



## Welfare implications of artificial rearing and early weaning in sheep

Fabio Napolitano<sup>a,\*</sup>, Giuseppe De Rosa<sup>b</sup>, Agostino Sevi<sup>c</sup>

<sup>a</sup> *Dipartimento di Scienze delle Produzioni Animali, Università degli Studi della Basilicata, via dell'Ateneo Lucano 10, 85100 Potenza, Italy*

<sup>b</sup> *Dipartimento di Scienze Zootecniche e Ispezione degli Alimenti, Università degli Studi di Napoli "Federico II", Via Università 133, 80055 Portici (NA), Italy*

<sup>c</sup> *Dipartimento PRIME, Università degli Studi di Foggia, via Napoli 25, 71100 Foggia, Italy*

Accepted 2 March 2007

Available online 7 May 2007

---

### Abstract

Soon after parturition a lasting and mutual ewe–lamb bond is established. However, in an increasing number of intensive sheep farms, lambs are separated from the dam at an early age. When artificial rearing is applied lambs are often kept with mothers for 2 days to allow the ingestion of maternal colostrum and then abruptly removed from their dams. Thus, lambs experience a marked emotional stress represented by the loss of the most relevant social model at this early stage of their behavioural development and a nutritional stress represented by the transition from maternal milk to a commercial milk substitute. These animals when exposed to open field tests show reduced levels of vocalization, are slower to initiate movements, spend less time in ambulatory behaviour and display an increased cortisol response than non-separated animals. In addition, artificial rearing performed on lambs from 2 days of age onward can cause decreased cellular and humoral immune responses. The main oral abnormal behaviour performed by artificially reared lambs is represented by sucking the navel or the scrotum of pen mates. This activity is evident from the initial days on reconstituted milk and lasts until weaning from milk. Attempts have been made to reduce the detrimental effects of early separation. Some of them mainly focus on the emotional aspects (it is recommended not to leave a lamb alone for artificial rearing), others aim at reducing the nutritional impact of artificial rearing (milk intake can be increased by offering a mix of ewe milk and a milk replacer during the first week and then gradually moved to a diet based only on milk substitute which results in higher growth rates). As compared with artificial rearing, early weaning performed at 3 months of age is associated with a later disruption of the mother–young bond and the consequent direct replacement of maternal milk by solid food. However, when they are given the chance, ewes and their lambs form long-term social

---

\* Corresponding author. Tel.: +39 0971 205078; fax: +39 0971 205099.

E-mail address: [napolitano@unibas.it](mailto:napolitano@unibas.it) (F. Napolitano).

associations which exceed the age of natural weaning, regarded as the end of the milk feeding period. Early weaned lambs emit an increased number of high pitched bleats immediately after weaning than before and this increment is still evident 2 days afterwards. Neither partial nor gradual separation from mothers is able to reduce the stress associated with early weaning. In conclusion, premature separation from mothers has clear and marked detrimental effects on various functions in lambs. For lambs maternal deprivation seems to be worse at 2 days (artificial rearing) than at 3 months of age (early weaning).

© 2007 Elsevier B.V. All rights reserved.

*Keywords:* Lamb; Artificial rearing; Weaning; Animal welfare; Behaviour

---

## 1. Introduction

In conventional dairy sheep production systems, lambs are suckled by their dams and either weaned (replacements) or slaughtered at an age of about 45–50 days. However, in an increasing number of specialised milk production farms, lambs are separated from the dam at an earlier age (0–2 days) and fed a milk replacer in order to increase the amount of milk available for cheese making. This technique is referred to as artificial rearing. Artificial rearing is also, albeit less frequently, performed in meat production systems to improve the reproductive performance of ewes, although in these systems weaning more often takes place at 3 months of age (early weaning).

In the present review we describe the formation and resolution of the ewe–lamb bond under natural conditions. Thereafter, we discuss the effects of premature dam–lamb separation, performed through artificial rearing or early weaning on behavioural, endocrine and immune responses of ewe and lamb. The techniques that may be used to mitigate the effects of a premature separation of lambs from mothers are also discussed.

## 2. Ewe–lamb relationship

### 2.1. Formation and maintenance of ewe–lamb bond

In mammals, a fundamental function of mothers is nursing their offspring and promoting the development of social behaviour. Soon after parturition a lasting and mutual ewe–lamb bond is established. The onset of this strong relationship is allowed by two main mechanisms: the maternal response of the ewe and the learning ability of the lamb. The maternal response is under hormonal control as demonstrated by the fact that maternal responsiveness of ewes toward newborn lambs follows the changes in blood estrogens with the highest percentage of animals showing maternal behaviour at parturition, when the estrogens concentration is the highest (Poindron and Le Neindre, 1980; Poindron and Lévy, 1990; Dwyer et al., 2004). Hormones also induce a sensitive period in post parturient ewes during which mothers develop selectivity. Further elements facilitating the onset of maternal behaviour in sheep are the vaginal stimulation operated by the foetus at parturition (Keverne et al., 1982) and the presence of amniotic fluid on the newborn lambs (Lévy et al., 1983). A marked responsiveness of ewes to newborn lambs can be observed in the first 4 h after parturition. The response of the ewe to the neonates includes low pitched bleating and vigorous licking which last about an hour and allow the mothers to learn how to distinguish their own lambs from alien lambs, the latter being actively rejected by head butting

(Alexander, 1988; Nowak et al., 1997). The maternal response tends to decline in the first 12 h after parturition and this can be assumed as the limit of the sensitive period (Poindron and Le Neindre, 1980; Lévy et al., 1991).

Most lambs are able to stand within 1–2 h (Arnold and Morgan, 1975; Slee and Springbett, 1986; Dwyer, 2003; Dwyer et al., 2005). Immediately after birth lambs are not able to distinguish their own mothers from other ewes. However, the ability to discriminate alien ewes improves with age. In sheep as in the other ungulates, the mother represents the most important stimulus with which the newborn lamb interacts. This interaction stimulates the lamb learning ability and the fact that the neonate is able to respond consistently to different anatomical regions of the ewe indicates the occurrence of early postnatal learning (Vince, 1993). As a consequence, lambs become able to distinguish their mothers from alien females within few hours after birth (Nowak and Lindsay, 1990). In particular, Nowak et al. (1990) observed that lambs are generally attracted by ewes within 18 h after birth, although a preference for their mothers is already evident at about 12 h of age (Val-Laillet and Nowak, 2006). At 3 weeks of age recognition is mainly based on ewe appearance (Alexander and Shillito Walser, 1978), although they can rely on other senses (i.e. hearing) to localise their mothers (Shillito, 1975).

Learning ability of newborn mammals in relation to mother recognition has been associated with rewards provided by parental care (Brake, 1981). The association of maternal cues with rewards deriving from the dam provides the basis for an early bond. In rats, tactile stimuli induce the development of the mother–young relationship (Alberts and May, 1984) and seem to inhibit most of the brain related changes occurring after maternal deprivation, as passive contacts suppress the response to stress (Levine, 2001). In new born lambs, attachment to the mothers seems to be feeding-mediated. Tactile stimulation provided by ewe licking seems not to be important (Goursaud and Nowak, 1999), whereas suckling within 24 h after birth plays a central role in the establishment of neonatal attachment to mothers (Vince et al., 1985; Nowak et al., 1997).

In particular, Nowak et al. (1997) observed that sucking has strong rewarding properties and plays a central role in the establishment of lamb preference towards their mothers, although once established, the maintenance of this social relationship is less dependent on food supply. These authors prevented lambs from reaching the udder of the mother at different times after birth. At 48 h of life, they assessed the ability of the lambs to distinguish their mothers from alien ewes using a two-choice test. If sucking was prevented during the first 6 h of life, lambs were not able to discriminate among the ewes, whereas if sucking deprivation was imposed to the lambs later in life (12–18 h *postpartum*) no effect on mother recognition was observed. Goursaud and Nowak (1999) demonstrated that the presence of colostrum in the gastrointestinal tract was as rewarding as a complete and successful sucking event in orienting lamb preference for the mother. Both milk ingestion and non-nutritive sucking induce the production of endogenous cholecystokinin which mediates the onset of the lambs' discriminative abilities (Nowak et al., 2001).

Once formed, the mother–young bond induces the pair to stay in close contact and at 60 days of age the average distance at pasture between ewes and lambs is about 5 m. At increasing age distances tend to increase and double (about 10 m) at 110 days of age (Arnold and Grassia, 1985; Bechet et al., 1989). This close relationship provides the lambs with the most important social model, on which the young relies for many functions. For example, lambs learn from mothers how to graze (Matthews and Kilgour, 1979) and which foods to eat or avoid (Thorhallsdottir et al., 1990). In fact, the two partners achieve a high degree of synchronisation (Bechet et al., 1989).

## 2.2. Resolution of ewe–lamb bond

It seems that the ewe maintains a close distance early in the lamb's life and thereafter the lamb plays an increasing part in maintaining the mother lamb attachment (Lynch et al., 1992). Under natural conditions milk provision is the main factor involved in the maintenance of a close mother–young relationship and a decrease in milk supply induces an increase in the distance between lamb and ewe, as the former will be engaged in an increasing grazing activity (Penning and Gibb, 1979). Jensen and Recen (1989) suggested that the mother, by continuously increasing the cost of suckling and decreasing the benefit, can gradually induce the young to stop suckling and wean itself which will occur when the benefit of feeding will overcome that of suckling. When the lambs grow older not only frequency (from 36 suckles per day at 1–2 weeks of age to 14 suckles per day at 6–7 weeks of age) and duration (from 41 s per bout at 1–2 weeks of age to 12 s per bout at 6–7 weeks of age) of suckling decline, but also the mother may become antagonistic if the young approach to suckle (Gordon and Siegmann, 1991). This latter behaviour can be interpreted within the context of the parental–offspring conflict theory, according to which offspring expect to receive more care than the parent is willing to give (Godfray, 1995). The changes in the digestive system which is almost completely developed by 8 weeks of age (Lyford, 1988), and in the lamb nutritional requirements can also play a role in the weaning process (Pryce, 1992). The whole weaning process is deemed gradual and depending on a number of factors (availability of solid food, breed, milk production, etc.), thus, a precise time for natural weaning cannot be specified, although for Bighorn sheep Berger (1979) indicates the age of about 120 days, depending on herbage availability which influences milk production of mothers.

The duration and strength of the post-weaning relationship between ewe and lamb can be affected by social (L'Heureux et al., 1995) as well as environmental factors (Lawrence, 1991; Rowell, 1991). Lawrence (1990, 1991) did not observe strong post-weaning relationships in wild and domestic ovids, whereas others showed that, when given the chance, ewes and their lambs form long-term associations which exceed the age of natural weaning, regarded as the end of the milk feeding period (Hinch et al., 1990; Rowell, 1991). Hinch et al. (1990) observed a general increase in spatial distance between family members with increasing age which was interpreted as indicative of a slow decline in association links, as they lasted more than 2.5 years. These authors also observed that such relationships were mainly due to the lambs which were attracted to their mothers. Therefore, along with Grubb and Jewell (1966), progressive natural weaning involves little or no negative effects on social groups of sheep as in a natural social environment, even when suckling is no longer performed, male lambs tend to remain integrated into the social group of the mother at least until the onset of the subsequent sexual season, whereas females may stay for much longer.

## 3. Effect of artificial rearing on lamb welfare

When artificial rearing is applied lambs are usually kept with mothers for 2 days to allow the ingestion of maternal colostrum and then abruptly removed from their dams, thus experiencing a marked emotional stress represented by the loss of the most relevant social model at this early stage of their behavioural development and a nutritional stress represented by the transition from maternal milk from the udder to a commercial milk substitute (24% crude protein, 25% fat on DM basis) from bucket (Napolitano et al., 1995).

### 3.1. Oral behaviour

In order to ensure an adequate level of welfare, animals should be allowed to perform their natural behavioural patterns (Farm Animal Welfare Council, 1993). When artificial rearing is performed, lambs cannot express their normal behaviour. As a consequence, they may express appetitive or consummatory behaviours directed towards inappropriate objects. In particular, Stephens and Baldwin (1971) observed that the main oral abnormal behaviour performed by artificially reared lambs was represented by sucking the navel or the scrotum of pen mates. This activity is evident from the initial days on reconstituted milk and lasts until weaning. As this non-nutritive sucking is usually performed while the other lambs feed, the subject being sucked may be disturbed in milk ingestion, while the animal performing the abnormal behaviour may ingest reduced amounts of food. In addition, non-nutritive sucking may induce increased levels of navel infections in subjects being sucked. In lambs this behaviour is performed even when the normal functional consequences of suckling have been already achieved, as in other young ruminants prematurely separated from their mothers (De Pasillé et al., 1992), thus indicating that the rewarding properties of sucking may be at least partially independent of the nutritive function. Toates and Jensen (1991) suggested that the performance of a behaviour itself can inhibit the motivation inducing that particular behaviour. At least in calves, non-nutritive sucking can contribute to satiety, thus reducing sucking motivation, although it does not involve food ingestion (De Pasillé et al., 1993). Increased postprandial levels of insulin and cholecystokinin were observed by De Pasillé et al. (1993) when calves were allowed to suck a dummy teat after the meal. These authors concluded that non-nutritive sucking can affect digestive hormone secretion, thus, deprivation of normal sucking can have detrimental effects on young ruminant welfare. In lambs, artificial rearing can induce a higher sucking activity (suckling + nibbling) than ewe rearing (Napolitano et al., 2002a). The authors suggest that this result may be attributed to the frustration caused by natural suckling deprivation.

### 3.2. Open field testing

Aversive events occurring during early life can alter animal's ability to cope with subsequent stressful circumstances. Open field testing has been widely used to assess the emotional stress induced by removal from home pens, isolation, exposure to a novel environment and handling. Such studies reported that early separation from the dam can have a marked effect on lamb behavioural response to this procedure (Napolitano et al., 1995, 2002a; Sevi et al., 1999, 2003). In particular, lambs reared without mothers show reduced levels of vocalization, are slower to initiate movements and spend less time in ambulatory behaviour than ewe-reared animals when exposed to open field tests. The higher activity observed in mothered lambs may be interpreted in terms of stronger motivation in contacting the dam.

A time-dependent behavioural response to isolation has been found by numerous authors which is independent from experimental treatments: at increasing age a corresponding reduction in latency to move and number of bleats have been observed, whereas duration of movement increases (Moberg et al., 1980; Sevi et al., 1999; Napolitano et al., 2003). These authors repeated the exposure of animals to the novel environment one to several times. Therefore, the changes observed in lamb behavioural response may be also attributed to experience and habituation. However, Napolitano et al. (1995) used different groups of various ages and confirmed that older lambs display a higher activity when subjected to open field

testing, possibly because they are less dependent on mothers, as also stated by Moberg and Arnold (1974).

It is believed that the behavioural response of young ruminants to an open field test is induced by a mix of motivations rather than by a single source of stimuli (Rushen, 2000; Vandenhede et al., 1998). In particular, the locomotive activity of an animal in a novel situation is likely to be the result of at least two tendencies, the need to locate resources such as cover and feed which in very young animals are represented by the mother, and the tendency to freeze to avoid predators. In these studies, ewe-reared subjects, displaying higher levels of ambulatory behaviour, possibly expressed a higher motivation to rejoin the dam, whereas behavioural inhibition may be the predominant response to fear in artificially reared lambs.

In artificially reared lambs kept in isolation and subjected to open field testing Moberg and Wood (1982) observed a non-functional stereotyped behaviour that they called flank touch and defined as “lamb reaching back and touching its flank with its muzzle”. The authors argued that in case of fear isolate lambs develop this self-directed behaviour in substitution of a behaviour that would normally be directed towards their mothers: joining their dams and suckle.

The presence of a stimulus within the arena changes the response of the lambs to open field testing as vocalizations and ambulatory behaviour tend to be inhibited (Moberg and Wood, 1982), whereas animals spend more time in investigative activities reflecting their interest towards the stimulus (Sevi et al., 2003). In particular, lambs reared artificially and in isolation from conspecifics remain withdrawn even in presence of the stimulus and are slow to make contact. Conversely, ewe-reared subjects and early separated lambs reared with peers display prompt interest in it, the latter also showing the longest time of contact (Moberg and Wood, 1982).

Although in some studies plasma cortisol response to isolation was not affected by rearing conditions (Moberg and Wood, 1982; Napolitano et al., 2002a,b), other authors (Sevi et al., 1999; Napolitano et al., 2003) observed a lower cortisol response in ewe-reared animals than in artificially reared lambs. These results are not necessarily in contrast, as cortisol increase after isolation is related to age. Younger animals, such as those used in the latter experiments, are still largely dependent on mothers and maternal separation can determine a higher cortisol response in these animals (Napolitano et al., 1995), whereas in older animals, such as those used in the former experiments, a lower perception of stress may reduce differences between dam-suckled and artificially reared lambs. In fact, the differences between ewe-reared and artificial reared lambs were observed up to 10 days of age, whereas in tests performed from 14 days onward lambs from different rearing groups exhibited similar adrenocortical responses.

### 3.3. Immune responses

The application of stressors and the consequent elevation of plasma cortisol concentrations have been associated with a reduction in immune responsiveness (Munck et al., 1984), although some studies rather showed a modulating effect of the hormone (Griffin, 1989).

A marked detrimental effect of maternal separation on various immune functions has been reported in different species (Bonnette et al., 1990; Gwazdauskas et al., 1978). In sheep, Napolitano et al. (1995) observed an altered humoral immune response as a consequence of early separation. In particular, the animals separated from their mothers at 2 days of age showed the lowest antibody titre to keyhole limpet hemocyanin (KLH) when compared with the analogous non-separated control group, whereas no differences were found between animals separated at a later stage (15 and 28 days of age) and the corresponding control. These differences were evident on both primary and secondary antibody responses, thus indicating a lasting immunosuppressive

effect of premature separation. However, such a decreased response could not be attributed to a reduced number of B cell because the lambs separated at 2 days and its control did not differ in the number of B cells, as assessed by flow cytofluorometric analysis. The authors suggested that their results could be due to a reduced level of cytokines stimulating B cell activity in animals subjected to premature maternal deprivation.

In subsequent studies (Sevi et al., 1999; Napolitano et al., 2002b), artificial rearing of lambs from 2 days of age onward determined a decreased *in vivo* cell mediated immune response to phytohemagglutinin (PHA) in terms of reduced skin thickening.

These results indicate that a thorough control of the environmental hygiene is a basic need for the application of artificial rearing. Although it was not the case in experimental studies, on-farm empirical data indicate that artificially reared lambs display increased levels of mortality (up to 10–15% from 0 to 3 weeks of age) and gastrointestinal affections as a possible consequence of inadequate management (low protection from temperature extremes, low environmental cleanliness, high stocking density, inadequate milk substitute temperature, concentration and availability, etc.) in relation to lamb reduced immuneresponsiveness (Coppinger et al., 1991; Minton et al., 1992). In addition, artificial rearing could have detrimental effects on vaccination programmes involving early separated lambs as a possible consequence of maternal deprivation induced immune suppression (Napolitano et al., 1995).

### 3.4. Growth rate

Detrimental effects of artificial rearing on lamb growth have been reported by different authors (Napolitano et al., 2002a; Sevi et al., 1999). However, neither Napolitano et al. (2002b) nor Sevi et al. (2003) found differences in weight gain between artificially and ewe-reared lambs, possibly because milk substitute was given *ad libitum*, thus allowing less abundant and more frequent meals with consequent increased dry matter ingestion and nutrient digestibility.

In addition to feeding needs the mother–young relationship involves emotional interactions that are essential for lamb postnatal activity. Lambs typically have a following behaviour (Winfield and Kilgour, 1976) and, when reared without their mothers, display reduced active and explorative behaviours as indicated by decreased ambulatory behaviour and activity in their time budgets (Napolitano et al., 2003).

An early separation from the mother is also likely to affect the solid feed intake of unweaned lambs. Napolitano et al. (2003) found that lambs reared with their mothers become accustomed to solid feed more rapidly than artificially reared lambs, while Bechet et al. (1989) observed that the mastication time of ewe-reared subjects at pasture (417 min/d) was 60% higher than in the corresponding separated group (259 min/d).

## 4. Minimising the stress of artificial rearing

Many attempts have been made to reduce the detrimental effects of early separation from the mother on lamb welfare. Some mainly focus on the emotional aspects related to maternal deprivation, others aimed to reduce the nutritional impact of artificial rearing.

### 4.1. Reducing emotional stress

Sheep are gregarious by nature (Lynch et al., 1992) and lambs prematurely separated from their dams try to compensate for the absence of maternal stimuli by higher levels of interaction

with pen mates. In fact, artificially reared lambs develop high levels of social interactions with pen mates, whereas ewe-reared lambs are less motivated in establishing new relationships with them (Napolitano et al., 2003). In addition, artificially reared lambs tend to show more positive social interactions with their pen mates (Zito et al., 1977; Napolitano et al., 2002a) and, when subjected to a discrimination test between pen mates and alien lambs spend longer times with their companions (Napolitano et al., 2003). Accordingly, Bechet et al. (1989) found that distances between individuals during grazing were lower for artificially reared animals than for ewe-reared lambs.

Lambs artificially reared in group display a significant modification of some behavioural response to open field testing (e.g. a higher level of vocalization) as compared to subjects kept in isolation (Moberg and Wood, 1982). Such differences may be attributed to the fact that, albeit peer reared animals also experienced maternal deprivation, they could benefit from the presence of the pen mates which may have contributed to the behavioural development of lambs.

Subjects exposed to open field testing in isolation emit more bleats than if tested with a social partner (Porter et al., 1995). In addition, lower rates of bleating expressed by lambs while subjected to open field testing as twin pairs compared to paired unfamiliar lambs suggest that mutual knowledge and familiarity can alleviate the emotional stress associated with maternal separation (Porter et al., 1995). The authors argued that although lambs under natural conditions prefer the mother as social partner (Nowak, 1990), they frequently interact with peers and congregate, often performing parallel locomotor playing, while the mother is involved in grazing activities. Thus, interactions with age mates can either play a substitution role for maternal contact in the case of naturally occurring periods of separation from dams or have positive effects on the welfare of lambs subjected to artificial rearing. Therefore, rearing the young with their peers should be recommended when maternal–neonatal bond is disrupted in order to provide the lambs with social stimulation.

In order to assess the stress deriving from total maternal deprivation or poor maternal care, after 24–30 h of colostrums feeding Napolitano et al. (2003) prevented a group of lambs from suckling. Thus, these animals received any kind of maternal stimuli (tactile, visual, olfactory, auditory) but not feeding which was provided by buckets. Conversely, another group was removed from their mothers and did not receive any maternal stimuli. The absence of the sucking stimulus, paired with the presence of the mother, prevented subjects to establish new substitutive bonds with their pen mates, as observed in separated lambs. In addition, the former group displayed reduced locomotion time, and higher latency time to move and cortisol levels during the isolation tests, as compared to separated animals. The authors concluded that the presence of mothers unable to fulfil lamb needs and expectations may be worse than no mothers at all.

Recover from emotional stress may be facilitated by the administration of gentle contacts by humans which may supply an additional social bond with subjects of a different animal species (Boivin et al., 2000). In sheep, the establishment of social relationship with members of other species has been previously observed (Cairns, 1966). Markowitz et al. (1998) showed that the initial days after birth could be the best period to develop this relationship, as the establishment of social preferences in lambs is very rapid (Nowak et al., 1990). As already reported, dam reared lambs separated from their mothers vocalise frequently. However, Biovin et al. (1997) showed that artificially reared lambs vocalise less in the presence of people than when alone. This effect is more apparent if the stockman that raised the lambs is present than if an unknown person is present. Recent studies (Tallet et al., 2006) showed that gentling *per se* increases affinity of artificially reared lambs for people, whereas feeding paired with gentling does not

induce any further improvement in this relationship. Based on these results the authors hypothesised that lambs may be able to develop a form of attachment to the stockperson which is independent from food provision. Biovin et al. (2001) found that gentling strongly encouraged the lambs reared without the mother to interact with the shepherd, whereas it did not induce affinity for humans in mothered lambs, thus confirming that the presence of the dam inhibits further socialization in young animals. In addition, Caroprese et al. (2006) showed that early separated animals may benefit, at least at immune level, from gentling treatment, thus reducing the risk of disease.

#### 4.2. *Reducing nutritional stress*

Artificial rearing techniques force the animals to a sudden change from maternal to reconstituted milk and deprive young animals of the maternal stimuli which facilitate suckling. Both factors may impair subsequent lamb performances. A stronger sucking response, a more rapid acceptance of the artificial teat during the first 3 days following the separation of lambs from their dams and a greater milk intake have been observed when lambs are fed ewe milk or a mix of ewe milk and a commercial milk substitute, as compared with subjects fed only milk substitute (Sevi et al., 1998, 1999). Although higher milk intakes led to faster growth in lambs receiving mixed milk in comparison with animals fed only milk substitute, both groups showed lower weight gains than those suckling from mothers, that benefited from maternal milk and more frequent meals. In addition, during an open field test the animals subjected to a gradual transition from maternal to reconstituted milk had a lower cortisol response in comparison to the lambs which experienced both the physical (diet change and lower milk consumption) and psychological stress (removal from their mothers). Lambs fed mixed milk also displayed an improvement in the cellular immune response (increased delayed type hypersensitivity to phytohemagglutinin) and in the behavioural response to open field test (reduced latency to move and increased duration of movement). These findings were confirmed by a subsequent study where dam-suckled lambs were compared to lambs separated from mothers but receiving either ewe milk or a mix of ewe milk and a milk replacer (50:50) during the first week and then both gradually moved (in 4 days) to a diet based only on milk substitute (Sevi et al., 2001). Both treatments proved to be effective in partially sustaining lamb welfare, as no differences were found in immune and endocrine responses and in growth between non-separated animals and test lambs. However, the authors concluded that even a gradual transition to a milk substitute may affect the behaviour of artificially reared lambs, as indicated by the reduced frequency of bleating expressed in the open field test. Increased levels of vocalization are generally considered a sign of stress (Alexander, 1977). However, in Sevi et al.'s study the low frequency of bleating was interpreted in terms of a reduced motivation to join the conspecifics.

Other studies aiming to reduce the negative effects of artificial rearing proposed procedures affecting both nutritional and emotional components of the stress associated with early separation. In particular, Sevi et al. (2003) performed a gradual transition from ewe-rearing to artificial rearing by separating lambs from their mothers during the daytime and rejoining them at night. However, these animals showed more behavioural, endocrine and immune disturbances, as well as a reduced weight gain, as compared to lambs subjected to sudden separation from the dams, thus the authors concluded that this strategy is not suitable to sustain the welfare of artificially reared subjects. Conversely, a delayed separation performed at 15 or 28 days of age rather than at 2 days determined a lower cortisol response to isolation, a higher humoral immune response and a higher growth rate (Napolitano et al., 1995).

## 5. Effect of early weaning on lamb welfare

When lambs are, even temporarily, separated from mothers they show evident signs of stress represented by increased levels of bleating and locomotion (Alexander, 1977). Both behaviours are aimed at maintaining contact with the ewe and help the lambs in localising, finding and identifying their mothers. Orgeur et al. (1998, 1999) observed that early weaning at 3 months of age induced lambs to emit an increased number of high pitched bleats immediately after weaning than before, and this increment was still evident 2 days after weaning. Increased vocalization and cortisol levels (the latter only for the first 60 min) were also observed in lambs weaned at 7 weeks (Mears and Brown, 1997), whereas no effect could be detected at any time after separation on  $\beta$ -endorphin concentration. Accordingly, Rhind et al. (1998) found that weaning at 4 months of age determined increased plasma cortisol concentrations, whereas no effect was observed on  $\beta$ -endorphin, or on antibody, lymphocyte and interferon- $\gamma$  responses to keyhole limpet haemocyanin. In this experiment a group of animals was immunised against ACTH. This treatment suppressed the post-weaning increase in cortisol level, although no effect on antibody response and interferon- $\gamma$  production was observed. The authors concluded that increased cortisol levels induced by weaning do not affect the immune response of lambs. In another study, the same age at weaning (4 months) had no significant effect on antibody production and experimental parasite infestation of lambs (Shaw et al., 1995).

Growth rate can be inhibited by early weaning (21–77 days) as the animals are slow in adapting to solid food consumption as a consequence of the physiological delay in ruminal development (Langland and Donald, 1975). Thus, in the weeks following weaning at 45 days, weight gain can drop due to a low consumption of grass and concentrate. The effect of weaning on growth is less marked in lambs separated from their dams at 65 days of age (Cañeque et al., 2001).

## 6. Minimising the stress of early weaning

Orgeur et al. (1998) measured the consequences of a separation progressively increased from 2 to 23 h per day over a period of 12.5 weeks before weaning which was definitively performed at 15.5 weeks of age, as compared to abrupt weaning performed at the same final age. Both methods allowed mutual communication through an open fence. The progressive weaning caused significant increments of lamb vocalization during the periods of temporary separation from mothers compared to non-separated lambs. At increasing time of separation, the vocal response was more evident during the hour before reunion, thus indicating that the increased separation was perceived by lambs as increasing discomfort. Bleating is a means of communication and can be used by lambs to be localised and identified by the dams (Morgan et al., 1975). Although at 3 months (complete weaning) these animals displayed lower levels of distress in terms of vocal activity, they suffered from the maternal separation several times and at an earlier age in comparison with subjects abruptly weaned. As a consequence, they were likely to experience a higher level of overall disturbance, as also indicated by an increased degree of parasite infestation in terms of number of excreted coccidial oocysts (Orgeur et al., 1998).

In a subsequent study (Orgeur et al., 1999), experimental animals were all abruptly weaned at 3 months. However, a group was maintained in visual and acoustic contact with their dams through an open fence (partial separation), whereas the other was moved to another barn and totally separated from mothers. Partial separation resulted in more pronounced signs of distress in terms of vocalization which was expressed more frequently and for a longer period of time. This result may be attributed to a possible frustration caused by the fact that lambs could

receive various stimuli from mothers but could not reach them to satisfy their social and nutritive needs.

Youssef et al. (1995) observed that lambs weaned at 3 months of age increased their bite rate, grazing and rumination time when grazed in group with ewes, albeit unfamiliar, thus indicating that the presence of experienced animals may positively affect their grazing performances and reduce the detrimental effects of maternal separation.

Protein supplementation enhanced the development of immunity to haemonchosis in weaning lambs of 4 months and reduced faecal worm egg counts (Shaw et al., 1995). Therefore, as also observed for artificially reared subjects, the reduction of the nutritional stress associated to a change in the diet of young animals may have beneficial effects on some indicators of welfare.

## 7. Effect of separation on ewe welfare

Repeated removal of lambs before the age of natural weaning (from 14 to 42 days of age) determined a marked behavioural response in ewes. After separation dams spend more time orientating and vocalising towards the lamb pen, standing with head raised and ears erect, and moving as compared to control animals (Cockram et al., 1993). These results, along with the decrease in times spent resting and ruminating while the lambs were absent, indicate that sheep perceive the separation from their lambs as aversive even at day 24 of treatment. Further signs of stress were limited to increased neutrophil concentration and decreased CD2 and T19 T-lymphocyte subpopulations. However, no effects of lamb removal was observed on either cortisol and  $\beta$ -endorphin levels or humoral and cellular immune responses. Accordingly, increased levels of vocalization after lamb removal were observed in ewes even if separation was progressively augmented from 2 to 23 h per day over a period of 12.5 weeks before weaning performed at 15.5 weeks of age (Orgeur et al., 1998). Orgeur et al. (1999) obtained similar results in ewes partially or totally separated from their lambs with alteration in behavioural responses and no effects at immune level. These authors also noticed that lambs seem to be more sensitive than ewes to the stress of separation as they vocalised more and exhibited a lower humoral immune response. They suggested that as the ewes were multiparous, they had already experienced the separation several times. However, these results can also be explained on the basis of the parental–offspring conflict theory, as mothers can rely on several offspring, whereas the lamb can only count on one mother. In addition, the former is dependent on the latter, but not vice versa.

Detrimental effects of separation have been detected on ewe behaviour and milk production even if only one of the twin lambs is removed within 24–36 h after parturition (Deligeorgis and Bizelis, 1998). In particular, separated ewes were observed standing more often, spent less time resting and gave lower milk yields than non-separated animals.

## 8. Conclusion

Premature separation from mothers has clear and marked detrimental effects on various functions of young animals, even in a precocial species such as sheep. Artificial rearing determines negative effects at behavioural, endocrine and immune levels, whereas early weaning performed at 3–4 months of age usually affects lamb behaviour only. Such findings are not surprising as lambs acquire increasing independence with age. In addition, it can be hypothesised that behavioural measurements are more sensitive for the detection of stressful conditions as compared to other commonly used endocrine or immune indicators of welfare.

Some methods aimed at alleviating the emotional (e.g. provision of substitutive social bonds) and/or nutritional stress (e.g. gradual transition from maternal to reconstituted milk) associated with the disruption of the mother–young relationship are able to improve, at least partially, lamb post-separation performances. Conversely, different methods based on gradual or partial separation from mothers are less effective in reducing the impact of both artificial rearing and early weaning, and in some cases their effects can be even worse than those caused by abrupt separation. In fact, the lambs are either forced to experience several times maternal deprivation or frustrated in reaching full contact with their mothers which exacerbate the negative effects of separation. Natural weaning is a gradual process involving complex mechanisms of mutual communication between ewes and their offspring which leads to minimal separation stress. However, such mechanisms are not activated before the age of natural weaning. Thus, at an early age animals perceive these farming or experimental practices as noxious.

## References

- Alberts, J., May, B., 1984. Non-nutritive, thermotactile induction of filial huddling in rat pups. *Dev. Psychobiol.* 17, 161–181.
- Alexander, G., 1977. Role of auditory cues in mutual recognition between ewes and lambs in Merino sheep. *Appl. Anim. Ethol.* 3, 65–81.
- Alexander, G., 1988. What makes a good mother? Components and comparative aspects of maternal behaviour in ungulates. *Proc. Aust. Soc. Anim. Prod.* 17, 25–41.
- Alexander, G., Shillito Walser, E.E., 1978. Visual discrimination between ewes by lambs. *Appl. Anim. Ethol.* 4, 81–85.
- Arnold, G.W., Morgan, P.D., 1975. Behaviour of ewe and lamb at lambing and its relationship to lamb mortality. *Appl. Anim. Ethol.* 2, 25–46.
- Arnold, G.W., Grassia, A., 1985. Spatial relationship between ewes and lambs. *Appl. Anim. Behav. Sci.* 14, 253–261.
- Bechet, G., Theriez, M., Prache, S., 1989. Feeding behaviour of milk-fed lambs at pasture. *Small Rumin. Res.* 2, 119–132.
- Berger, J., 1979. Weaning conflict in Desert and Mountain Bighorn sheep (*Ovis canadensis*): an ecological interpretation. *Z. Tierpsychol.* 50, 188–200.
- Biovin, X., Nowak, R., Després, G., Tournadre, E., Le Neindre, P., 1997. Discrimination between shepherds by lambs reared under artificial conditions. *J. Anim. Sci.* 75, 2892–2898.
- Biovin, X., Nowak, R., Terrazas Garcia, A., 2001. The presence of the dam affects the efficiency of gentling and feeding on the early establishment of the stockperson–lamb relationship. *Appl. Anim. Behav. Sci.* 72, 89–103.
- Boivin, X., Tournadre, E., Le Neindre, P., 2000. Hand-feeding and gentling influence early weaned lamb's attachment responses to their stockperson. *J. Anim. Sci.* 78, 879–884.
- Bonnette, E.D., Kornegay, E.T., Lindemann, M.D., Notter, D.R., 1990. Influence of two supplemental vitamin E levels and weaning age on performance, humoral antibody production and serum cortisol levels of pigs. *J. Anim. Sci.* 687, 1346–1353.
- Brake, S.C., 1981. Suckling infant rats learn a preference for a novel olfactory stimulus paired with milk delivery. *Science* 211, 506–508.
- Cairns, R.B., 1966. Development, maintenance, and extinction of social attachment behaviour in sheep. *J. Comp. Physiol. Psychol.* 62, 298–306.
- Cañeque, V., Velasco, S., Diaz, M., Perez, C., Huidobro, F., Lauzurica, S., Manzanares, C., Gonzalez, J., 2001. Effects of weaning age and slaughter weight on carcass and meat quality of Talaverana breed lambs raised at pasture. *Anim. Sci.* 73, 85–95.
- Caroprese, M., Napolitano, F., Albenzio, G., Annicchiarico, G., Musto, M., Sevi, A., 2006. Influence of gentling on lamb immune response and human–lamb interaction. *Appl. Anim. Behav. Sci.* 99, 118–131.
- Cockram, M.S., Imlah, P., Goddard, P.J., Harkiss, G.D., Waran, N.K., 1993. The behavioural, endocrine and leucocyte response of ewes to repeated removal of lambs before the age of natural weaning. *Appl. Anim. Behav. Sci.* 38, 127–142.
- Coppinger, T.R., Minton, J.E., Reddy, P.G., Blecha, F., 1991. Repeated restraint and isolation stress in lambs increases pituitary-adrenal secretions and reduces cell-mediated immunity. *J. Anim. Sci.* 69, 2808–2814.

- Deligeorgis, S., Bizelis, J., 1998. Effects of early weaning system on milk production and the pre- and post-weaning behaviour in Karagouniko ewes and their lambs. In: *Proceedings of the Sixth International Symposium on the Milking of Small Ruminants*, vol. 95. EAAP Publication, pp. 298–301.
- De Pasillé, A.M.B., Metz, J.H.M., Mekking, P., Wiepkema, P.R., 1992. Does drinking milk stimulate suckling in young calves? *Appl. Anim. Behav. Sci.* 34, 23–36.
- De Pasillé, A.M.B., Christopherson, R., Rushe, J., 1993. Non-nutritive sucking by the calf and postprandial secretion of insulin, CCK, and gastrin. *Physiol. Behav.* 54, 1069–1073.
- Dwyer, C.M., 2003. Behavioural development in the neonatal lamb: effect of maternal and birth-related factors. *Theriogenology* 59, 1027–1050.
- Dwyer, C.M., Gilbert, C.L., Lawrence, A.B., 2004. Prepartum plasma estradiol and postpartum cortisol, but not oxytocin, are associated with interindividual and breed differences in the expression of maternal behaviour in sheep. *Horm. Behav.* 46, 529–543.
- Dwyer, C.M., Calvert, S.K., Farish, M., Donbavand, J., Pickup, H.E., 2005. Breed, litter and parity effects on placental weight and placentome number, and consequences for the neonatal behaviour of the lamb. *Theriogenology* 63, 1092–1110.
- Farm Animal Welfare Council, 1993. Report on priorities for Animal Welfare and Research. Farm Animal Welfare Council, Surbiton, UK.
- Godfray, H.C.J., 1995. Evolutionary theory of parent–offspring conflict. *Nature* 376, 133–138.
- Gordon, K., Siegmann, M., 1991. Suckling behaviour of ewes in early lactation. *Physiol. Behav.* 50, 1079–1081.
- Goursaud, A.P., Nowak, R., 1999. Colostrum mediates the development of mother preference by newborn lambs. *Physiol. Behav.* 67, 49–56.
- Griffin, J.F.T., 1989. Stress and immunity: a unifying concept. *Vet. Immunol. Immunopathol.* 20, 263–312.
- Grubb, P., Jewell, P., 1966. Social grouping and home range in feral Soay sheep. *Symp. Zool. Soc. London* 18, 179–210.
- Gwazdauskas, F.C., Gross, W.B., Bibb, T.L., McGillard, M.L., 1978. Antibody titres and plasma glucocorticoid concentrations near weaning in steer and heifer calves. *Can. Vet. J.* 19, 150–154.
- Hinch, G.N., Lynch, J.J., Elwin, R.L., Green, G.C., 1990. Long-term associations between Merino ewes and their offspring. *Appl. Anim. Behav. Sci.* 27, 93–103.
- Jensen, P., Recen, B., 1989. When to wean—observation from free-ranging domestic pigs. *Appl. Anim. Behav. Sci.* 23, 14–25.
- Keverne, E.B., Levy, F., Poindron, P., Lindsay, D.R., 1982. Vaginal stimulation: an important determinant of maternal bonding in sheep. *Science* 219, 81–83.
- Langland, J.P., Donald, G.E., 1975. The intakes and growth rate of grazing Border Leicester × Merino lambs weaned at 21, 49 and 77 days. *Anim. Prod.* 21, 175–181.
- Lawrence, A.B., 1990. Mother–daughter and peer relationships of Scottish hill sheep. *Anim. Behav.* 39, 481–486.
- Lawrence, A.B., 1991. Mother–daughter bonds in sheep. *Anim. Behav.* 42, 683–685.
- Levine, S., 2001. Primary social relationships influence the development of the hypothalamic–pituitary–adrenal axis in the rat. *Physiol. Behav.* 73, 255–260.
- Lévy, F., Poindron, P., Le Neindre, P., 1983. Attraction and repulsion by amniotic fluids and their olfactory control in ewe around parturition. *Physiol. Behav.* 31, 687–692.
- Lévy, F., Gervais, R., Kindermann, U., Litterio, M., Poindron, P., Porter, R., 1991. Effects of early postpartum separation on maintenance of maternal responsiveness and selectivity in parturient ewes. *Appl. Anim. Behav. Sci.* 31, 101–110.
- L'Heureux, N., Lucherini, M., Festa-Bianchet, M., Jorgenson, J.T., 1995. Density-dependent mother–yearling association in bighorn sheep. *Anim. Behav.* 49, 901–910.
- Lyford, S.J., 1988. Growth and development of the ruminant digestive system. In: Curch, D.C. (Ed.), *The Ruminant Animal*. Prentice-Hall, New Jersey, pp. 44–63.
- Lynch, J.J., Hinch, G.N., Adams, D.B., 1992. The Behaviour of Sheep. Biological principles and Implications for Production, vol. X. CAB International, Wallingford, UK., p. 237.
- Markowitz, T.M., Dally, M.R., gursky, K., Price, E.O., 1998. Early handling increases lamb affinity for humans. *Anim. Behav.* 55, 573–587.
- Matthews, L.R., Kilgour, R., 1979. Learning and associated factors in ruminant feeding behaviour. In: *Proceedings of the 5th International Symposium Ruminant Physiology*. Clermont-Ferrand, (Chapter 6), pp. 123–144.
- Mears, G.J., Brown, F.A., 1997. Cortisol and b-endorphin responses to physical and psychological stressors in lambs. *Canad. J. Anim. Sci.* 77, 689–694.
- Minton, J.E., Coppinger, T.R., Reddy, P.G., Davis, W.C., Blecha, F., 1992. Repeated restraint and isolation stress alters adrenal and lymphocyte functions and some leukocyte differentiation antigens in lambs. *J. Anim. Sci.* 70, 1126–1132.

- Moberg, P.D., Arnold, G.W., 1974. Behavioural relationship between merino ewes and lambs during the four weeks after birth. *Anim. Prod.* 19, 169–176.
- Moberg, G.P., Anderson, C.O., Underwood, T.R., 1980. Ontogeny of the adrenal response of lambs to emotional stress. *J. Anim. Sci.* 51, 138–142.
- Moberg, G.P., Wood, V.A., 1982. Effect of differential rearing on the behavioural and adrenocortical response of lambs to a novel environment. *Appl. Anim. Ethol.* 8, 269–279.
- Morgan, P.D., Boundy, C.A.P., Arnold, G.W., Lindsay, D.R., 1975. The roles played by the senses of the ewe in the location and recognition of lambs. *Appl. Anim. Ethol.* 1, 139–150.
- Munck, A., Guyre, P.M., Holdbrok, J., 1984. Physiological functions of glucocorticoids in stress and their relation to pharmacological actions. *Endocr. Rev.* 5, 25–44.
- Napolitano, F., Marino, V., De Rosa, G., Capparelli, R., Bordi, A., 1995. Influence of artificial rearing on behavioural and immune response of lambs. *Appl. Anim. Behav. Sci.* 45, 245–253.
- Napolitano, F., Braghieri, A., Cifuni, G.F., Pacelli, C., Girolami, A., 2002a. Behaviour and meat production of organically farmed unweaned lambs. *Small Rumin. Res.* 43, 179–184.
- Napolitano, F., Cifuni, G.F., Pacelli, C., Riviezzzi, A.M., Girolami, A., 2002b. Effect of artificial rearing on lamb welfare and meat quality. *Meat Sci.* 60, 307–315.
- Napolitano, F., Annicchiarico, G., Caroprese, M., De Rosa, G., Taibi, L., Sevi, A., 2003. Lambs prevented from suckling their mothers display behavioural, immune and endocrine disturbances. *Physiol. Behav.* 78, 81–89.
- Nowak, R., 1990. Mother and sibling discrimination at a distance by three- to seven-day-old lambs. *Dev. Psychobiol.* 23, 285–295.
- Nowak, R., Lindsay, D.R., 1990. Effect of breed and litter size on mother discrimination by 12-h-old lambs. *Behaviour* 115, 1–13.
- Nowak, R., Poindron, P., Putu, I.G., 1990. Development of mother discrimination by single and multiple newborn lambs. *Dev. Psychobiol.* 22, 833–845.
- Nowak, R., Murphy, T.M., Lindsay, D.R., Alster, P., Andersson, R., Uvnäs-Moberg, K., 1997. Development of a preferential relationship with the mother by the newborn lamb: importance of the sucking activity. *Physiol. Behav.* 62, 681–688.
- Nowak, R., Breton, G., Mellot, E., 2001. CCK and development of mother preference in sheep: a neonatal time course study. *Peptides* 22, 1309–1316.
- Orgeur, P., Mavric, N., Yvore, P., Bernard, S., Nowak, R., Schaal, B., Lévy, F., 1998. Artificial weaning in sheep: consequences on behavioural, hormonal and immuno-pathological indicators of welfare. *Appl. Anim. Behav. Sci.* 58, 87–103.
- Orgeur, P., Bernard, S., Naciri, M., Nowak, R., Schaal, B., Lévy, F., 1999. Psychological consequences of two different weaning methods in sheep. *Reprod. Nutr. Dev.* 39, 231–244.
- Penning, P.D., Gibb, M.J., 1979. The effect of milk intake on the intake of cut and grazed herbage by lambs. *Anim. Prod.* 29, 53–67.
- Poindron, P., Le Neindre, P., 1980. Endocrine and sensory regulation of maternal behaviour in the ewe. *Adv. Study Behav.* 11, 75–119.
- Poindron, P., Lévy, F., 1990. Physiological, sensory and experiential determinants of maternal behaviour in sheep. In: Krasnegor, N.A., Bridges, R.S. (Eds.), *Mammalian Parenting*. Oxford University Press, Oxford, UK, pp. 133–156.
- Porter, R.H., Nowak, R., Orgeur, P., 1995. Influence of a conspecific agemate on distress bleating by lambs. *Appl. Anim. Behav. Sci.* 45, 239–244.
- Pryce, C.R., 1992. A comparative systems model of the regulation of maternal motivation in mammals. *Anim. Behav.* 43, 417–441.
- Rhind, S.M., Reid, H.W., McMillen, S.R., Palmarini, G., 1998. The role of cortisol and  $\beta$ -endorphin in the response of the immune system to weaning in lambs. *Anim. Sci.* 66, 397–402.
- Rowell, T.E., 1991. Till death us do part: long-lasting bonds between ewes and their daughters. *Anim. Behav.* 42, 681–682.
- Rushen, J., 2000. Some issues in the interpretation of behavioural responses to stress. In: Moberg, G.P., Mench, J.A. (Eds.), *The Biology of Animal Stress—Basic Principles and Implications for Animal Welfare*. CABI, UK, pp. 23–42.
- Sevi, A., Casamassima, D., Danese, G., 1998. The effect of type of milk on sucking response of artificially reared lambs. *Zootec. Nutr. Anim.* 24, 85–93.
- Sevi, A., Napolitano, F., Casamassima, D., Annicchiarico, G., Quarantelli, T., De Paola, R., 1999. Effect of gradual transition from maternal to reconstituted milk on behavioural, endocrine and immune responses of lambs. *Appl. Anim. Behav. Sci.* 64, 249–259.
- Sevi, A., Napolitano, F., Casamassima, D., Dell'Aquila, S., 2001. Effect of milk source on welfare and weight gain of lambs. *Anim. Welfare* 10, 163–172.

- Sevi, A., Caroprese, M., Annicchiarico, G., Albenzio, M., Taibi, L., Muscio, A., 2003. The effect of a gradual separation from the mother on later behavioural, immune and endocrine alterations in artificially reared lambs. *Appl. Anim. Behav. Sci.* 83, 41–53.
- Shaw, K.L., Nolan, J.V., Lynch, J.J., Coverdale, O.R., Gill, H.S., 1995. Effects of weaning, supplementation and gender on acquired immunity to *Haemonchus contortus* in lambs. *Int. J. Parasitol.* 25, 381–387.
- Shillito, E.E., 1975. A comparison of the role of vision and hearing in lambs finding their own dams. *Appl. Anim. Ethol.* 1, 369–377.
- Slee, J., Springbett, A., 1986. Early postnatal behaviour in lambs of ten breeds. *Appl. Anim. Behav. Sci.* 15, 229–240.
- Stephens, D.B., Baldwin, B.A., 1971. Observations on the behaviour of groups of artificially reared lambs. *Res. Vet. Sci.* 12, 219–224.
- Tallet, C., Veissier, I., Boivin, X., 2006. Human contact and feeding as rewards for the lamb's affinity to their stockperson. *Appl. Anim. Behav. Sci.* 94, 59–73.
- Thorhallsdottir, A.G., Provenza, F.D., Balph, D.F., 1990. The role of the mother in the intake of harmful foods by lambs. *Appl. Anim. Behav. Sci.* 25, 35–44.
- Toates, F.M., Jensen, P., 1991. Ethological and psychological models of motivation—towards a synthesis. In: Meyer, J.A., Wilson, S. (Eds.), *From Animals to Animats*. MIT Press, Cambridge, pp. 194–205.
- Val-Laillet, D., Nowak, R., 2006. Socio-spatial criteria are important for the establishment of maternal preference in lambs. *Appl. Anim. Behav. Sci.* 96, 269–280.
- Vandenheede, M., Bouissou, M.F., Picard, M., 1998. Interpretation of behavioural reactions of sheep towards fear-eliciting situations. *Appl. Anim. Behav. Sci.* 58, 293–310.
- Vince, M., 1993. Newborn lambs and their dams: the interaction that leads to suckling. *Adv. Study Behav.* 22, 239–268.
- Vince, M.A., Lynch, J.J., Mottershead, B.E., Green, G.C., Elwin, R.L., 1985. Sensory factors involved in immediately postnatal ewe/lamb bonding. *Behaviour* 94, 60–84.
- Winfield, C., Kilgour, R., 1976. A study of the following behaviour in young lambs. *Appl. Anim. Ethol.* 2, 235–243.
- Youssef, M.Y.I., Philips, C.J.C., Metwally, M., 1995. The effect of pre-weaning grazing experience and presence of adult ewes on grazing behaviour of weaned lambs. *Appl. Anim. Behav. Sci.* 44, 257–281.
- Zito, C.A., Wilson, L.L., Graves, H.B., 1977. Some effects of social deprivation on behavioural development of lambs. *Appl. Anim. Ethol.* 3, 367–377.