic goats (*Capra hircus*), in which bidirectional vocal recognition has also been
350 observed (Briefer & McElligott, 2011), are classified as a hider species, despite the fact that some
351 researchers have reported that they do not display hiding behaviour under some domestic settings
352 (Rudge, 1970; Tennessen & Hudson, 1981). We hypothesise that early social integration with other
353 conspecifics observed in both cattle and goats has favoured bidirectional recognition in these
354 species.

355

356 The wild ancestors of domestic cattle are extinct (Bradley & Magee, 2006). However, feral
357 populations of ancient cattle breeds and other closely related bovid species might provide evidence
358 of the anti-predator strategy that existed before this species was domesticated. For example,
359 Chillingham cattle offspring are reported to hide (Hall, 1986), and Maremma cattle have been
360 observed displaying both hider and follower strategies in the early weeks of life, depending on the
361 availability of cover (Vitale et al., 1986). It may be more generally true that attempts to divide
362 ungulates into hiders and followers, and to make predictions about mother-offspring recognition
363 based on this dichotomy without considering intermediate behavioural patterns (Ralls, Kranz, &

364 Lundrigan, 1986), are flawed. Extensive research about maternal behaviour in captive ungulates
365 (Ralls et al., 1986; Ralls, Kranz, & Lundrigan, 1987) has led to the conclusion that the hider-follower
366 dichotomy is an overly simplistic characterization of the mother-offspring predator avoiding strategy,
367 which is not effective in describing the whole range of behavioural patterns adopted by ungulates.

368

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

382

383 Our results show that the age of the calf is an important factor in determining a cow's response to
384 playbacks. Mothers of younger calves tended to respond more strongly than mothers of older calves
385 to playbacks in general. The mother-offspring relationship weakens over time as the calf grows and
386 becomes more independent, both in modern domestic cattle (Thomas, Weary, & Appleby, 2001; von
387 Keyserlingk & Weary, 2007), and in ancient breeds (Maremma cattle; Vitale et al., 1986), and other

388 ungulates such as American bison, *Bison bison* (Green, 1992). By contrast, even though a decrease in
389 responsiveness in older calves might be expected as they become more independent from their
390 mother with regards to feeding (i.e. weaning period) and less vulnerable to predators (Thomas et al.,
391 2001; von Keyserlingk & Weary, 2007; Estes & Estes, 1979; Green, 1992; Vitale et al., 1986), there
392 was no reciprocal tendency in this study for older calves to pay less attention to playbacks of their
393 mother's calls. This is probably linked to the strength of the attachment of calves to their mothers,
394 which does not seem to decrease with age even after weaning (Veissier & Le Neindre, 1989).

395

396 Conclusion

397 Unlike previous studies aimed at testing cattle mother-offspring recognition (e.g. Barfield et al., 1994;
398 Marchant-Forde et al., 2002), our study was carried out on free-range animals, where cows and
399 calves are allowed to graze undisturbed outdoors in relatively large fields. Our findings strongly
400 suggest that, under these conditions, individual vocal recognition between domestic cows and calves
401 is bidirectional, and that the response of mothers is at least partly influenced by their own calf's age.
402 Despite cattle being classified as a hider species, the recognition process thus seems more similar to
403 what has been observed in follower species (Espmark, 1971; Sèbe et al., 2007) than in other hider
404 species (Torriani et al., 2006). In order to understand how and why this pattern exists in a domestic
405 setting, we need a greater understanding of the conditions under which individual recognition has
406 evolved. Detailed comparative behavioural studies of domestic, feral and wild ungulates are needed
407 to determine the differences in parent-offspring interactions within and among species (Ralls et al.,
408 1986, 1987), beyond the simple classification of species as "hidiers" or "followers" (Fisher et al., 2002;
409 Ralls et al. 1986).

410

411

412 Figure legends

413 Figure 1. Proportion of cows responding to playbacks of their Own (dark bars) or a different (Other)
414 calf (light bars). Four different behavioural responses were recorded, and these are presented in
415 order of the strength of the response (i.e. from ear movement/look towards the speaker to calling
416 back/meeting calf), with the strongest response on the right (Binomial GLMM: * $P < 0.05$, *** $P <$
417 0.001 , NS = non-significant). Error bars are 95 % confidence intervals from the binomial distribution.

418

419 Figure 2. The effect of the age of a cow's calf on the likelihood that she would respond to playbacks
420 of calls from Own and Other calves. Data shown are the mean age (+/- SEM) of the calves belonging
421 to tested cows, which either did not (striped bars) or did (stippled bars) respond to playbacks, for the
422 four behavioural measures. The behavioural responses are presented in order of strength: (a) Ear
423 movements or looking towards speaker. (b) Directing the body towards speaker or standing up. (c)
424 Walking towards speaker. (d) Calling back or meeting their own calf (Binomial GLMM).

425

426 Figure 3. Proportion of calves responding to playbacks from Own (dark bars) and Other cows (light
427 bars). Four different behavioural responses are presented in order of the strength of the response of
428 the observed reaction to the playback trial, from left to right (Binomial GLMM, * $P < 0.05$, *** $P <$
429 0.001). Error bars are 95 % confidence intervals from the binomial distribution.

430

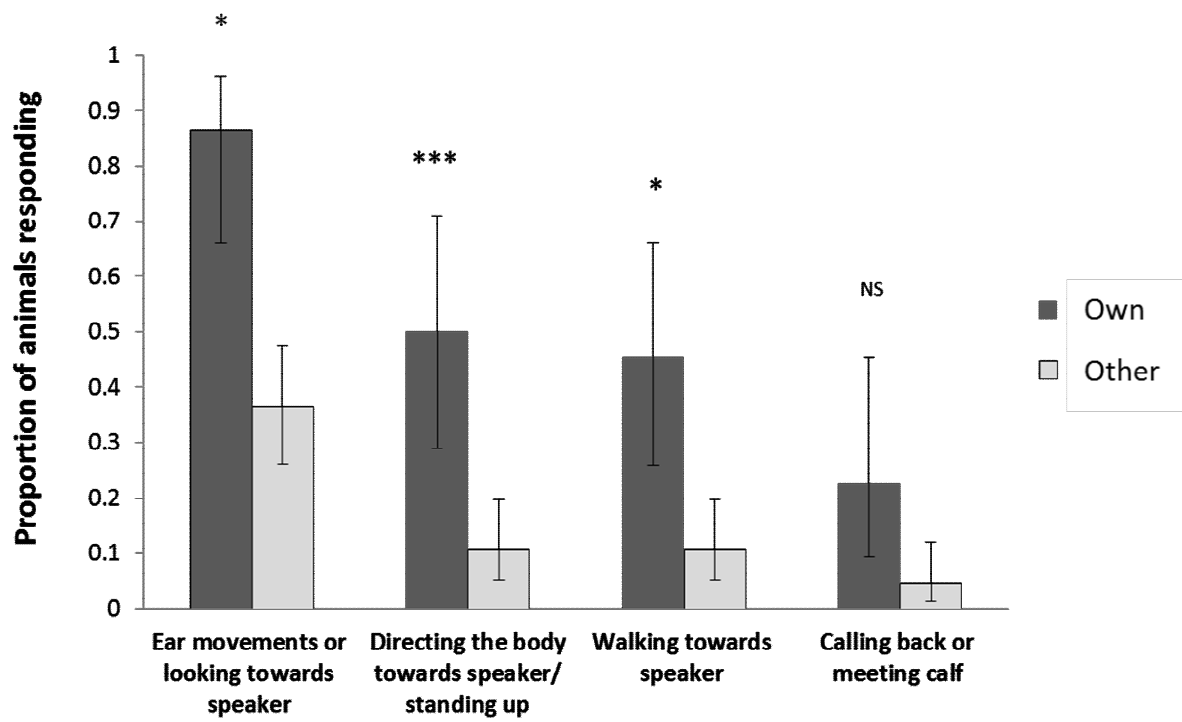
431 Figure 4. Average (+/- SEM) latency to respond in one of four ways (1. Ear movements and/or looking
432 towards speaker; 2. Directing the body towards speaker or standing up; 3. Walking towards speaker;
433 4. Calling back and/or meeting their own calf or mother) to playbacks of calls from Own and Other
434 animals in cows and calves (Wilcoxon signed-rank test: ** $P < 0.01$, NS = non-significant).

435 Acknowledgments

436 We thank Catherine, Desire and David Hackett for their help and access to the animals on their farm
437 on Radcliffe on Trent, Nottinghamshire, UK. MPdIT was funded by the National Council of Science
438 and Technology, Mexico (CONACYT) PhD (scholarship No. 304365), and EFB by a Swiss National
439 Science Foundation fellowship.

440

441 Figure 1

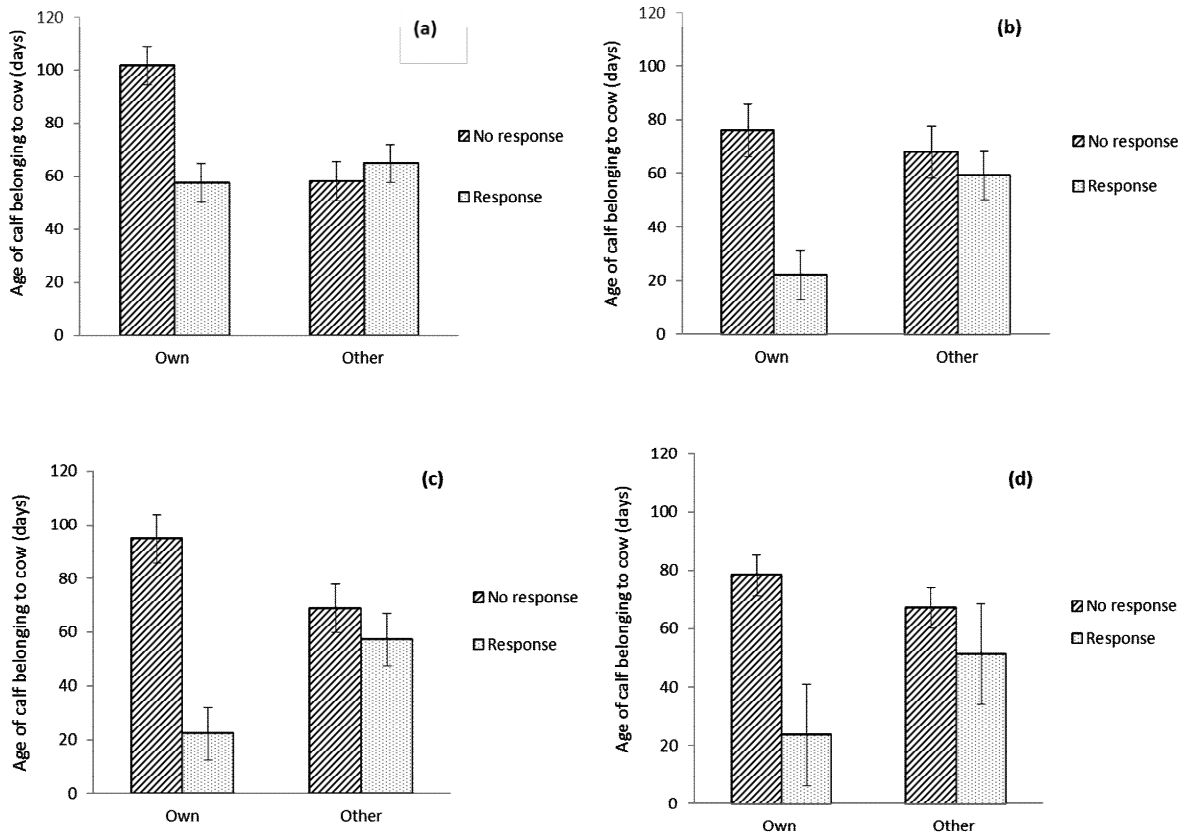


442

443

444

445 Figure 2

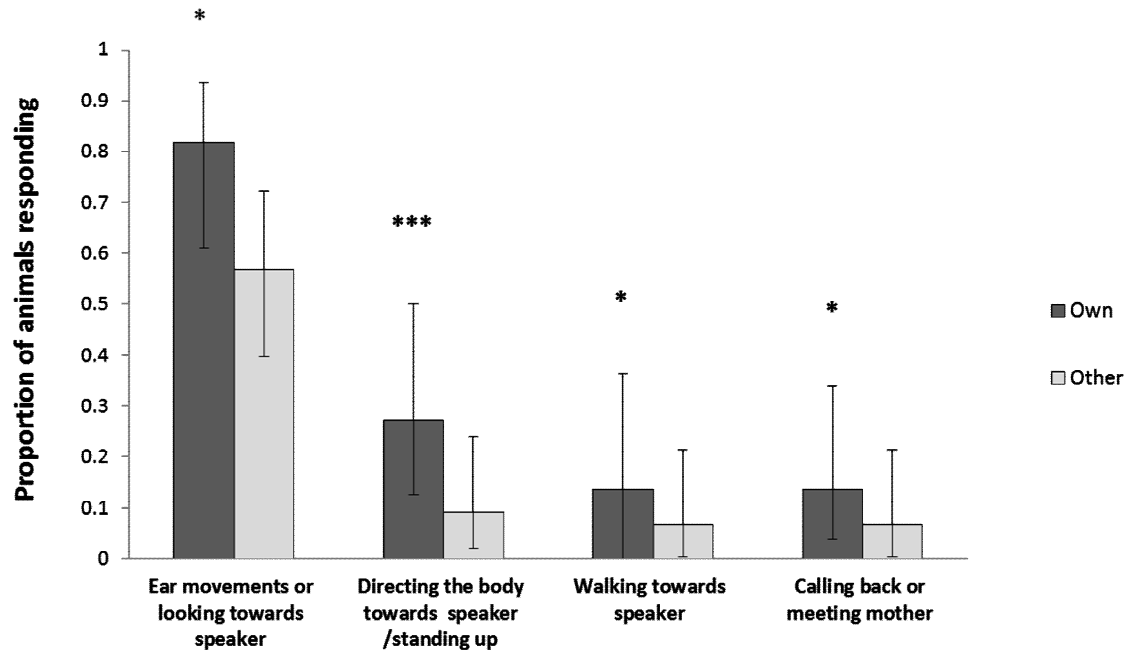


446

447

448

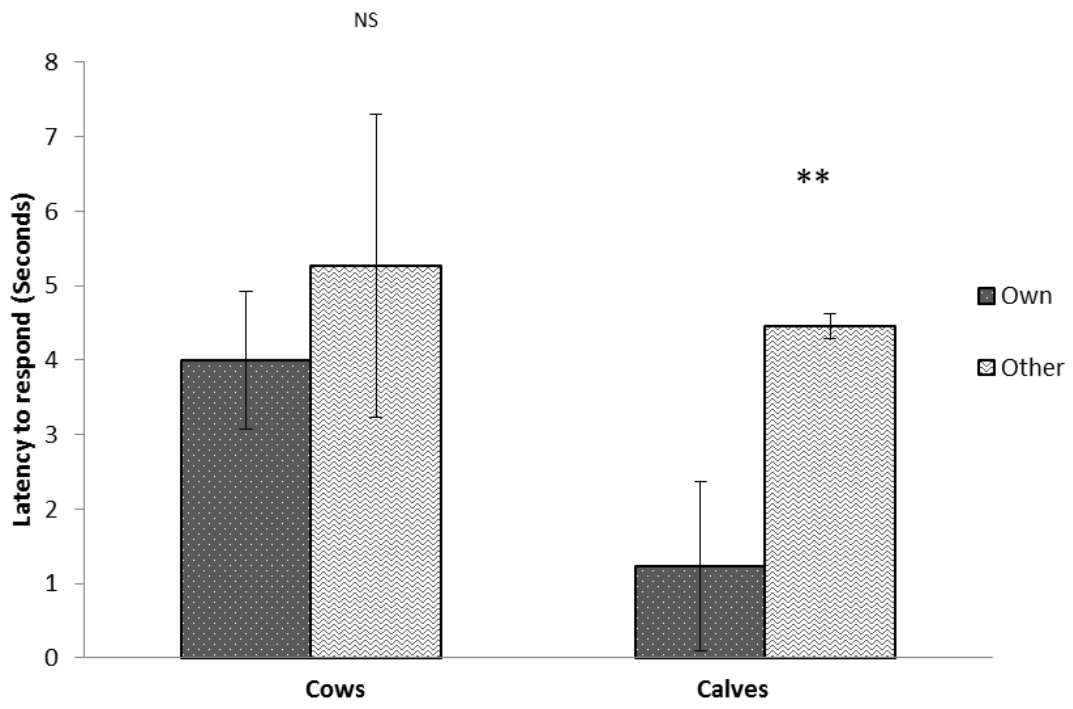
449 Figure 3



450

451

452 Figure 4



453

454

455 References

- 456 Alexander, G. (1977). Role of auditory and visual cues in mutual recognition between ewes and lambs
457 in Merino sheep. *Applied Animal Ethology*, 3, 65-81.
- 458 Alexander, G. (1978). Odour, and the recognition of lambs by merino ewes. *Applied Animal Ethology*,
459 4, 153-158.
- 460 Alexander, G., & Shilito, E. E. (1977). The importance of odour, appearance and voice in maternal
461 recognition of the young in merino sheep (*Ovis aries*). *Applied Animal Ethology*, 3, 127-135.
- 462 Arave, C. W., & Albright, J. L. (1981). Cattle behaviour. *Journal of Dairy Science*, 64, 1318-1329.
- 463 ASAB. (2012) Guidelines for the treatment of animals in behavioural research and teaching. *Animal*
464 *Behaviour*. 83, 301-309.
- 465 Barfield, C. H., Tang-Martinez, Z., & Trainer, J.M. (1994). Domestic calves (*Bos taurus*) recognize their
466 own mothers by auditory cues. *Ethology*, 97, 257-264.
- 467 Boersma, P., & Weenink, D. (2009). Praat: doing phonetics by computer. Retrieved from
468 <http://www.praat.org/>.
- 469 Bouissou, M. F., Boissy, A., Le Neindre, P., & Veissier, I. (2001). The social behaviour in cattle. In L. J.
470 Keeling, & H. W. Gonyou (Eds.), *Social behaviour in farm animals*. (pp. 113-145). Oxon, UK.:
471 CABI Publishing.
- 472 Bradley, D.G., & Magee, D.A. (2006). Genetics and the origins of domestic cattle. In M. A. Zeder, D. G.
473 Bradley, E. Emshwiller, & B.D. Smith (Eds.), *Documenting domestication: new genetic and*
474 *archaeological paradigms*. (pp 317–328). London, U.K.: University of California Press.
- 475 Briefer, E., & McElligott, A. G. (2011). Mutual mother-offspring vocal recognition in an ungulate ruminant
476 species (*Capra hircus*). *Animal Cognition*, 14, 585-598.

477 Broad, K.D., Curley, J.P., & Kaverne, E.B. (2006). Mother-infant bonding and the evolution of
478 mammalian social relationships. *Philosophical Transactions of the Royal Society B*, 361,
479 2199-2214.

480 Charrier, I., Aubin, T., & Mathevon. (2010). Mother-calf vocal communication in Atlantic walrus: a
481 first field experimental study. *Animal Cognition*, 13, 471-482.

482 Coulon, M., Deputte B.L., Heyman, Y., Richard, C., & Delatouch, L. (2007). Visual discrimination by
483 heifers (*Bos taurus*) of their own species. *Journal of Comparative Psychology*, 121, 198-204.

484 Coulon, M., Deputte B.L., Heyman, Y., & Baudoin C. (2009). Individual recognition in domestic cattle
485 (*Bos taurus*): Evidence from 2D- images of heads from different breeds. *PLOS ONE*, 4, 1-8.

486 Craig, C. (2000). Goldwave V. 5.11. Goldwave, St John's. Retrieved from <http://goldwave.com/>

487 Espmark, Y. (1971). Individual recognition by voice in reindeer mother-young relationship. *Behaviour*,
488 40, 295-301

489 Estes, R. D., & Estes, R. K. (1979). The birth and survival of wildebeest calves. *Zeitschrift für*
490 *Tierpsychologie*, 50, 45-95.

491 Fisher, D. O., Blomberg, S. P., & Owens, P. F. (2002). Convergent maternal care strategies in ungulates
492 and macropods. *Evolution*, 56, 167-176.

493 Flower, F. C., & Weary, D. M. (2003). The effects of early separation on the dairy cow and calf. *Animal*
494 *Welfare*, 12, 339-348.

495 Green, W. C. H. (1992). The development of independence in bison: pre-weaning spatial relations
496 between mothers and calves. *Animal Behaviour*, 43, 759-773.

497 Hall, S. J. G. (1986). Chillingham cattle: dominance and affinities and access to supplementary food.
498 *Ethology*, 71, 201-215.

- 499 Jensen, P. (2001). Parental behaviour. In Keeling, L. J., & Gonyou, H. W. (Eds.), *Social Behaviour in*
500 *farm animals* (pp. 59-81). U.K.: CABI Publishing
- 501 Langbein, J., & Raasch, M. L. (2000). Investigations on the hiding behaviour of calves at pasture.
502 *Archives für Tierzucht-Archives of Animal Breeding*, 43, 203-210.
- 503 Lent, P. C. (1974). Mother-infant relationships in ungulates. In V. Geist & F. Walther (Ed.), *Behaviour*
504 *of ungulates and its relation to management*. (pp. 14-55). Morges, Switzerland: IUCN
505 Publications.
- 506 Lickliter, R., & Heron J. R. (1984). Recognition of mother by newborn goats. *Applied Animal Behaviour*
507 *Science*, 12, 187-192.
- 508 Lingle, S., Rendall, D., & Pellis, S. M. (2007). Altruism and recognition in the antipredator defence of
509 deer: 1. Species and individual variation in fawn distress calls. *Animal Behaviour*, 73, 897-
510 905.
- 511 Marchant-Forde, J. N., Marchant-Forde, R. M., & Weary, D.M. (2002). Responses of dairy cows and
512 calves to each other's vocalisations after early separation. *Applied Animal Behaviour*
513 *Science*, 78, 19-28.
- 514 McGregor, P. K. (1992). Quantifying responses to playback: one, many, or composite multivariate
515 measures. In P. K. McGregor (Ed.) *Playback and Studies of Animal Communication* (pp. 79-
516 96). New York: Plenum Press.
- 517 Nowak, R., Porter, R., Lévy, F., Orgeur, P., & Schaal, B. (2000). Role of mother-young interactions in
518 the survival of offspring in domestic mammals. *Reviews of Reproduction*, 5, 153-163.
- 519 Padilla de la Torre, M., Briefer, E.F., Reader, T., & McElligott, A. G. (2015). Acoustic analysis of cattle
520 (*Bos taurus*) mother-offspring contact calls from a source-filter theory perspective. *Applied*
521 *Animal Behaviour Science*, 16, 58-68.

522 Pitcher, B.J., Briefer, E.F., McElligott, A. G. (2015). Intrasexual selection drives sensitivity to pitch,
523 formants and duration in the competitive calls of fallow bucks. *BMC Evolutionary Biology*,
524 15, 149

525 Pitcher, B.J., Harcourt R.G., & Charrier, I. (2010). Rapid onset of maternal vocal recognition in a
526 colonially breeding mammal, the Australian sea lion. *PLOS ONE*, 5, 1-7.

527 Price, E. O. (1984). Behavioural aspects of animal domestication. *Quarterly Review of Biology*, 59,
528 419-422.

529 R Development Core Team. (2009). R Foundation for Statistical Computing. Vienna: Austria.
530 Retrieved from <http://www.R-project.org>.

531 Ralls, K., Kranz, K., & Lundrigan B. (1986). Mother-offspring relationships in captive ungulates:
532 variability and clustering. *Animal Behaviour*, 34, 134-145.

533 Ralls, K., Kranz, K., & Lundrigan B. (1987). Mother-Young relationships in captive ungulates: spacial
534 and temporal patterns. *Zoo Biology*, 6, 11-20.

535 Rudge, M.S. (1970). Mother and kid behaviour in feral goats. *Zeitschrift für Tierpsychologie*, 27, 687-
536 692.

537 Sèbe, F., Nowak, R., Poindron, P., & Aubin T. (2007). Establishment of vocal communication and
538 discrimination between ewes and their lamb in the first two days after parturition.
539 *Developmental Psychobiology*, 49,375-386.

540 Tennessen, T., & Hudson, R. (1981). Traits relevant to the domestication of herbivores. *Applied*
541 *Animal Ethology*, 7, 87-102.

542 Thomas, T. J., Weary, D. M., & Appleby, M. C. (2001). Newborn and 5-week-old calves vocalize in
543 response to milk deprivation. *Applied Animal Behaviour Science*, 74, 165-173.

544 Tibbetts, E. A., & Dale, J. (2007). Individual recognition: it is good to be different. *Trends in Ecology*
545 *and Evolution*, 22, 529-537.

546 Torriani, M. V. G., Vannoni, E., & McElligott, A. G. (2006). Mother-young recognition in an ungulate
547 hider species: a unidirectional process. *American Naturalist*, 168, 412-420.

548 Tucker, C.B. (2009). Behaviour of cattle. In P. Jensen (Ed.), *The Ethology of domestic animals*. (pp.
549 151-160). UK.: CABI

550 Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection*
551 *and the descent of man, 1871-1971*. (pp. 136-179). Chicago: Aldine-Atherton.

552 Veissier, I., Le Neindre, P. (1989). Weaning in calves : Its effects on social organization. *Applied*
553 *Animal Behaviour Science*, 24, 43-54.

554 Vitale, A. F., Tenucci, M., Papini, M., & Lovari, S. (1986). Social behaviour of the calves of semi-wild
555 Maremma cattle, *Bos primigenius taurus*. *Applied Animal Behaviour Science*, 16, 217-231.

556 von Keyserlingk, M. A. G., & Weary, D. M. (2007). Maternal behaviour in cattle. *Hormones and*
557 *Behaviour*, 52, 106-113.

558 Watts, J. M., & Stookey, J. M. (2000). Vocal behaviour in cattle: the animal's commentary on its
559 biological processes and welfare. *Applied Animal Behaviour Science*, 67, 15-33.

560 Zeder, M. A. (2012). Pathways to Animal Domestication. P. Gepts, T. R. Famula, R. L. Bettinger, S. B.
561 Brush, A. B. Damania, P. E. McGuire, & C. O. Qualset (Eds.), In *Biodiversity in Agriculture:*
562 *Domestication, Evolution, and Sustainability*. (pp. 227-259). U.K.: Cambridge University
563 Press.

564

565

566 Table 1. Results of binomial generalised linear mixed models testing the effect of the playback
 567 treatment (Own or Other), the age of the calf providing the playback call, and the interaction
 568 between the two, on the probability that cows would respond (four behavioural responses). The age
 569 of the calf belonging to the Own or Other cow, and the date of the playback trial, were also tested as
 570 covariates. Because Own and Other animals were tested with playbacks simultaneously, the playback
 571 trial was fitted as a random effect.

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

572

573

574 Table 2. Results of binomial generalised linear mixed models testing the effect of the playback
 575 treatment (Own or Other cow), the age of the calf, the interaction between the two, and the date of
 576 the playback trial, on the probability that calves would respond (four behavioural responses).
 577 Because Own and Other animals were exposed to playback simultaneously, playback trial was fitted
 578 as a random effect.

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

579

580

581 **Supplementary Material**

582 **SM1:**

583 Example of cow playback sequence:

584 Sequence with 5 cow calls interspersed with 2.7 s of silence intervals created for the playbacks to
585 calves.

586 **SM2:**

587 Example of calf playback sequence:

588 Sequence with 3 calf calls interspersed with 2.8 s of silence intervals created for the playbacks to
589 cows.

590

591 Highlights

592

- 593 • We investigated vocal recognition in cattle using playback experiments
- 594 • Mother-offspring vocal recognition in cattle is a bidirectional process
- 595 • Calf age is an important factor in determining a cow's response to playbacks
- 596 • Mothers respond more to playbacks when their calf is younger

597

598

599