

## Mother–young vocal communication and acoustic recognition promote preferential nursing in sheep

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### SUMMARY

**In mammals with precocial neonates, exclusive maternal care and investment depend on mutual mother–young recognition. In sheep, this is ensured by rapid olfactory recognition of the neonate by its mother. However, recent studies suggest that other processes may participate in preferential maternal care. We investigated the possibility that acoustic communication promotes preferential nursing of the lamb. In the first of two studies, we examined the association between nursing and vocal activity in ewes and their lambs during the first 2 weeks of lactation. As early as 3 and 6 h postpartum, vocal activity was preferentially concentrated before nursing and by day 15 all vocal activity occurred within 2.5 min before nursing. In the second study, we tested the responses of ewes and lambs at 15 days postpartum to the playback of recorded bleats of their partner or from unrelated ewes and lambs. When playback was performed 30 min after a nursing episode, both ewes and lambs responded to bleats of their partner but not to bleats from alien subjects. When playback was performed 5 min after nursing, ewes did not respond to any lamb's bleats, while lambs continued responding to the bleats of their mothers, but significantly less than 30 min after nursing. Nursing therefore appears to play an important role in structuring very early vocal communication between the mother and her neonate. In turn, if the motivational state of the members of the mother–young dyad is adequate, this ensures the display of mutual acoustic recognition and prepares them for preferential nursing before maternal olfactory recognition of the lamb comes into play.**

Key words: mother–young interactions, motivation, suckling, bleats, maternal behaviour, selectivity, playback, ewe, lamb.

### INTRODUCTION

In mammals, maternal investment is a key determinant of reproductive fitness, as young are unable to survive without milk and adequate maternal care (Walser, 1978; Clutton-Brock, 1991). This is particularly true in gregarious species in which reproduction is highly synchronised and many young are born within a limited time of the year; if the mother provides milk to non-kin young she may reduce her investment in her own offspring (González-Mariscal and Poindron, 2002; Poindron et al., 2007). In such situations, mother–young recognition at the time of suckling is critical to maximise maternal investment. Sheep constitute a good example of mammals living in large groups with synchronised seasonal breeding, in which mutual mother–young recognition ensures exclusive care of their own progeny (Lynch et al., 1992; Poindron et al., 2007).

In this species, olfaction has long been recognized as the critical sensory modality controlling exclusive acceptance of the mother's own lamb at nursing (Bouissou, 1968; Alexander, 1978; Kendrick et al., 1997; Lévy and Fleming, 2006). The process of parturition facilitates ewes' rapid familiarisation with the individual smell of their neonates (Kendrick et al., 1997; Lévy et al., 2004), which in turn ensures selective access to the udder as early as 2 h postpartum in the large majority of mothers (Poindron et al., 1980; Keller et al., 2003). Nonetheless, despite the critical role of maternal olfactory recognition and selective nursing of the newborn lamb in early maternal investment, several other factors in the mother, but also

in the lamb, may contribute further to preferential maternal investment. First, maternal olfactory recognition is functional only at a very short distance (<0.25 m) (Alexander and Shillito, 1977a; Alexander, 1978) and discrimination of young at greater distances necessarily involves visual and/or acoustic modalities. Second, recognition of the mother by her lamb is also important for its survival and hence for maternal reproductive success (Nowak and Lindsay, 1992), and this depends on visual and acoustic cues (Nowak, 1991; Terrazas et al., 2002). Therefore, visual and acoustic distance recognition by both ewes and lambs are likely to facilitate preferential suckling and maternal investment.

While it is well established that ewes and lambs recognise each other through both visual and acoustic cues (Lindsay and Fletcher, 1968; Poindron and Carrick, 1976; Alexander and Shillito, 1977a; Alexander and Shillito, 1977b; Alexander and Shillito-Walser, 1978; Terrazas et al., 1999), vocal recognition is likely to play a primary role at a distance, since it can take place at much greater distances than allowed by visual recognition (Hinch et al., 1987) or when mother and young cannot see each other (Shillito, 1975; Poindron and Carrick, 1976; Shillito-Walser et al., 1981). Also, vocal communication is an important component regulating early mother–young interactions (Vince, 1993), when both the mother and her neonate show an intense peak of vocal activity in the first 3 h following the birth of the lamb (Sèbe et al., 2007). Furthermore, ewes and lambs display a preference for each other based solely upon vocal cues soon after parturition (at 24 h in

ewes and 48 h in lambs) (Sèbe et al., 2007) and recognise the individual acoustic signature of their kin soon afterwards (Searby and Jouventin, 2003).

Taken together, these results suggest that mutual vocal recognition plays a significant role in the development of preferential nursing by ewes of their own lambs and that this may occur quite rapidly after parturition. Moreover, early suckling activity is critical for the lamb to develop a preference for its mother, which also depends on mother–young vocal communication and recognition (Nowak, 1990; Nowak, 1991; Terrazas et al., 2002; Sèbe et al., 2007). Therefore, our hypothesis was that vocal communication and the display of acoustic recognition by ewes and their lambs would be closely associated with nursing. To investigate this possibility we carried out two separate studies to analyse the establishment of acoustic communication between the ewe and her lamb and the conditions under which mutual ewe–lamb vocal recognition occurs during the first 2 weeks after birth.

In the first study, we tested the hypothesis that if vocal communication plays a role in preferential suckling, some pattern of association between these two components of the mother–young relationship should emerge within a few days of parturition. To this end, we recorded and analysed spontaneous nursing behaviour and vocal activity of mother–young dyads during the first 2 weeks of lactation, to see whether vocal behaviour in ewes and lambs would peak just before nursing.

In the second study, we investigated further the role of acoustic recognition at the time of nursing, by testing the response of ewes and lambs to the playback of bleats of their own or an alien partner. This was performed at 2 weeks postpartum, as the results of the first study indicated that at this time we could reliably assume vocal communication to be established. In addition, we took into account the time at which the tests were carried out relative to the last nursing bout, because the context in which a sensory signal is emitted, such as the motivational state of the receiver, can influence the display of the receiver's behavioural response (Snowdon and Hausberger, 1997; McGregor, 2005a; Engh et al., 2006). The role of the motivational context of the receiver in the display of mother–young vocal recognition has not been documented in sheep. Therefore, we tested the response of ewes and lambs to the playback of bleats either 5 or 30 min after a nursing episode. We considered that these two intervals represented a sufficient difference in motivation to suckle because in the first study we found that most nursing occurred at intervals ranging from 30 to 60 min at 2 weeks postpartum. The second study also clarified the causal relationships between vocal behaviour and nursing.

## MATERIALS AND METHODS

### Study 1: relationship between the vocal activity of the ewe and her lamb and nursing during the first 2 weeks after parturition

#### Animals and management conditions

The study was conducted at the INRA Research Centre of Nouzilly, France. Fourteen Ile-de-France ewes and their 16 lambs (12 singles and four twins) were used. Reproduction had been controlled and planned to obtain births spread over a period of 2 weeks, in order to maximise the number of animals that could be observed individually during the first 24 h postpartum. Five days before parturition, ewes were put into a communal pen (50 m<sup>2</sup>). When a ewe was about to give birth, she was penned individually and kept there with her young for 6 h to allow adequate development of mother–young relationships. At 6 h postpartum, mothers and lambs were transferred to an adjacent pen with other ewes and lambs in which they could interact socially with non-kin. The size of the pen was adjusted regularly so that the density of mother–young dyads always remained in a range of 5 to 7.5 m<sup>2</sup> per dyad.

#### Behavioural observations

Ewes and lambs emit basically two categories of bleats (Dwyer et al., 1998; Hersher et al., 1963; Lévy et al., 1996; Sèbe et al., 2007), easily distinguishable by the human ear and by the opening of the mouth: (1) low-pitched bleats (quiet vocalisations emitted with the mouth closed); and (2) high-pitched bleats (loud calls emitted with the mouth open). These two types of vocalisation were both taken into account in the present study. The time and number of vocalisations of the 14 ewes and their 16 lambs were directly recorded by an observer during six observation sessions, each lasting 3 h, from the time of lambing until day 15 postpartum (see Fig. 1 for details). All animals were observed at 0–3, 3–6, 12–15 and 24–27 h postpartum. However, due to some overlapping with the last parturitions, only 11 ewes were observed at 6 and 15 days. For all sessions, the vocal activity was recorded by focal observations of each mother–young unit separately on video. Therefore, during each session of observation, the behaviour of ewes and their lambs was video recorded and thereafter analysed in the laboratory, using Observer Video-Pro XT software (Noldus et al., 2000). In all sessions and for all subjects, nursing episodes were identified (at least 1 min of sucking by the lamb in one suckling bout or several bouts separated by a maximum interval of 5 s). No other such episodes occurred within a period ranging from 25 min prior to a target suckling bout until 10 min after it ended. In this paper, we use

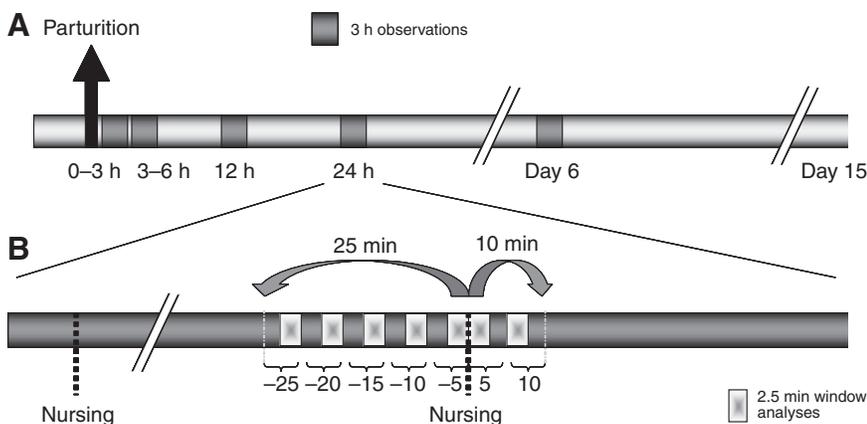


Fig. 1. Schematic representation of the experimental protocol for the study of vocal exchanges between ewes and their lambs from parturition to day 15 postpartum. (A) Representation of 3 h observation periods from lambing to day 15 postpartum. (B) Representation of 2.5 min time-window analyses of focal sampling in relation to a nursing event.

the terms nursing and suckling to refer to the feeding of the lamb by the dam according to the definitions of Hall and colleagues (Hall et al., 1988). During these 35 min, vocalisations of the ewe and her lamb were quantified in windows of 2.5 min of focal sampling, each separated by 2.5 min intervals (Fig. 1), in order to obtain an accurate estimation of vocalisation timing in relation to the feeding of the lamb. The vocal behaviour of each animal was then analysed over the 35 min period. In addition, the global vocal activity of the mother–young dyad during this time was assessed by summing the vocal activity of the ewe and her lamb.

#### Statistical analyses

The results are presented as medians and lower and upper quartiles. Because of the lack of normality of the data and small sample size, non-parametric statistical tests were used (Siegel and Castellan, 1988). Since the vocal behaviour of singles and twins, or of their mothers, did not differ, they were combined to form a single group of lambs.

Within each 35 min period, the vocal activity in the various 2.5 min windows was compared by the Friedman test, followed by the Wilcoxon signed-ranks test for pairwise comparisons, with Bonferroni correction for multiple comparisons. In addition, separate comparisons were carried out, on the one hand between the five 2.5 min windows of the 25 min before nursing, and on the other hand between the 2.5 min window just before nursing and the two 2.5 min windows after nursing. Comparisons between the various times of the study were carried out by a Friedman test, taking the percentage of bleats emitted in the last 2.5 min before nursing relative to the total number of bleats emitted in the 25 min before nursing. The significance level was set at  $P=0.05$ , with bilateral probabilities. Statistica V.6.0 software (2002; StatSoft, Tulsa, OK, USA) was used for the statistical analyses.

### Study 2: experimental responses of ewes and their lambs at 15 days postpartum to the playback of bleats relative to suckling

#### Animals and management conditions

Animals were drawn from a total flock of 80 Ile-de-France ewes and their 110 lambs maintained in the grounds of INRA Research Centre of Nouzilly, France. Ovulations had been synchronised so that all experimental ewes gave birth within a period of 1 week each year. Subjects were tested at 15 days postpartum over a period of 2 years. Ewes were kept permanently indoors in pens at a density of 30 animals per 100 m<sup>2</sup>. They were fed dehydrated lucerne, maize, straw and vitamin and mineral supplement, and had free access to water. Recording of bleats and playback experiments were performed 2 weeks after lambing.

#### Bleat recording

At 15 days ( $\pm 1$  days) of age, each lamb was individually caught and placed in a small pen inside the barn while its mother was kept 1 m away, so that visual contact was always maintained. The vocalisations of the mothers and their lambs were recorded 1 day before the playback tests. Vocalisations exchanged between each mother and her lamb were recorded at the same time using a Marantz PMD 670 digital recorder (Marantz Europe, Eindhoven, The Netherlands; sampling frequency: 32,000 Hz) connected to a Beyer dynamic microphone M88 TG (Heibronn, Germany; frequency response:  $\pm 2.5$  dB within the range 20–20,000 Hz). The distance between the microphone and the head of the recorded animal was 1 m.

Only high-pitched bleats (i.e. loud calls emitted with the mouth open; see Fig. 2) were recorded (Dwyer et al., 1997; Dwyer et al., 1998), as this is the main type of vocalisation emitted by ewes and lambs at this stage of the mother–young relationship (Sèbe et al., 2007). Sound files were then transferred to a computer for subsequent broadcast.

#### Playback procedure

Ewe calls were played back to 37 lambs and lamb calls to 31 ewes in their living pen in the barn. Mothers and offspring were not separated from each other or from the other ewes and lambs of the same group. Animals were studied focally (i.e. one dyad at a time). Tests were performed after 16:00 h, when the daily routine maintenance of the animals had ceased.

Three different bleats, from the same animal, separated by 2.5 s of silence were played back. Selected recordings were free of bleats from other animals and had a signal (dB) to noise (dB) ratio higher than 25 in all cases. The recordings were played at a volume and tone similar to that of the natural voices of lambs as controlled by a sound level meter. A computer connected to a unidirectional loudspeaker (TANNOY coaxial 80 W/6  $\Omega$  Tannoy Ltd, Coatbridge, UK) was used for the playback. The loudspeaker was placed 1 m outside a corner of the animals' pen and playback was carried out when subjects were 3–6 m from the loudspeaker. In addition, the following conditions had to be met for the test to occur. (1) Subjects involved in the test (kin or non-kin) had to be visually separated and at least 2 m away from each other. (2) The subject to be tested must not have been eating or lying with eyes closed. (3) The exact time of the last nursing ( $>5$  s) had to be known, since it was one of the experimental parameters studied.

Each tested individual was subjected to two playback sessions: bleats of the kin mother or young (hereafter referred to as 'kin bleats') and bleats of another unrelated ewe or lamb from the same living pen (hereafter referred to as 'non-kin bleats'). To avoid habituation

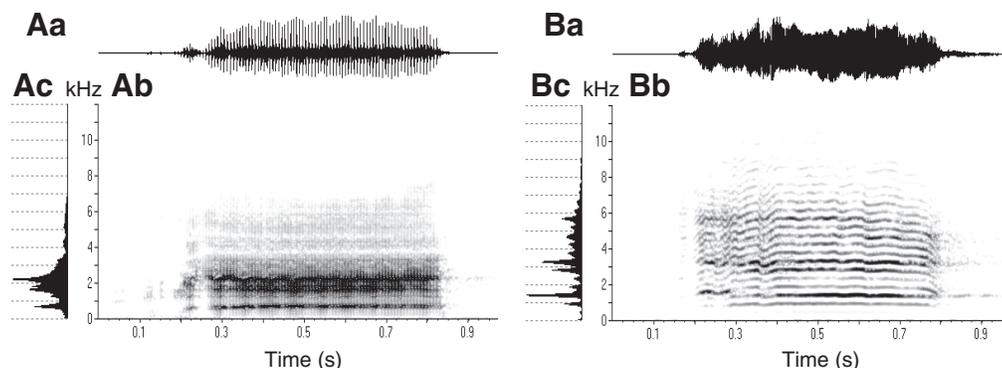


Fig. 2. Spectrograms (b), oscillograms (a) and mean spectrum (c) of the two studied and used calls in the playback experiment: (A) high-pitched bleats of mothers and (B) high-pitched bleats of lambs (window size: 512 points, overlap: 87.5%).

(McGregor, 1992), each lamb was never tested more than twice, with a minimum of 1 h between the two playback sessions. Half of the animals were tested with kin bleats first and the other half with non-kin bleats first. The non-kin bleats used in the test came from animals from the same group. Hence, bleats from non-kin mothers came from ewes that were at the same stage of lactation as the mother of the lamb to be tested, and bleats from non-kin lambs came from lambs of the same age as the lamb of the ewe to be tested. For each tested subject, the two playback sequences were carried out on the same day and they were separated by at least 1 h and one suckling. To test the effect of the interval between suckling and playback of the vocalisations on the response by the tested subject, we performed the playback either 5 or 30 min after suckling. The intervals of 5 and 30 min were chosen because in study 1 we had found that ewes nurse their lambs generally between one and two times per hour at 2 weeks of lactation, which is also consistent with the literature (Ewbank, 1964; Fletcher, 1971; Schirar et al., 1989). We therefore inferred that comparing the responses of ewes and lambs to acoustic playback 5 or 30 min after a suckling episode would offer a substantial difference regarding the motivation to nurse (mother) and suck (lamb). Each lamb and ewe was then allocated at random to one of four experimental groups and observed under the following stimulus conditions. Group 1: behavioural responses of mothers to bleats of lambs 30 min after nursing ( $N=16$ ); group 2: behavioural responses of mothers to bleats of lambs 5 min after nursing ( $N=15$ ); group 3: behavioural responses of lambs to bleats of ewes 30 min after suckling ( $N=19$ ); and group 4: behavioural responses of lambs to bleats of ewes 5 min after suckling ( $N=18$ ).

All groups were independent of each other, while the condition for the type of bleat (kin or non-kin) was tested with the same subjects.

#### Criteria of response

Under natural conditions, when recognised, a call can elicit various responses from the receiver: interruption of ongoing activity, vocalisations, orientation towards the source (head or head and body), approaching the source (McGregor, 1992; Charrier et al., 2002a; Searby and Jouventin, 2003; Ligout et al., 2004; Sèbe et al., 2007) and eventually reunion of the two members of the dyad, as subjects were in the same pen at the time of testing. We took into account these five response categories during the playback and the minute following the last played-back bleat. The responses of each subject were quantified by allocating points each time the tested animal displayed one of the following behaviours. (i) Interruption of behaviour within 2 s after the emission of a bleat: 1 point. (ii) Looking towards loudspeaker within 2 s after the emission of a bleat: 1 point. 'Looking' was defined as the rear-front axis of the head of the animal being oriented directly towards the loudspeaker. (iii) Approaching the loudspeaker ( $>1$  m) during the playback or the following minute of observation: 1 point. (iv) Bleats emitted during the playback or the following minute of observation. The number of allocated points for this variable ranged from 0 to 4. Each time the subject vocalised within 2.5 s after the playback of one bleat, it was given 1 point. Thus, an animal could obtain a total of 3 points for immediate 'response' to the playback of the three bleats. In addition, if the subject emitted more bleats during the rest of the test (1 min after playback of the third bleat), he was given one additional point. A major weight was given to this variable because, in other studies (Shillito-Walser et al., 1981; Searby and Jouventin, 2003), the bleating rate has been shown to be positively correlated with recognition. (v) Reunion of mother and young during the playback or the following minute of observation, ending with

suckling: 1 point. When none of these behaviours were recorded during the testing session, the subject obtained a score of 0 points. Thus, the score of an individual could range from 0 to 8 points.

#### Statistical analyses

The results are presented as medians and lower and upper quartiles. Because of the discontinuous nature of the data and their lack of normality, non-parametric statistical tests were used.

In each group, Wilcoxon tests were used to compare the behavioural responses of subjects to kin *versus* non-kin bleats. Mann–Whitney *U*-tests were used for comparisons of responses between groups.

In all cases, the significance level was set at  $P=0.05$ , with bilateral probabilities.

## RESULTS

### Study 1: relationship between the vocal activity of the ewe and her lamb and nursing during the first 2 weeks after parturition

#### Pattern of the pooled vocal activity of the mother–young dyad in relation to nursing activity

During the first 3 h after parturition, the number of bleats of the dyad did not differ significantly between all the various 2.5 min windows of the 35 min period around nursing (Friedman:  $N=14$ ,  $d.f.=6$ ,  $P=1$ ).

During the period 3–6 h after parturition, the number of bleats differed significantly between the various windows of sampling (Friedman:  $N=14$ ,  $d.f.=6$ ,  $P<0.001$ ; Fig. 3). The vocal activity was significantly higher just before nursing than 25 and 20 min before nursing (Wilcoxon:  $N=14$ ,  $P<0.05$ ), while no difference was found between the period just before nursing and the two periods after (Friedman:  $N=14$ ,  $d.f.=2$ ,  $P=0.8$ ). Similar results were found at 12 h and 24 h postpartum (Friedman tests, total:  $N=14$ ,  $d.f.=6$ ,  $P<0.001$ ; before nursing:  $N=14$ ,  $d.f.=4$ ,  $P<0.001$ ; after nursing:  $N=14$ ,  $d.f.=6$ ,  $P>0.076$ ; Fig. 3).

At days 6 and 15, there was also a significant structuring of the vocal activity around nursing (Friedman test, total:  $N=11$ ,  $d.f.=6$ ,  $P<0.01$ ; before nursing:  $N=11$ ,  $d.f.=4$ ,  $P<0.01$ ; after nursing:  $N=14$ ,  $d.f.=6$ ,  $P<0.05$ ; Fig. 3). Furthermore, at day 6, the vocal activity just before nursing was significantly higher than that 10 min before or during the two 2.5 min windows after suckling (Wilcoxon tests:  $N=11$ ,  $P<0.05$ ). At day 15, the vocal activity just before nursing was significantly higher than that at any other period (Wilcoxon tests:  $N=11$ ,  $P<0.05$  for five comparisons and  $P<0.07$  for one comparison; Fig. 3). There was a peak of vocalisations during the last 2.5 min before nursing on day 15 (Fig. 3). Moreover, the percentage of bleats emitted during the 2.5 min preceding nursing relative to the total number of bleats emitted in the 25 min before nursing increased significantly with time during the six observation sessions, 0–3 h, 3–6 h, 12 h, 24 h, day 6 and day 15 (Friedman test:  $N=8$ ,  $d.f.=5$ ,  $P<0.018$ ; Fig. 4). Three to six hours after parturition, the percentage of the pre-nursing vocal activity occurring just before nursing was higher than that during the first 3 h after parturition (Wilcoxon test:  $N=14$ ,  $P=0.002$ ). This percentage did not differ significantly between 3–6 h, 12 h, 24 h and day 6 after parturition (Wilcoxon tests:  $P>0.1$ ). Finally, at day 15, this percentage was 100% and differed significantly from the percentage at day 6 (Wilcoxon test:  $N=8$ ,  $P=0.046$ ).

**Relationship between the vocal activity of mothers and nursing**  
During the first 3 h after parturition and like the global vocal activity of the mother–young dyad, the vocal activity of the ewes in the

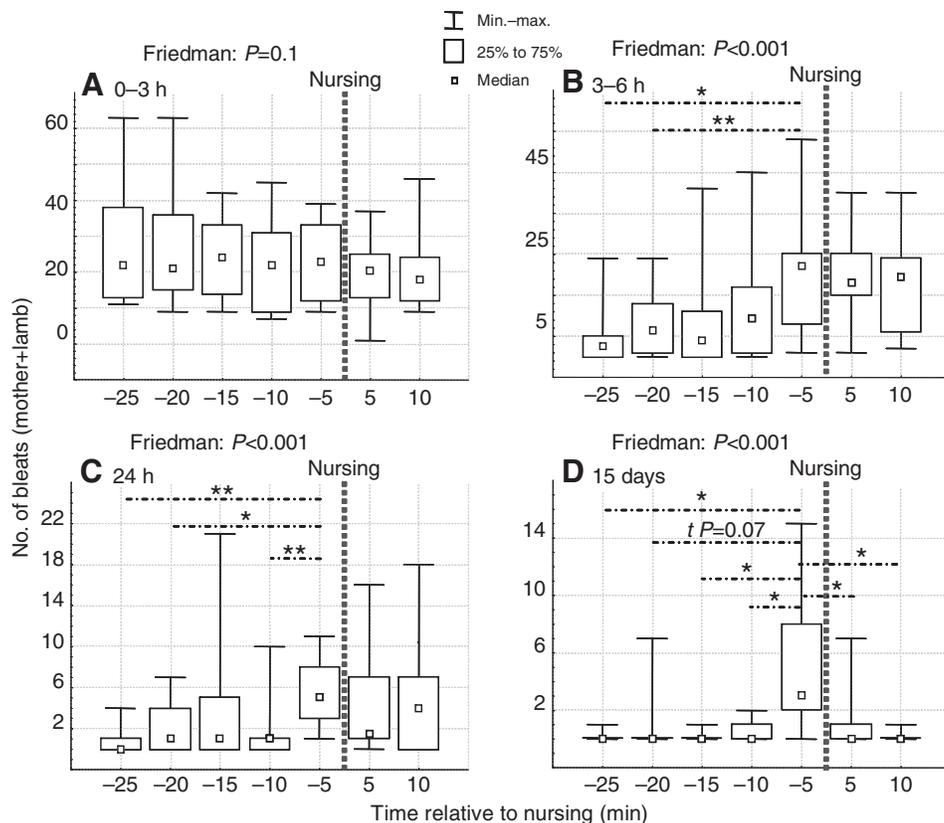


Fig. 3. Box-plot representation of vocal activity of ewe-lamb dyads (medians, lower and upper quartile) during 2.5 min observation windows, from 2 days before parturition (ewes only) to 15 days postpartum at the time of nursing. Vocal activity (A) at 0–3 h postpartum, (B) at 3–6 h postpartum, (C) at 24 h postpartum, and (D) at 15 days after lambing. (Friedman tests followed by Wilcoxon signed-ranks tests for pair-wise comparisons with Bonferroni correction for multiple comparisons:  $t$ :  $P < 0.1$ ; \* $P < 0.05$ ; \*\* $P < 0.01$ .)

35 min period around nursing did not differ between all the various 2.5 min windows (Friedman test:  $N = 14$ ,  $d.f. = 6$ ,  $P = 1$ ).

In contrast, at all other observation times (3–6 h, 12 h, 24 h, day 6 and day 15) the number of bleats differed significantly between all the various 2.5 min windows of each 35 min period (Friedman:  $N = 14$ ,  $d.f. = 6$ ,  $P < 0.001$ ). The vocal activity was highest just before

nursing in all cases (Friedman:  $N = 14$ ,  $d.f. = 4$ ,  $P < 0.01$ ), but this activity just before nursing did not differ from that in the two windows after nursing at 3–6 h, 12 h and 24 h (Friedman:  $N = 14$ ,  $d.f. = 2$ ,  $P > 0.18$ ). Nonetheless, at day 6 and day 15 the number of bleats by the mother after nursing decreased significantly relative to the last 2.5 min before nursing (Friedman test, total:  $N = 14$ ,  $d.f. = 2$ ,  $P < 0.05$ ).

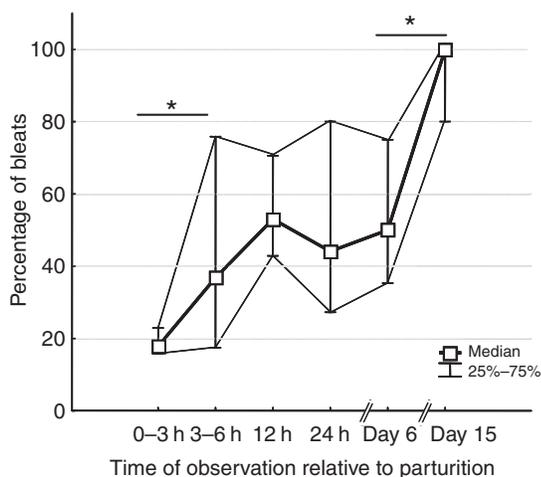


Fig. 4. Proportion of the vocalisations of ewes and lambs during the 2.5 min observation window just preceding nursing, relative to the total number of vocalisations emitted during the five 2.5 min observation windows in the 30 min before nursing (Wilcoxon test: \* $P < 0.05$ ). Note that at 3–6 h postpartum, vocal activity is already significantly more concentrated just before suckling than in the first 3 h postpartum, and this continues to increase over time (main effect of time, Friedman test:  $N = 8$ ,  $d.f. = 5$ ,  $P < 0.018$ ).

Relationship between the vocal activity of lambs and nursing As for the mothers, between birth and 3 h after birth, the vocal activity of newborn lambs did not differ between the various 2.5 min windows of the 35 min period around nursing (Friedman:  $N = 14$ ,  $d.f. = 6$ ,  $P = 0.24$ ).

At 3–6 h, 12 h, day 6 and day 15 after parturition, the number of bleats differed significantly between the various 2.5 min windows of each 35 min period (Friedman:  $N = 14$  or 11,  $d.f. = 6$ ,  $P < 0.01$ ), whereas this was not the case at 24 h (Friedman:  $N = 14$ ,  $d.f. = 6$ ,  $P = 0.37$ ). At 3–6 h, 12 h, day 6 and day 15 after parturition the vocal activity increased significantly before nursing (Friedman:  $N = 14$  or 11,  $d.f. = 4$ ,  $P < 0.05$ ) and decreased significantly after nursing (Friedman test:  $N = 14$  or 11,  $d.f. = 2$ ,  $P < 0.05$ ).

**Study 2: experimental responses of ewes and their lambs at 15 days postpartum to the playback of bleats relative to suckling**

Behaviour of ewes following the playback of lambs' bleats (groups 1 and 2)

When playback was performed 30 min after suckling, kin lamb bleats elicited significantly higher scores than non-kin lamb bleats (Wilcoxon test:  $N = 16$ ,  $P < 0.001$ ; Fig. 5A) and in the former case, playback was followed by mother–young reunion in 37% of tests with kin bleats, usually ending with suckling, *versus* 0% with non-

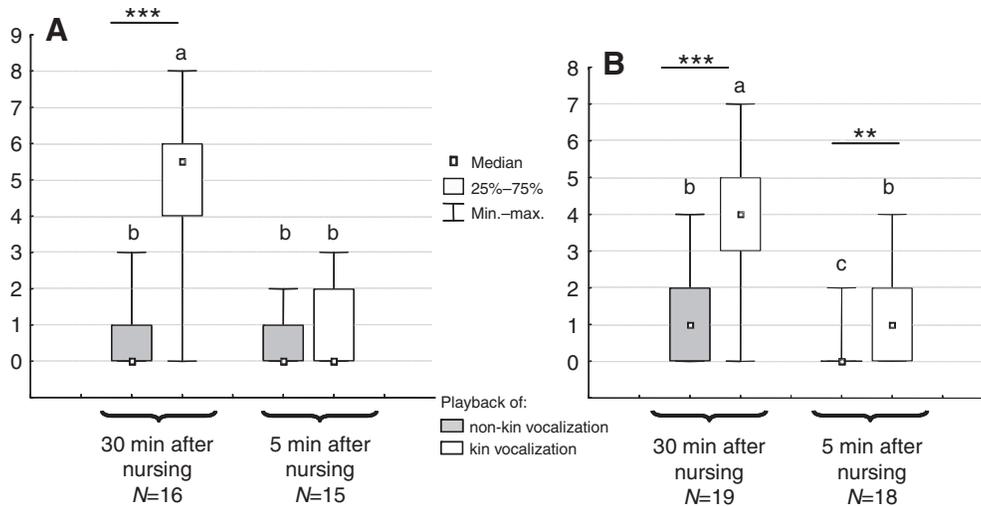


Fig. 5. Responses of ewes (A) and lambs (B) to the playback of vocalisations from an alien or own lamb or an alien versus own mother, respectively, 30 or 5 min after suckling (Wilcoxon test: \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ). Significantly different values are marked with different letters.

kin bleats (Fisher's exact test,  $P = 0.009$ ). In contrast, when playback of the bleats of the kin lamb was carried out 5 min after suckling, it did not result in higher scores than the playback of bleats of a non-kin lamb (Wilcoxon test,  $N = 16$ ,  $P = 0.29$ ; Fig. 5A). The mothers' scores resulting from the playback of non-kin lamb bleats 30 min after suckling did not differ from those obtained 5 min after suckling (Mann-Whitney:  $P = 0.76$ ). In addition, mother-young reunion was never observed with non-kin bleats.

#### Behaviour of lambs following the playback of kin or non-kin mothers' bleats (groups 3 and 4)

The playback of the kin mother's bleats at both 30 and 5 min after suckling elicited higher scores in lambs than the playback of bleats from non-kin mothers at the same times (Wilcoxon:  $N = 19$  or  $18$ ,  $P < 0.005$ ; Fig. 5B). In addition, playbacks of kin mother's bleats 30 min after suckling resulted in significantly higher scores than playback of kin mother's bleats 5 min after suckling (Mann-Whitney:  $P < 0.001$ ). However, the proportion of mother-young reunions following playback of the kin mother's bleats 30 min after nursing (20%) did not differ significantly from that following playback 5 min after nursing (38%). Finally, following the playback of bleats from a non-kin mother, the scores of the lambs were significantly higher 30 min after suckling than 5 min after suckling (Mann-Whitney:  $P < 0.005$ ; Fig. 5B) although we never observed mother-young reunion in this experimental situation. Also, the proportion of mother-young reunions following playback of bleats of the kin mother differed from that following playback of bleats of non-kin mothers (30 min after nursing: 20% versus 0%, Fisher's exact test,  $P = 0.052$ ; 5 min after nursing: 38% versus 0%, Fisher's exact test,  $P = 0.004$ ).

#### DISCUSSION

The above results support the hypothesis that the timing of vocal activity of ewes and their lambs, and the display of reciprocal acoustic recognition are closely associated with nursing and may facilitate preferential mother-offspring interactions. The concentration of vocal activity just before nursing and the preferential responses by the two members of the dyad to the playback of each other's bleats rather than to bleats from non-kin indicate that acoustic communication is of particular importance for the manifestation of exclusive care of the young. The results of the playback experiment indicate that vocal behaviour is not merely

used to maintain contact, because animals were responsive to playback mainly when motivation for feeding was likely to be high. Thus, mutual acoustic recognition between lambs and mothers ensures a high probability of preferential maternal nursing, even before the final step of olfactory maternal recognition that usually takes place when the lamb reaches the udder (Lindsay and Fletcher, 1968; Poindron, 1976; Poindron et al., 1980). While it is well established that vocalisations represent an important element of mother-young interactions (Nowak, 1990; Vince, 1993; Dwyer et al., 1998), this is the first experimental evidence demonstrating its biological significance for preferential maternal investment.

#### Early postpartum association of mother-young vocal communication with nursing

The development of a preference for the mother is entirely dependent on suckling in sheep (Nowak et al., 1997). The association of vocal activity by the mother and her lamb with nursing, which was marked at 2 weeks of lactation, develops very soon after parturition. Evidence for nursing-dependent structuring of vocal behaviour in ewes and lambs was present at 3-6 h after parturition, indicating that acoustic communication has already started to develop at that time. This is likely to be the result of a number of converging factors. Both ewes and lambs display intense vocal activity that peaks during the first 3 h following parturition (Poindron et al., 1980; Shillito-Walser et al., 1984; Dwyer et al., 1998; Sèbe et al., 2007) thus providing a propitious context for the establishment of vocal communication and hearing recognition. Since the lamb starts to suck within the first hour after birth, it is likely that nursing begins to play a reinforcing role in vocal activity very early on, thus providing a basis for the two members of the dyad to learn each other's vocal identity. In the lamb, this is likely to depend on the well-established reinforcing influence of colostrum intake on the development of a preference for the mother (Nowak et al., 1997; Val-Laillet et al., 2004; Nowak and Poindron, 2006). The reinforcement of vocal activity by nursing is also consistent with the shaping of neonatal behaviour by stimuli associated with suckling, which can have a calming effect and facilitate learning, as reported in a wide range of species, including rats, rabbits, dogs, sheep and humans (Nowak, 2006). Also, it must be kept in mind that the bleating activity of the mother in the early postpartum period has a very high frequency of occurrence, more than 10 times higher than that of the lamb (Sèbe et al., 2007). Consequently it is likely

to play a driving and determinant role in the association between nursing and vocal communication between the mother and her young. Hence, nursing may facilitate lambs' learning of the vocal signature of the mother, as has been shown for olfactory or acoustic cues in human babies (Alegria and Noirot, 1978; Noirot and Alegria, 1983; Nowak, 2006). This is the first evidence that an early postpartum relationship exists between mother–young vocal communication and both recognition and nursing. Thus, the results suggest that nursing and the natal context may play an important role in vocal learning between lambs and their mothers.

Interestingly, a pattern of association between vocal activity and nursing was also present within 6 h postpartum in ewes and their lambs. This implies that in the ewe the initial activation of vocal behaviour by intrinsic factors associated with parturition (Dwyer et al., 1998; Sèbe et al., 2007) gives precedence to factors provided by the lamb and by nursing itself. Therefore, nursing appears to be reinforcing not only in the neonate but also in the mother. This is supported further by the results of study 2, showing that mothers responded to the playback of their lamb's bleats 30 min after nursing but not just after, when their motivation to nurse was likely to be low. Together with the early increase of vocalisations by the lamb observed before nursing, the rewarding effect of nursing appears to rapidly promote the reinforcement of vocal communication between the mother and her neonate and the establishment of mutual acoustic recognition and preferences.

The association of an increased peak of vocal activity with the imminence of nursing is not limited to the initial postpartum hours: our results suggest that the first coupling of vocal activity with nursing during the 6 h immediately postpartum is followed by a second increase of this coupling between 6 and 15 days postpartum, as illustrated in Fig. 4. This dynamic probably reflects the establishment of nursing behaviour within the context of the mother–young vocal relationship or/and the change in the mother–young spatial relationship, which increases with the age of the lambs and their motor activity. Within a few days after birth, lambs tend to form play groups, thus reducing the contact with their dam (Lynch et al., 1992). In addition, an important change in maternal behaviour takes place by the end of the first week postpartum. During the first week postpartum, lambs are allowed to suck whenever and for as long as they want, generally staying close to their dams (Ewbank, 1964; Hess et al., 1974; Graves et al., 1977; Lynch et al., 1992). Then, at about 7 days of lactation, mothers begin to control the duration of nursing bouts, and this becomes the rule within a few days (Gordon and Siegmann, 1991). It is therefore likely that this increasing limitation of access to the udder imposed by the dam, combined with increasing mother–young distance and independent activity of the lamb (Lynch et al., 1992), reinforces the advantage of and need for vocal communication to promote nursing.

#### **Importance of nursing for the display of mother–young vocal recognition in ewes and lambs**

The results of study 2 provide important information regarding the factors controlling mother–young vocal communication. The difference in the responses to each other's played-back bleats by the mother and the lamb before and after suckling indicates that vocal communication depends strongly on the motivational state of the receiver, as suggested by the results of study 1 on spontaneous communication and nursing. Both mothers and young responded better to playback performed 30 min after nursing than when it was performed just after nursing. In fact, mothers totally failed to respond to the bleats of their lambs just after a nursing episode, indicating that the motivation to nurse must be a primary determinant of vocal

communication in mothers under undisturbed conditions. This is also partly true for lambs, as they responded significantly more to playback 30 min after suckling than 5 min later. Nonetheless, their response 5 min after suckling was still higher than that for playback of non-kin mother's bleats. This may suggest that the lambs are not fully satiated after a nursing episode and/or that it is easier for lambs to find their way back to their mothers only 5 min after having been in contact with them. This is especially likely in the case of twins, when maternal milk production may not be sufficient to meet the needs of two lambs (Treacher, 1983; Hinch, 1989). Another non-exclusive explanation for the persistence of some response of lambs immediately after nursing is that the oral stimulation provided by sucking is rewarding independently of the intake of milk (Nowak, 2006). It contributes to the psychobiological attachment of the lamb to its mother, and this may be another strong motivation for the lamb to reunite with its mother, independently of its prandial state. The level of satiety also appears to modulate the response to non-kin bleats, as at 30 min the response of lambs to non-kin mother bleats was higher than at 5 min. While this response remained lower than that to kin bleats, it underlines the major role played by context and the fact that the response depends not only on recognition of the signal but also on motivational state.

The results of study 2 also demonstrate that one important function of vocal communication is to allow inter-individual recognition before nursing. Mothers and lambs responded very specifically to the bleats of their kin, thus reducing the probability of nursing between non-kin subjects before olfactory identification of the lamb had taken place. In other words, preferential maternal investment at nursing is already conditioned by vocal communication and mutual acoustic recognition before the animals come in contact. Although the actual rejection of an alien lamb at the udder depends on olfactory inspection by the ewe when the animals are in physical contact (Lévy et al., 2004), the present results indicate that acoustic recognition does play an active role in promoting preferential nursing between ewes and their own lambs in spontaneously occurring mother–young interactions, at least at the age of 2 weeks. Further studies are warranted to investigate the exact time at which acoustic recognition starts to play such a role. Nonetheless, the emergence of some association between vocal activity and nursing as early as 6 h postpartum (study 1), together with the early acoustic recognition existing between ewes and their lambs (Dwyer et al., 1998; Searby and Jouventin, 2003; Sèbe et al., 2007), suggests that it is probably already functional long before 2 weeks postpartum. This function of acoustic recognition for preferential maternal investment is likely to be even more important when animals are at pasture, where inter-individual distances between animals are much greater than in the present study. This probably also applies to other domestic and wild species in which mother–young acoustic recognition has been documented [e.g. goats (Ruiz-Miranda et al., 1993; Terrazas et al., 2003); reindeer (Espmark, 1971); red deer (Vankova and Malek, 1997; Torriani et al., 2006); fur seals (Charrier et al., 2001; Charrier et al., 2002a); wolves (Goldman et al., 1995); and bats (Balcombe, 1990; Balcombe and McCracken, 1992)].

#### **Conclusion**

Mother–young vocal communication and recognition in sheep is well structured and biologically significant at the time of nursing, ensuring effective maternal care that is selectively directed towards the mother's own young, a function that had not been considered previously for this sensory modality in sheep. Like olfactory cues in sheep and other species (Poindron et al., 1980; Montigny et al.,

2006; Nowak and Poindron, 2006), bleats serve as an organising signal anticipatory of feeding rhythm. The present study demonstrates the importance of nursing and of motivational context in the display of vocal mother–young communication and recognition in sheep. These results suggest that mother–young vocal communication and nursing are associated, and that this association may facilitate the development of mutual vocal recognition. In addition, these results highlight the major role played by context learning in the development of filial and maternal bonding. The behavioural response of the recipient depends not only on the signal itself but also on a rapid periodic change of motivational context in both the transmitter and the recipient. This is somewhat similar to results reported in other species, such as the seal, although it occurs over a much longer period in seals. Thus, the responsiveness of fur seal pups to maternal calls during the mother's absence varies according to their motivational state, which is itself related to internal nutritional balance (Charrier et al., 2001; Charrier et al., 2002b). More generally, this is congruent with the social modelling theory that suggests that input must be referentially and contextually applicable to elicit a socially appropriate response (Bandura, 1977; McGregor, 2005b). The motivational context associated with nursing appears fundamental to a full understanding of the communication network at play in mother–young relationships.

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