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

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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.

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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 rosmasus*

58   *rosmasus,* 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

recognition process of mothers by offspring, at least in 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; and reindeer, *Rangifer tarandus*; Espmark, 1971).

Cattle are a facultative hider species; when calves are artificially provided by 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; Langbein & Raasch (2000); von Keyserlingk & Weary, 2007; Watts & Stookey, 2000). Isolation to give birth is an important preliminary step in the formation of the mother-offspring 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 vocalisations (Barfield, Tang-Martinez, & Trainer, 1994; Marchant-Forde, Marchant-Forde, & Weary, 2002). However, there has been no definitive test of maternal recognition of calf vocalisations. 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. (2002), mothers were separated from 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° 93´ 72", 1° 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

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158   directional microphone, connected to a Maranzt 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 ± 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 ± SD; range = 0 - 3 times), and each calf 1.31 ± 1.12 times

218   (mean ± 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 ± 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 ± 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.

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255

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 ± SEM.

274

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).

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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

Discussion

We investigated if 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; Tucker, 2009; von Keyserlingk & Weary 2007; 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 recognise 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 vocalisations 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 bi-directional individual recognition by vocal cues between mothers and offspring in domestic cattle. Comparative studies using domestic and closely related wild species 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).

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

Torriani et al., 2006), the results of our study reveal that cows and calves display bidirectional individual vocal recognition. This important finding 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, and three 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 (*Capra hircus*), 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 hypothesise 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 anti-predator 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, &

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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 "hiders" 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).
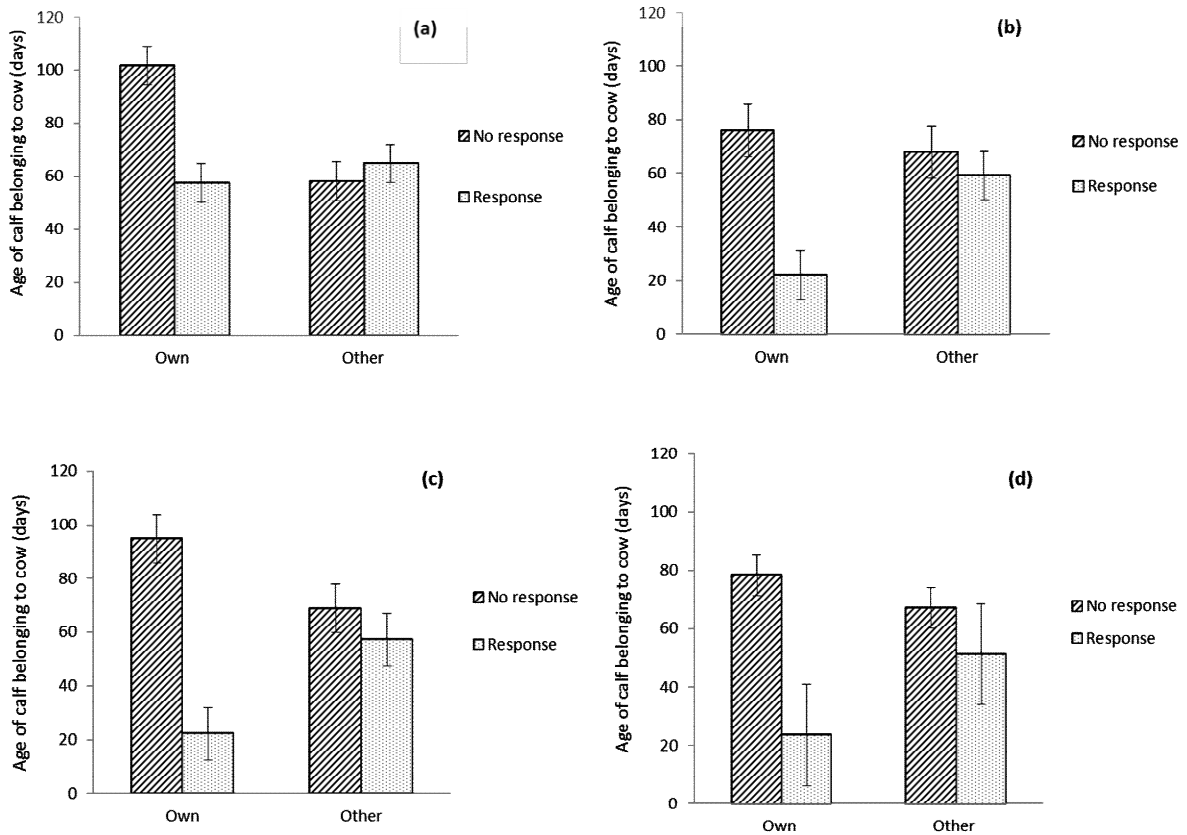
440

441   Figure 1
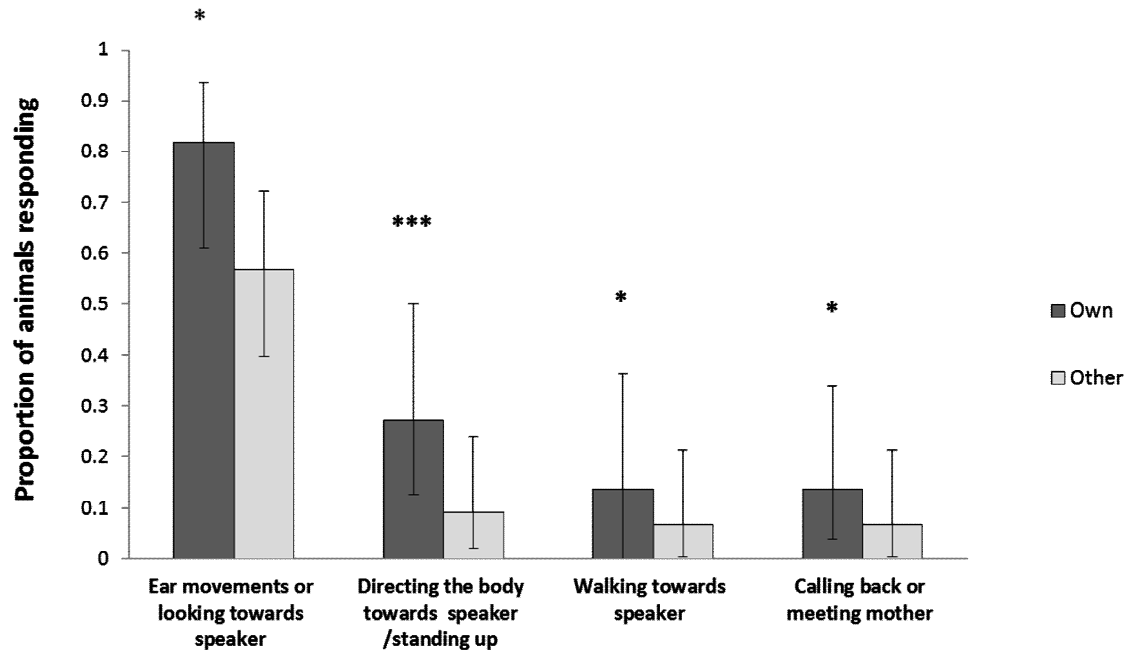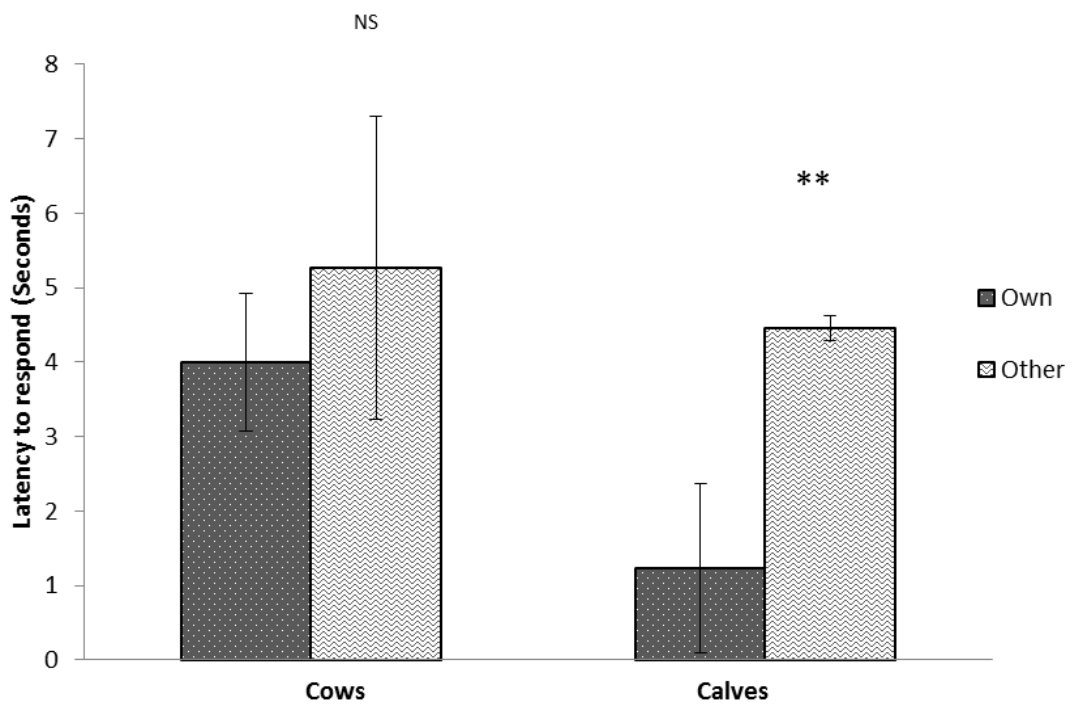

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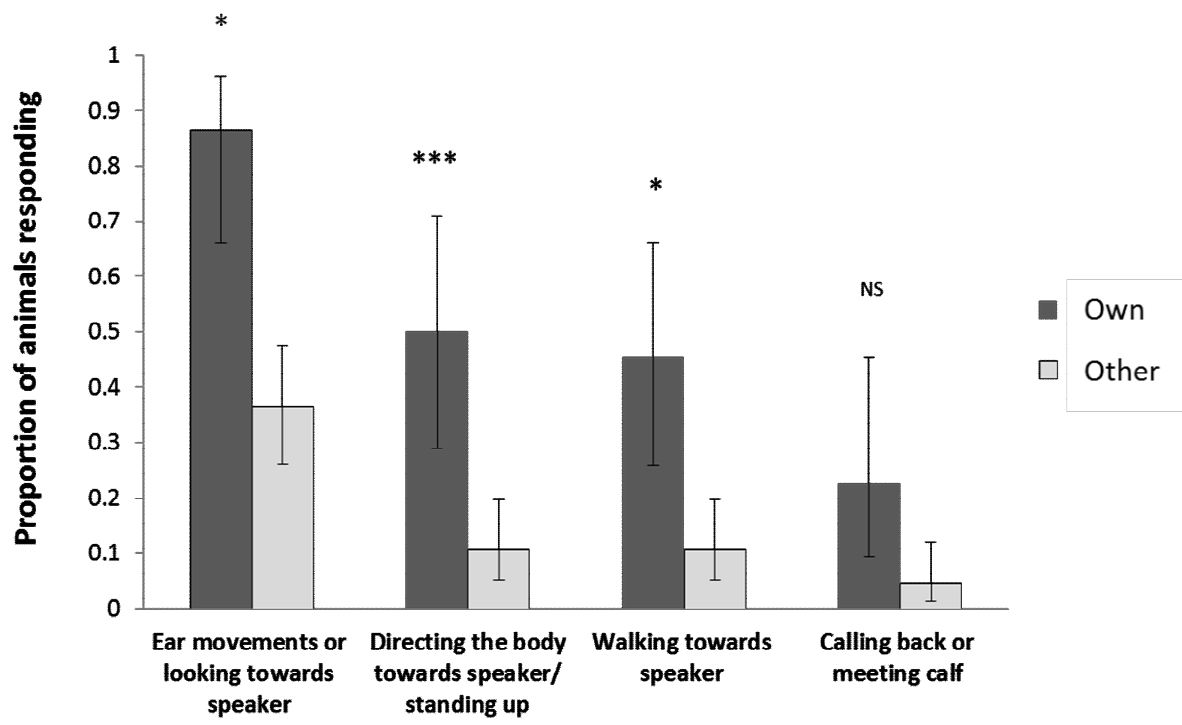
449   Figure 3

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451

452   Figure 4

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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 hider

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.

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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

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