



Mother–offspring recognition via contact calls in cattle, *Bos taurus*



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

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

Torriani, Vannoni, & McElligott, 2006; walrus, *Odobenus rosmarus rosmarus*: Charrier, Aubin, & Mathevon, 2010; Australian sea lion, *Neophoca cinerea*: Pitcher, Harcourt, & Charrier, 2010; goats, *Capra hircus*: Briefer & McElligott, 2011).

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

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

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

Cattle are a facultative hider species; when calves are artificially provided with high vegetation, they spend time using it for concealment, suggesting that the absence of hiding behaviour in domesticated cattle may largely be a result of the lack of cover (Bouissou, Boissy, Le Neindre, & Veissier, 2001; Jensen, 2001; von Keyserlingk & Weary, 2007; Langbein & Raasch, 2000; Watts & Stookey, 2000). Isolation to give birth is an important preliminary step in the formation of the 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 vocalizations (Barfield, Tang-Martinez, & Trainer, 1994; Marchant-Forde, Marchant-Forde, & Weary, 2002). However, there has been no definitive test of maternal recognition of calf vocalizations. One study reported that dairy cows display a poor ability to respond preferentially to their own calves' calls

(Marchant-Forde et al., 2002), but this evidence comes from experiments conducted in the artificial conditions of a dairy farm. In Marchant-Forde et al.'s (2002) study, mothers were separated from their calves within 24 h of birth, and playbacks were performed indoors. It therefore remains unknown whether parent–offspring recognition in this species under more natural conditions is uni- or bi-directional.

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

METHODS

Study Site and Subjects

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

Sound Recording

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

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