EVALUATION OF STRATEGIES FOR LAMBING MANAGEMENT

A Thesis

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Master of Science

by

Natasha Lee Pettifor

January, 2012

ABSTRACT

Predicting ewe maternal success and measuring maternal bond strength remain, to an extent, topics of mystery. The optimization of management strategies will always be an important goal for any livestock farmer. Optimizing maternal success at lambing time is an essential point of focus for any farmer hoping to profit from his or her flock of sheep. As more is understood about the behavioral tendencies related to maternal success, management systems will be tailored to lower labor requirements, making sheep farming less stressful for those involved and encouraging the growth of the sheep industry. Any tactic that can work toward the goals of decreased labor and increased production, while preserving or enhancing animal welfare, should continue to be thoroughly explored. Allowing for and encouraging the natural expression of innate behaviors to achieve these goals, particularly including maternal behavior, will remain an important area of focus in keeping sheep production viable.

BIOGRAPHICAL SKETCH

Natasha Pettifor was born in Naples, Florida on November 16^{th}, 1982. While still in high school, she volunteered in molecular biology and biochemistry laboratories at the University of Florida College of Veterinary Medicine and Florida Gulf Coast University. After graduation from Gulf Coast High School in 2001, she briefly attended the University of South Florida, during which time she worked in a molecular biology research laboratory at the College of Medicine studying the role of an upstream AUG in the regulation of nitric oxide synthase. In 2003, Natasha transferred to New College of Florida, where she was delighted to work for three years in the laboratory of her undergraduate mentor, Dr. Katherine Walstrom, on projects ranging from various examinations of RNA helicase A in the C. elegans germline to the identification of novel RNA transcripts extracted from coral mucus samples. While at New College, Natasha participated in an NSF REU internship at Indiana University in Bloomington in the laboratory of Dr. William Timberlake, assisting with a project of stereotyped behaviors in zoo walruses and conducting research on spatial learning in rats. This research would become her undergraduate honors thesis, "Spatial Learning in the Floor Maze with *Rattus norvegicus",* under the guidance of Dr. Gordon Bauer. Natasha graduated from New College of Florida in 2006, and after another brief stint at the University of South Florida, began her Master's work at Cornell University under Dr. Michael Thonney in the Department of Animal Science, in 2008. Since then, she has studied maternal behavior in ewes and learned much about the practice of running a sheep farm. She has spoken regularly to local sheep and goat farmers through Cooperative Extension activities, and presented a poster at the 2010 Joint Annual Meeting of the American Society of Animal Science. She plans to continue her PhD work in this same area, as an expansion of her current research.

To Giggi

ACKNOWLEDGMENTS

The author wishes to thank, above all, Dr. Michael L. Thonney, advisor and chairperson of the author's special committee, for his invaluable help, advice and support in the manifestation of this project and the innumerable other learning opportunities which the author has been afforded. Without his assistance and encouragement, none of this would have been possible.

The author also wishes to thank Dr. Daniel Brown and Dr. Robert Johnston for their help and advice in serving as members of the author's committee.

Many thanks are extended to Lisa Furman as manager of the Cornell Sheep Farm, the functional operation of which enables this and further sheep production research. Thanks also to tatiana Stanton, for her assistance with research tasks, and also to numerous sheep farm interns and employees whose labor made this research achievable.

Table of Contents

BIOGRAPHICAL SKETCH III

ACKNOWLEDGMENTS V

LIST OF FIGURES VII

LIST OF TABLES VIII

CHAPTER ONE MATERNAL CARE AND BONDING IN SHEEP 1

Ewes' bonds toward their lambs 3

Lambs' bonds toward their dams 9

CHAPTER TWO TEMPERAMENT AND MEASURES OF MATERNAL ABILITY 15

CHAPTER THREE MANAGEMENT 32

CHAPTER FOUR EVALUATION OF ALTERNATIVE STRATEGIES IN LAMBING MANAGEMENT 45

Materials and Methods 47
- Experiment 1 47
- Experiment 2 54

Results 58
- Experiment 1 58
- Experiment 2 61

Discussion 65

CONCLUSIONS 71

WORKS CITED 73

LIST OF FIGURES

Figure 1. Pathways involved in the onset of maternal responsiveness in the ewe (Poindron et al., 2007a).......... 4

Figure 2. This figure from Sébe et al. (2010) shows the results of lamb exposure to high and low vocalizations from their own and unfamiliar dams. The y-axis is a measure of lamb response, where negative scores represent stronger response. The white box in each column shows responses to the lamb's own mother, while gray boxes refer to unfamiliar dams. (a) shows responses to low and high pitched beats; (b) shows responses to high pitched bleats for ewes hidden out of sight; (c) shows responses to high-pitched recoded bleats and (d) shows responses to low-pitched recorded bleats. 13

Figure 3. Diagram of the lambing pen in Experiment 1, with distances and cubicle locations shown.......... 49

Figure 4. Example of a path taken (shown by the arrows) during the MMBS test. 52

Figure 5. Diagram of the 2-choice testing setup, with a ewe shown as having entered the testing pen through a gated chute system. 53

Figure 6. Distribution of modified maternal behavioral scores by lambing location 60

Figure 7. Mean percent of time spent oriented to offspring in the two choice test. 61

Figure 8. Mean Weight Per Day of Age (WPDA) for lambs in both treatment groups and seasons 63

Figure 9. Mean WPDA for each group, by ewe age 64

LIST OF TABLES

Table 1. Rubric for Modified Maternal Behavior Score 51
Table 2. Number of ewes in each category 55
Table 3. Maternal Behavior Score Rubic, as used in Experiment 2 (O'Connor, 1996). ... 55
Table 4. Ethogram for focal observations of lactating ewes on pasture. 56
Table 5. Initial linear model used to quantify the effect of experimental variables on weight per day of age (WPDA). 57
Table 6. Cubicle use and area in experiment 1. 58
Table 7. Effect of lambing location on weight per day of age (WPDA), modified maternal behavior score (MMBS), and percentage of time (Time) spent by the ewes facing their own lambs in a two-choice test. 59
Table 8. Numbers of lambs for various categories. 61
Table 9. Effect of lambing type, season, and litter size on grams of weight per day of age (WPDA)[a]. 62
Table 10. Analysis of variance for weight per day of age (WPDA). 64

Chapter One

Maternal Care and Bonding in Sheep

As a general rule, mammalian mothers make a sizeable investment into maternal care. Most can recognize their own young shortly after birth and can differentiate between their own and alien young at any point between birth and weaning. Mothers of many species, including rats and mice, willingly accept foreign young introduced to their litters after parturition despite this discriminatory ability. In contrast, other species, particularly including ruminants, form exclusive bonds to specific neonates within a few hours of birth. These neonates must be present during a hormonally-driven sensitive period, and must exhibit at least some of a specific set of cues for the dam to accept the infant and form this exclusive bond.

The origins of the need for this selective and exclusive bonding can be understood by examining the ecological history of flocking ruminants such as sheep. Living in large social groups, without nesting sites or dens, young ruminants are precocious and can stand and run within a few hours of birth, and must be able to easily reunite with their dam upon separation. The dams of wild or extensively-managed sheep and goats generally separate from the flock for long enough to give birth and form a secure bond with their offspring, but return to the flock before the young are more than a couple days of age. Flock structure offers some safety from predation, but with a large number of individuals in a small area, a strong mother-to-offspring bond is necessary if young ruminants are to receive adequate maternal care and not become lost or disoriented in the crowd, and if the mother is not to mistakenly distribute her limited resources to foreign offspring (Porter et al., 1991).

The bonding process occurs internally, as a series of hormonal events, and externally, as a series of behaviors linked by modal perception. The hormonal processes underlying maternal bonding in small ruminants are similar to or the same as those involved in other mammalian species, though the resulting behaviors and cues are often more species-specific, adapted to flock life and range or pastoral conditions, among other factors.

The sensitive period for maternal bonding in sheep and goats begins during birth or a short time before giving birth, and bonding appears to occur within 2.5 to 6 hours, with some individual variation. This period has been suggested to be an example of imprinting in adulthood (Poindron et al., 2007b). The activation of the sensitive period that allows for formation of this bond is driven by a series of hormonal processes, reinforced by learning and experience.

Behaviorally, after the hormonally driven contractions that physically account for the mechanism of birth, ewes and lambs follow a script that ensures fitness and bonding. On the ewe's side, licking the lamb and uttering low-pitched bleats and rumbles are important post-natal behaviors. The lamb opens its eyes at once and has been functionally listening since before birth; visual and auditory stimuli are immediately relevant to the newborn lamb. The low-pitched noises and licking of the ewe calm the lamb and depress its movements, while movement by the ewe makes the lamb more energetic. The lamb shakes its head, raises its ears and begins a pattern of behavior that results in standing: it raises onto its sternum, then knees, then straightens its rear legs and finally its forelegs (Vince, 1993).

As the lamb stands, it begins its search for the udder. The cues that lead the lamb to the correct location are primarily visual and tactile. The lamb instinctively makes “munching” movements with its mouth in response to touch on the top of its face and will place its head under any object that projects at about head height. Additionally, the wool-free areas of a sheep’s underbelly, particularly the udder and inguinal area, are much more warm than insulated, wool-covered areas, so the lamb may use this to locate the udder. Lambs stereotypically begin searching around the neck of the ewe and progress toward the udder along the side. A cooperative and responsive ewe will arch her back and lift her hind leg to allow the lamb easier access to the udder. While repeated circling can be detrimental to nursing, it appears that a ewe turning in a circle can work to help the lamb’s progression toward the udder. When a ewe circles, she brings the lamb back to her head, in an appropriate position to begin the udder-seeking sequence once again (Vince, 1993).

Ewes’ bonds toward their lambs

Preparation for maternal behavior begins during pregnancy. Circulating progesterone, known in part for it’s actions in maintaining pregnancy, rises slowly during the course of gestation, and falls sharply just before labor begins. While progesterone drops, estrogen levels rise. Estradiol is the primary estrogen in sheep, and this combination of falling progesterone levels combined with increased circulating estradiol is known to trigger the onset of maternal behaviors. At this same time, prolactin levels are also increasing; this hormone as well is known to play a role in maternal behavior but is best known for its role in milk production (Kendrick and Keverne, 1991).

The hormonal state that drives maternal behavior can often be observed before the birth process, with ewes showing an attraction to amniotic fluid and general maternal responsiveness for several hours preceding birth. In most cases, and particularly for primiparas (first-time mothers), vaginocervial stimulation (VCS) at the time of birth is necessary to stimulate neural oxytocin-based systems, leading to full-strength maternal responses. Physical stretching and general physical sensations in the vagina, cervix and uterus cause oxytocin release and increased activity of oxytocinergic neurons in widespread areas of the brain. This is one of the pathways shown in Figure 1. Areas of particular importance are the paraventricular nucleus of the hypothalamus (PVN), the medial preoptic area (MPOA), the bed nucleus of the stria terminalus (BNST) and the main olfactory bulb (MOB) (Kendrick, 2000).

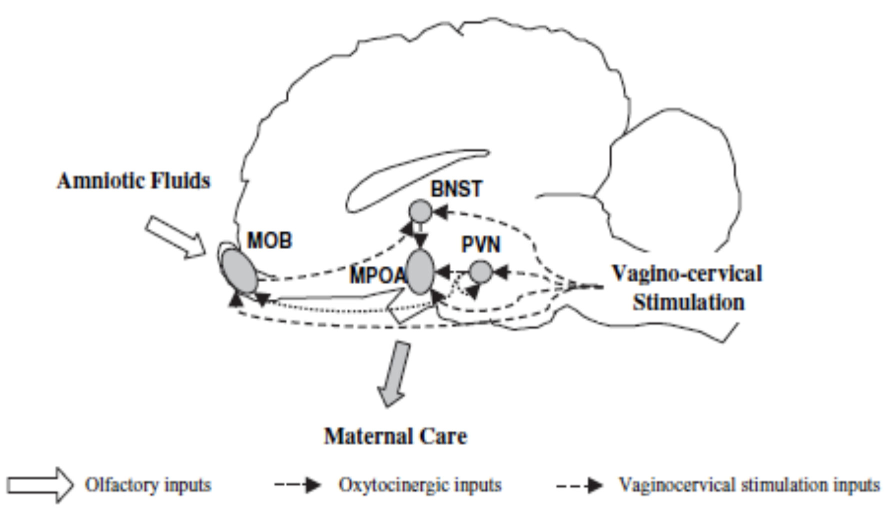

Figure 1. Pathways involved in the onset of maternal responsiveness in the ewe (Poindron et al., 2007a).

As mentioned above, VCS is necessary for the induction of the full range of maternal behaviors in inexperienced ewes. Lévy et al. (1992) demonstrated that this is related to oxytocin (OT) levels, as measured in the cerebrospinal fluid (CSF). This was accomplished by peridurally anesthetizing primparous ewes prior to labor, completely inhibiting afferent input from the nerves in the genital tract and surrounding motor nerves. In one experiment, OT levels were compared between these anesthetized ewes and non-anesthetized counterparts, and while the results were not completely unambiguous, OT was significantly higher in the group that did not receive peridural anesthesia. In a second experiment, a group of all-primiparous ewes received peridural anesthesia, and maternal responsiveness was measured by amount of licking and lack of rejection behaviors. Intracerebroventricular (ICV) infusions of OT were given to non-maternal ewes. This ICV OT was sufficient to instate maternal behavior in the non-maternal ewes, and these effects were found to be long-lasting. These results all support the idea that VCS, through nerve inputs from the genital region, results in OT release that is necessary for a full maternal response in nulliparous ewes

In addition to general maternal responses such as licking, bleats, and decreased rejection behaviors, VCS appears to facilitate an attraction toward amniotic fluid. When the peridurally anesthetized ewes in the experiment of Lévy et al. (1992) were offered a choice between feed troughs containing amniotic fluid or free of amniotic fluid, significantly more "maternal" ewes chose to eat from the amniotic fluid-containing trough, and to spend more time at that trough, while non-maternal ewes, and ewes tested 2 days prior to parturition spent significantly more time at the amniotic fluid-free trough. The role of VCS in this increased attraction to amniotic fluid can be related to the importance of VCS in not just maternal responsiveness, but also in the development of maternal selectivity. Exposure to amniotic fluid and increased oxytocinergic neuronal activity in the main olfactory bulb related to the smell of the amniotic fluid plays an important role in the development of selective olfactory memories, the first step in sheep maternal selectivity.

Maternal exposure to young over extended periods (at minimum, several days) can create maternal behavior without an initial burst of oxytocin, but the presence of the initial burst driven by VCS allows for a time-sensitive, rapid and selective enhancement of the classical neurotransmitter systems that drive bond formation (Kendrick and Keverne, 1991). Kendrick (2000) suggests that this triggered sensitive period could have evolved as an evolutionary mechanism to fast-track the initiation of maternal behaviors and drives, a particularly useful trait in a species that needs to bond quickly to its young and rejoin its social group in a short period of time.

Maternal experience causes permanent morphological changes in the brain, and that the effect of past experience helps drive bond formation in sheep. The effects on lambs of having an experienced ewe for a dam have been studied in numerous fashions. Older ewes are more successful mothers (Hatcher et al., 2010; O'Connor et al., 1985; Sawalha et al., 2007), and multiparous ewes (having experienced multiple parities) are less emotionally reactive and fearful (Vierin, 2002).

In addition to measures of production, multiparous ewes display different underlying hormonal states. They only require short-term treatment with progesterone and estrogen before ICV oxytocin will initiate maternal behavior. In primiparous ewes, in contrast, a much longer course of hormone treatment, 6-8 weeks worth – enough to induce lactation – is necessary before ICV oxytocin is sufficient to initiate maternal behavior (Kendrick and Keverne, 1991).

Maternal behavior in sheep can be seen as two sets of processes: 1) maternal responsiveness; and 2) maternal selectivity. Maternal responsiveness is the general willingness to accept and care for young, while selectivity is a result of the discriminative bond in ungulates having precocial young. Responsiveness occurs immediately at and even before birth, while selectivity requires time to develop, a result of hormonal processes and the learning of specific cues; particularly olfactory but also visual and auditory cues. In sheep, the bonding process requires as little as 2 to 4 hours, though selectivity does not persist for as long in ewes with only a few hours of exposure as in ewes with a week of exposure. In the former case, 24 hours of separation was enough to eliminate selectivity, while in the latter case, it appeared to take 3 days of separation for the ewe to fail to retain selectivity (Keller et al., 2003; Levy, 2008).

Olfactory learning drives the development of selectivity, but olfaction is not completely necessary for lamb identification. Ewes that are separated from – but can smell – their lambs form normal selectivity. But, if a barrier such as glass, through which odors cannot pass, separates ewe and lamb, then selectivity does not form normally. The same is true for ewes rendered anosmic (generally by flushing the olfactory epithelia with a corrosive liquid or ablating the main olfactory bulb.) Anosmic ewes will eventually, over the course of weeks, develop selectivity toward lambs with which they are consistently associated, rejecting foreign lambs attempts at nursing, but never showing the level of maternal aggression toward foreign lambs seen in non-anosmic control ewes. This suggests that olfactory cues may drive aggression toward foreign lambs, above their role in discrimination. At only 12 hours post-parturition, anosmic ewes do show preference for their own lamb in a two-choice test, but do not show rejection behaviors toward foreign lambs. It appears that olfaction is required for discrimination at the udder and is used at close distances, while auditory and visual cues are necessary for distance recognition and are sufficient for lamb identification after 12 hours (Ferreira et al., 2000).

The particular cues used for non-olfactory recognition between ewes and their lambs have been the subject of a moderate number of investigations. Sébe et al. (2007) examined the ability of ewes to discriminate between their own and alien young on only the basis of auditory cues. The ewes used in the study were kept in claiming pens for 6 hours after giving birth before being moved to communal mixing pens. Two-choice tests of discrimination were performed at 6, 24 and 48 hours after parturition for ewes and 12, 24 and 48 hours of age for lambs. To test ewe identification of lambs, ewes were presented with a choice between their own lamb on one side of a testing pen, and an alien lamb on the opposing side of the pen. Lambs were hidden behind an opaque canvas, at a distance from which ewes would not be able to use olfactory cues. Lambs were tested in the same procedure, with ewes hidden behind opaque canvas. The time which the ewe or lamb being tested spent in "proximity zones" (areas closest to each hidden individual) was recorded and time spent near the ewe's own lamb used as a measurement of lamb discrimination. Ewes were able to discriminate their own lambs' vocalizations as early as 24 hours after parturition, while lambs were able to identify their dams at 48 hours of age.

While sheep have become well known for facial recognition in the past few years (Kendrick et al., 2001), it does not appear to play a large role in visual recognition of lambs. Kendrick (1996) easily trained sheep to discriminate between pictures of faces of adult sheep, but discrimination for lamb faces had very low rates of success. However, some studies have shown that ewes can recognize their own lambs when olfactory and acoustic cues are removed; particularly Lindsay and Fletcher (1968), who found that recognition of lambs by their dams was reduced but not entirely eliminated under such circumstances. However, this study also found reduced recognition in ewes exposed to only olfactory and acoustic cues, and the methods are fairly different from those used in more modern discrimination tasks. One example of this was the use of a T-maze, with 6 ewes tested a total of 90 times. In more recent ewe-lamb discrimination work discrimination responses by ewes declined noticeably after the third trial, as ewes learn that they cannot reach their lambs (Sébe et al., 2007). While the paper of Lindsay and Fletcher (1968) has been repeatedly cited as evidence for visual recognition, most recent publications focus on "recognition at a distance," a combination of auditory and visual cues, and the specific area of visual recognition would be well-served by further study.

Lambs' bonds toward their dams

While the ewe forms a selective bond toward her lamb within a few hours, the lamb does not show much selectivity for at least the first day. Lambs do display preferential reactions toward their own dam immediately after birth. For example, a paper by Vince and Ward (1984) describes increased heart rate responses to the odor of a lamb's own dam compared to the scent of an alien dam. This suggests some priming for future learning by exposure in utero.

Terrazas et al. (2002) tested this by allowing lambs to choose between pairs of intact and anosmic maternal ewes, where each pair contained both the lamb's dam and a foreign dam. The anosmic ewes were unselective, showing indiscriminate maternal responsiveness to any lamb. When presented with intact ewes, lambs reliably correctly chose their own dam, but when presented with anosmic ewes, which would respond with equal maternal drive to any lamb presented, lambs choices did not differ significantly from chance. It appears that at a day of age, lambs respond to general maternal cues and do not actively discriminate in favor of their own mothers, though they do appear to show the start of learning this distinction. This was later corroborated by the Sébe (2007) study, in which lambs could not discriminate their own mothers at 12 or 24 hours of age based on auditory cues, but could make this discrimination at 48 hours.

Bonding of lambs to their mothers appears to be driven by opioid action. This was explored by Shayit et al. (2003), where newborn lambs were given single injections of the opioid antagonist naltrexone and then observed and tested to measure the strength of the bond lambs formed toward their mothers. Naltrexone-treated lambs showed significantly shorter latencies to nurse immediately after birth, but at 24 and 48-hour tests, the naltrexone-treated lambs failed to spend significantly more time near their own dam than near an alien ewe compared with lambs in the control groups. This result, described next, supports the theory that opioid receptors are important in the formation of the lamb's bond to its mother. Exactly how opioid actions affect the individual steps in the bonding process is incompletely understood.

The Shayit et al. (2003), study had lambs choose between their own and an alien mother. The dams of naltrexone-treated lambs emitted significantly fewer low-pitched bleats once their lambs had approached them, when compared to the mothers of control (untreated) lambs. Yet, alien ewes did not vocalize any differently toward naltrexone-treated lambs than they did toward untreated lambs. Vocalizations were the only measure of maternal interest recorded, so this does not include the effect of behaviors such as licking, posture, and activity levels, which may have affected the lamb's response toward their dams. Additionally, naltrexone-treated lambs were not significantly more likely than chance to approach their own mothers before approaching an alien ewe at the initiation of the choice test, while control lambs did approach their own dams first at levels significantly above chance. In combination with the Nash et al. (1996) study, these results could indicate a decreased ability of the opioid-deprived lambs to identify and react to maternal cues. Shayit et al. (2003), suggested that this lessened response indicates a weakened relationship or strength of maternal bond between these lambs and their mothers.

Once lambs do learn the individual characteristic of their mothers, they appear to depend primarily on acoustic recognition at a distance, and this auditory discrimination appears to have solidified by 48 hours of age. Most studies of vocal recognition have used lambs of over one week of age. Sébe et al. (2007) showed that lambs and ewes use auditory discrimination at much younger ages than usually tested in these studies.

In a recent experiment, Sébe et al. (2010) explored recognition of individual acoustic signatures in 48-hour-old lambs, comparing recognition, response to and acoustic signatures of high- and low-pitched bleats from the ewes. The distinction between low- and high-pitched bleats had never been previously examined. Low bleats or rumbles are made with the mouth closed and only produced when the lamb is very near, less than one meter away. High-pitched bleats are used when the lamb is over a meter away, and have been the focus of all previous studies on vocal recognition in lambs and ewes. Lambs were tested in one of four treatment groups, each using a two-choice test essentially identical to the one used by Sébe et al. (2007). Ewe vocalizations were recorded 8 hours before testing for use in the tests. Results are shown in Figure 2. The first group was presented with pre-recorded low and high pitched bleats from an unfamiliar mother and lambs showed no preferential choice for either low or high-pitched bleats. The remaining three groups were presented with auditory stimuli from either their own or an unfamiliar mother. In the second group, lambs exposed to live calls from two ewes significantly chose their own dams over unfamiliar dams. In this test, the ewes only produced high-pitched calls, as the lambs were out of sight and at a distance. Lambs in the third group were presented with pre-recorded high-pitched bleats from their own and an unfamiliar mother, while the fourth group was presented with equivalent low-pitched bleats. Somewhat surprisingly, lambs did not significantly respond to recorded high-pitched bleats from either ewe, but they did respond strongly and significantly to the recorded low bleats from their own mother. Since lambs could recognize their own mother on the basis of her produced live but not pre-recorded high bleats, it appears that a back-and-forth communication is necessary for discrimination at a distance (by high bleats), while the low bleats or rumbles contain an acoustic signature which lambs can identify by 48 hours of age.

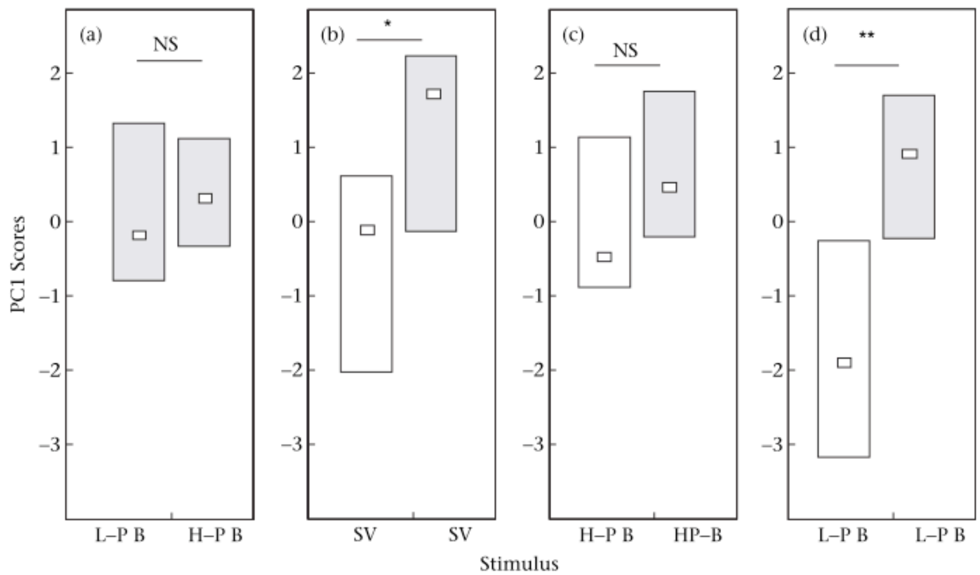

Figure 2. This figure from Sébe et al. (2010) shows the results of lamb exposure to high and low vocalizations from their own and unfamiliar dams. The y-axis is a measure of lamb response, where negative scores represent stronger response. The white box in each column shows responses to the lamb's own mother, while gray boxes refer to unfamiliar dams. (a) shows responses to low and high pitched beats; (b) shows responses to high pitched bleats for ewes hidden out of sight; (c) shows responses to high-pitched recoded bleats and (d) shows responses to low-pitched recorded bleats.

Torriani et al. (2006) suggested that selection pressure for recognition is greater on a young animal than on its dam; the associated cost to the individual is obviously much greater. This view was supported by their finding that young fallow deer could recognize their dams' individualized vocalizations, but the dams could not discriminate between the calls of their own and alien young. Fallow deer, however, are a hider species, as is the domestic goat. Hider ungulates leave their young hidden while out foraging, and the young responds selectively to the individual call of the mother upon her return. In contrast, sheep are a follower species, with the young moving about alongside or relatively close to the mother and the rest of the flock. Follower species show two-way auditory recognition, with both mother and offspring able to identify each other based on their contact calls (Torriani et al., 2006). This correlates with the Sébe et al. (2010) study; two-way communication by high-pitched calls was necessary and sufficient for discrimination, while the high-pitched calls themselves were not sufficient without the direct exchange of contact calls.

On the whole, the behavioral and endocrine processes surrounding birth and rearing in sheep are specifically evolved and tailored to maximize lamb survival. Altricial lambs minimize predation risks by spending only a few hours to a few days on the birth site, after which their tight bond with their dam ensures that her resources are delivered specifically to her genetic offspring and none other. Adaptations in communication, using different modalities and different variations of the same modality, allow the ewe-lamb pair to maintain contact. Individual signatures, both acoustic and olfactory, encourage the lamb to know it's own mother. Hormonal processes direct the entire progression, from the ewe's initial drive for amniotic fluid to memory formation and the stable bond created and remaining weeks after the initial burst of bonding hormones has tapered off.

Chapter Two

Temperament and Measures of Maternal Ability

Numerous factors are known to influence lamb survival, from sex and birth weight to age of dam, breed, and ewe nutrition. Some of these factors can best be controlled with management; others can be easily selected for in breeding programs. One facet of lamb survival that is still the subject of inquiry is the role of maternal care: How can a ewe's ability be quantified and predicted, and what is the role of temperament in maternal success?

Successful maternal skills can vary depending on the management system in place. Ewes giving birth and raising lambs on pasture may face a different set of pressures than those lambing in an intensive indoor system. One of the longest-running and most commonly used predictors for maternal success on pasture is maternal behavior score, but the reliability of this measurement has been called into question in recent years. Other measures of temperament, judging ewes as calm or anxious, or as more or less active, or judging their levels of discomfort in challenging situations, have been suggested as potential predictors of maternal ability.

Maternal behavior score, or MBS, is a measure of the distance which a ewe, having lambed on pasture, flees while her lambs are being handled for ear-tagging and other processing. This processing almost always occurs within the first 24 hours of birth; in many flocks it occurs within 12 hours of birth. In addition to ear-tagging, lambs may be paint-numbered, tail-docked, weighed and otherwise handled. The specific procedures vary among flocks and farms. Ewe MBS has been the subject of a number of publications since the mid-1980s, with a variety of resulting conclusions as to its usefulness as an indication of maternal ability or success, generally measured as lamb survival and/or lamb weight gain.

The first report of maternal behavior score as a potential predictor of maternal success was by O'Connor et al. (1985) in a study examining 1146 pasture-lambing New Zealand ewes of six different genotypes. Three measures of survival were examined – from birth to weaning, birth to tagging and tagging to weaning; weaning weights were also used as a measure of maternal success. O'Connor et al. (1985) found increases in survival from birth until tagging and birth until weaning correlated with better MBS, as did weaning weights, though not as strongly. Weaning weight most significantly increased with genotype and birth weight. MBS most significantly was influenced by ewe age, genotype, and litter size. The strongest effect of MBS on survival from birth to weaning was for quads, with moderate effects for twins and triplets; no significant effect of MBS was seen for singles. These effects persisted when litter size was corrected for, even though dams of larger litters had significant increases in MBS with increases in litter size. No significant ewe age effect was found for survival from birth until weaning, despite the significant increase in MBS with increase in dam age.

Ten years later, an update was published. Using a flock of 73 Scottish Blackface ewes, O'Connor (1996) collected ewe weights, lamb birth and weaning weights, MBS and focal animal behavioral observations. The rubric used for MBS was slightly altered in the second publication, with scores ranging from 1 through 6 rather than through 5. In the new rubric, a score of 6 was given to ewes who made contact with (or "nuzzled") their lambs during tagging. A growth coefficient, “B”, was used as a measure of lamb growth and maternal success. This measure was derived from nine lamb live weight estimates. The results were very similar to those reported in the 1985 study (O'Connor et al., 1985), with “B” significantly positively correlated with MBS and negatively correlated with litter size. B was negatively correlated with ewe live weight before lambing, which is explainable by the fact that ewes with larger litters will tend to weigh more before giving birth so it is merely a reflection of litter size. The strongest correlation between lamb survival and MBS was found at the increase between a MBS of two and a MBS of three, predicting an average increase in lamb growth from 189 to 204 grams per day.

In the report by O’Connor (1996), 15-minute focal behavioral observations were collected for each ewe-lamb set during weeks 1, 3, 6, and 14. Behaviors which may be described as indicators of ewe alertness were quantified: head up scanning, allowing or denying sucking attempts, approaching lamb(s), vocalizing, and the proportion of time a ewe spent within 1 m of her lamb(s). The only one of these to show a significant negative correlation with growth rate was time spent near a ewe’s lamb. It was suggested that this was due to lambs of ewes producing sub-optimal levels of milk remaining close to their dams with hope of additional sucking opportunities. There was a positive correlation between ewe head up and ewe vocalizations and MBS, suggesting that MBS is a good predictor of ewe attentiveness, an important factor in successful lamb rearing.

A few years later, Lambe et al. (2001) examined MBS and weight gain in 847 Scottish Blackface ewes lambing in lowland paddocks. The MBS was a 6-point scale as in O’Connor (1996), and lamb survival and maternal success was assessed by four measures: average lamb weight gain from tagging (less than 24 hours of age) to marking (average age of 42 days), average lamb weight gain from tagging to weaning (average age of 120 days), number of lambs dying from birth to marking, and average number of lambs dying from birth to weaning. Across all measures, parity and MBS were not significantly correlated with lamb traits. MBS did approach significance for the number of lambs dying between birth and marking and birth and weaning, and ewes receiving an MBS of 1 were significantly more likely to lose lambs than ewes in any other MBS class. Of particular note is that all of the MBS of 1 were given to ewes with little or no lambing experience. A moderate and positive genetic correlation between MBS and average weight of lambs raised to weaning was found. The authors suggested that this could indicate that the major source of variation in MBS was environmental, not genetic. They suggested that the estimates of heritability and repeatability (0.13 and 0.32, respectively) could be substantial enough to include MBS as a trait selected for in the breeding process.

In 2005, Everett-Hincks et al. (Everett-Hincks et al., 2005) published a study exploring similar relationships in a large Coopworth flock. This flock had been using a scoring system similar to O'Connor's (1985) original 5-point MBS for over 25 years, and annually culling any ewes scoring 1 or 2. Everett-Hincks et al. (2005) looked at two measurements of maternal success- litter survival, litter size at weaning divided by litter size at birth; and lamb survival, a binomial trait in which any lamb surviving to weaning was scored a 1, while any that died were scored 0. Additionally, lamb survival was looked at separately for all lambs born as twins or triplets. The model used included the effects of litter size, birth year, lamb sex, age of dam and MBS.

MBS was significantly higher in dams giving birth to triplets than in those giving birth to twins or singles. These authors and others suggest that this effect may be a response to a greater amount of stimuli, as more lambs produce more of the noises, movements, and smells, to which a ewe is programmed to react in the period after giving birth. MBS was also found to increase over the course of the season, corresponding to known (but not measured) increases in shepherding intensity. This may be due to ewes becoming more accustomed to the presence of people, and so responding with less fear at tagging.

Litter survival was found to decrease as litter size increased, corroborating many past studies; however, it did also correlate with MBS, increasing as MBS increased, despite the correlation between MBS and litter size. This correlation between litter survival and MBS was particularly strong as ewes increased from MBS of 1 or 2 (scores which were grouped for statistical analysis) to an MBS of 3. Above 3, the effect of increased MBS was minimal. Lamb survival, on the contrary, decreased as MBS increased. Everett-Hincks et al. (2005) report a "major" decrease in lamb survival for ewes scoring 3 compared to ewes scoring 1 or 2. Additionally, very low heritability and repeatability were found for litter survival and MBS, particularly in comparison to the Lambe et al. (2001) study. The Lambe et al. (2001) study, however, used flocks which had never been selected for MBS, compared to the flock used in the Everett-Hincks et al. (2005) study, which had been heavily selected for MBS over a large number of generations. In fact, Everett-Hincks et al (2005) concluded that there would be little to be gained from continued selection for MBS and litter survival In the Coopsworth flock they studied.

Salwalha et al. (2007) evaluated MBS as one of a number of factors in a large study of lamb survival in a flock of Scottish Blackface sheep which had been selected for a variety of traits, but not MBS. Dams with an MBS of 1 had a significantly higher proportion of stillborn lambs; this is likely to account for these ewes receiving scores of 1; otherwise, lambs from ewes receiving scores of 1 were found to have lower hazard rates of postnatal mortality (though not significantly.) In the report by Lambe et al. (2001) ewes with dead lambs were included with those receiving scores of 1 as well, which likely influenced the overall survival statistics for that score class. Salwalha et al. (2007) found a negative but non-significant correlation between MBS and postnatal survival overall, and conclude that selection for MBS would not reduce postnatal survival rates.

Hatcher et al. (2009) also examined MBS as part of a larger study of lamb survival, using records of 3666 Australian Merino dams over an 8 year period. The "MBS" used in this study was somewhat different than the one used in most other published studies; it was referred to as a "maternal bond score" and rates 1 as the best score, with a ewe maintaining close proximity to her lambs, while 4 is the lowest possible score, indicating that a ewe leaves and ignores her lambs. While the scoring rubric is a bit different, it likely quantifies the same behavior as the distance which a ewe flees at tagging. In contrast to Everett-Hincks et al (2005), MBS was found to be highly repeatable and moderately heritable, but it was once again found to have quite low correlation with lamb survival, and any correlations that were not practically zero had very high SE. As a result, Hatcher et al. (2009) concluded that MBS is a "very poor indirect selection criteria [sic]."

The reason most often suggested for the poor reliability of MBS as a selection criterion for lamb survival is that it measures ewe temperament, not maternal ability. What is really measured may well be the ewe's reaction to the presence of humans. A number of experiments, particularly a series done at the University of Western Australian, have focused specifically on measuring this aspect of temperament and relating it to maternal ability and lamb survival, as well as to stress reactions.

Divergent lines of Merino sheep based on temperament have been bred at the University of Western Australian since 1990 (Beausoleil et al., 2008; Bickell et al., 2009a; Bickell et al., 2010a; Bickell et al., 2010b; Bickell et al., 2009b; Blache and Bickell, 2010) Individual lambs at 3 months of age are evaluated and classified according to the results of two tests: an arena test measuring locomotor activity and a test of social isolation. The arena test creates a conflict of motivation by presenting lambs with a group of flock-mates separated from the individual by a human. The isolation test records agitation (a combination of movement and vocalization) when lambs are placed inside a solid plywood box for one minute. This isolation test was proposed to quantify fearfulness as a temperament trait. The combined results from these two tests were used to place lambs into "More Active" or "Less Active" flocks, also referred to in some, particularly earlier, publications as "nervous" and "calm" flocks. More Active sheep were generally classified as being more fearful or anxious but this connection between behavioral response and the temperament trait "fearfulness" has not been validated and has been questioned in recent years (Beausoleil et al., 2008).

In wild bighorn sheep, bolder ewes have lower lamb mortalities and are less likely to fall victim to predation than are "shy" ewes. Bickell et al. (2009b) suggest that in general, a more reactive temperament is advantageous in a natural setting, where vigilance against predation plays an important role in evolutionary fitness. In contrast, farm-bred sheep were proposed to benefit from lowered emotional reactivity.

The two flocks in Western Australia resulting from years of divergent selection based on being More or Less Active have been the basis for multiple studies on maternal temperament. One line of research describes the More Active line as “nervous” and the Less Active line as “calm”. These descriptors are based primarily on the Murphy et al. (1998) study describing the behavior of the divergent lines, and reporting that calm ewes spent more time grooming their lambs and emitting more low-pitched bleats than do nervous ewes. Bickell et al. (2009b) reported increased cortisol levels in sheep from the MA line after exposure to noisy machinery; this result also contributed to the “calm” and “nervous” descriptors.

The division between temperaments has much potential usefulness in part because it is so consistent over age. Even one week old lambs from each divergent line showed measurable differences in behavioral response to stressors (Bickell et al., 2009a). These traits are conferred genetically and not behaviorally through maternal care patterns: a cross-fostering study by Bickell et al. (2009a) demonstrated that a lamb’s behavior was predicted by the behavior of its genetic mother and was not affected by the behavioral phenotype of the ewe raising it.

Bickell et al. (2009b) tested recognition and preference between ewes and lambs belonging to each line. While calm mothers did emit more low bleats, in almost all other measures recorded, no difference was found between lines. Sheep from each line did differ in their locomotor activity, as would be expected, but this difference did not appear to have any effect on bonding. Bickell et al date do report that "more unexpectedly nervous ewes seemed more prone to react positively in the initial stage of the test", as nervous ewes were more likely to spend more time near their own lamb during the first minute of a choice task.

Bickell et al. followed their 2009 studies (Bickell et al., 2009a; Bickell et al., 2009b), performed in the barn, with a 2010 publication (Bickell et al., 2010b) focusing on ewes from the same divergent lines, but lambed outdoors rather than in pens in a barn. They suggested that the effects of temperament on maternal behavior could have been minimized or negated by the intensive management system in a barn or by the presence of human observers. In the 2010 study, single-bearing primiparous and multiparous ewes were lambed outdoors and observed by remote-controlled recording devices. Some effect of temperament was found, in that "calm" ewes licked their lambs more, while the lambs of "nervous" ewes had decreased latencies to stand. After the initial period, however, both groups spent the same amount of time sucking and neither group showed any significant difference in mortality.

In contrast to Bickell's labeling of the MA and LA flocks as calm and nervous, (Beausoleil et al., 2008) used the same divergently selected flocks at the University of Western Australia to conducted studies testing whether increased locomotor activity in the arena task really was a sign of fearfulness. Using the same arena test used to classify lambs as more or less active, Beausoleil et al. (2008) found that the MA sheep had a significantly decreased latency to approach the human, and spent significantly more overall time near the human. Additionally, a cortisol assay was performed on blood drawn prior to and immediately after the arena test; while there was no difference between flocks prior to the arena test, there was a weak flock effect on cortisol levels at the end of the arena test, with MA sheep having lower plasma cortisol levels than LA sheep. As a result, Beausoleil et al. (2008) et al suggest that MA sheep are in fact more bold and not more nervous.

Boissy et al. (2007) published a genetic analysis focused on social reactivity as a measure of temperament quite similar to that studied by Bickell et al. Lambs from eight genotypes were exposed to tests of novelty, exploration and reactivity to humans. As an example, they noted that Romanovs, known in the literature as emotionally reactive, did show more behaviors indicative of fear, including a high frequency of low bleats and, as in the Bickell studies (2009a; 2010a; 2010b; 2009b; 2010), a low level of locomotion. The consensus seems to be that more emotionally reactive sheep are less likely to be active, but whether this can be extended to the period after birth is debatable or even unlikely, as ewes are in a very different context in each situation.

While MBS and “more active”/”less active” temperaments cannot be directly compared, it could be speculated that lower MBS ewes are “more active” – after all, they are defined by moving farther from the human at the time of tagging. However, a ewe that runs away and comes back, moved around but was exploring would earn a score of 3 (in the O’Connor scoring), and as the jump from 2 to 3 was seen as a significant one, this distinction could mark a difference in temperament.

One possibility for bridging this gap is a test of “arena behavior”, suggested by Kilgour (1998). Temperaments were compared between two flocks of Merinos, one divergently selected for lamb-rearing ability and one unselected, by means of an arena test, very similar to one of the tests used for selecting the “more active” and “less active” animals in Bickell et al. (2010b; 2009b) and Beusoileil (Beausoleil et al., 2008). Ewes were selected for the “fertility flock” on the basis of rearing performance: any ewe failing to raise a lamb was removed from the flock, and ewes raising twins were preferentially included in the flock. Rams were selected on the basis of their dam’s performance. The arena test measured the total distance moved by an animal during ten minutes spent in an arena containing a human seated in front of a group of sheep.

Kilgour (1998) found the “fertility flock” ewes and rams traveled significantly less than ewes and rams from the unselected flock, at all three ages tested (6, 12, and 20 months). Fertility flock rams and ewes also bleated less at 6 and 12 months, though the effect was no longer significant at 20 months of age. He suggested that fertility flock animals move and bleat less due to lower levels of stress and agitation; this agrees with the cortisol study done by Beausolieil et al. (2008), in which “less active” flock animals had lower levels of cortisol compared to the “more active” sheep.

Approaching from another direction, Viérin et al. (2002) and Viérin and Bouissou (2001) presented ewes in two studies with three fear-eliciting tests, one of which was similar to the arena tests used by Kilgour (1998), Bickell (2010b; 2009b) and Beausoleil (2008), and an isolation test, which is somewhat comparable to the agitation measured by the box test. (The nature of the measurements of the box test prevents any direct comparison.) Viérin and Bouissou (2001) tested two groups of pregnant ewes (at 40 and 140 days of pregnancy) and one group of non-pregnant ewes. In their second study (Vierin, 2002) the ewes tested were divided into three classes: nulliparous ewes that had never lambed, primiparous ewes, which had lambed once and been weaned three weeks prior to testing, and multiparous ewes, which had lambed multiple times and had also been weaned three weeks prior to lambing.

The three tests used were an isolation test, in which the ewe was separated from its flockmates; a "surprise effect" test in which a red ball was dropped from the ceiling, and a "human presence" test similar to the arena test, but with the human entering the arena after the ewe, and the object of the ewe's attention a known feed trough rather than conspecifics. A "fear score" was calculated based on the frequency of behaviors related to the fear or absences of fear, including: latency to eat, total feeding time, number of walking bouts, number of glances at and latency to sniff the stimulus, and time spent far from the stimulus and near a known exit. This fear score was interpreted as a representation of the level of fear an animal experienced.

When pregnant ewes were compared to non-pregnant ewes, they displayed significantly fewer signs of fear in the both the isolation and surprise tests. In these tests, pregnant ewes walked and stopped with lower frequency, reared against the wall and pawed with lower frequency, and crossed fewer squares. In the isolation test, pregnant ewes tended to bleat less often and in the surprise test, with higher latency. Both pregnant and non-pregnant ewes responded similarly to the human test, with the only difference in behavior a lower occurrence of rearing against the wall by pregnant ewes. Fear scores for ewes on the 40th day of pregnancy and the 140th day of pregnancy did not differ significantly in any of the three tests.

Multiparous ewes were found to show significantly lower levels of fear in every situation, compared to nulliparous and primiparous ewes. In the isolation test, nulliparous ewes immobilized more frequently and spent more time immobile. In the surprise test, multiparous and primiparous ewes both showed significantly less fear than nulliparous ewes, while nulliparous ewes crossed more squares and spent more time in the area close to the stimulus (red ball). In the human test, multiparous ewes showed significantly less fear, but nulliparous and primiparous ewes did not differ in their fear scores; the only item which differed was the rate of bleating.

An interesting comparison between the Viérin (Vierin, 2002) and Viérin and Bouissou (2001) studies and the Bickell (2010b; 2009b) and Beausoleil (2008) studies is the interpretation of the predictive factor “number of squares crossed.” In Beausoleil (2008), “More Active” sheep crossed more squares, had lower latency to investigate the human in the arena, and had lower levels of plasma cortisol after arena testing. In Viérin et al. (2001, 2002), squares crossed was counted as a sign of fear- and it did correlate with other more straightforward behavioral signs of fear, such as escape attempts and bleating. One possible interpretation is that in the UWA flock (used in Beausoleil (2008) and Bickell (2010b; 2009b)) has been bred for boldness and so their movements were more explorative and less emotionally reactive in nature. Beausoleil (2008) suggests that, since cortisol levels in both groups rose evenly after shearing, and since the stress response is less elevated in response to stressors over which the individual has perception of control, the More Active ewes had a greater perception of control over their environment in the arena test.

While low levels of fear could be a potential indicator of maternal ability, the Viérin (2002) study suggests that these emotional reactions certainly can change over time. This agrees with something generally regarded as common knowledge by sheep farmers: older, more experienced ewes are considerably easier to shepherd. This also supports, unsurprisingly, the often-observed result that ewe age is a good predictor of lamb survival (Everett-Hincks et al., 2005; Hatcher et al., 2010; Lambe et al., 2001; Sawalha et al., 2007). The high repeatability of maternal care seen over parities for ewes is somewhat counter to the idea that maternal ability improves over time. Although a flock of more easily handled ewes, even if not independently objectively better mothers, could make life easier on the farmer, in turn allowing for improved management and increased shepherding.

While the UWA studies (Beausoleil et al., 2008; Bickell et al., 2009a; Bickell et al., 2010a; Bickell et al., 2010b; Bickell et al., 2009b) have focused on divergent temperament lines, one avenue of divergent selection inherently including known differences in temperament has had fairly significant attention paid as well: breed differences. The distinction between "highland" and "lowland" or "intensively" and "extensively" managed flocks has been documented, such as in contrasts between Scottish Blackface sheep, an extensively managed highland breed known for high levels of maternal care and Suffolk sheep, an intensively managed breed known for weaker maternal ability (Dwyer and Lawrence, 2005). Intensively managed breeds often have been selected for specific and desirable traits, such as carcass traits and very often, wool characteristics. Selection in these breeds has not focused on maternal care or skill; intensive farming and management practices often make up for the lowered care provided by ewes, though usually at a labor cost to the farm. Extensively managed breeds, in contrast, often lamb without supervision and have to rely on maternal skill to raise their offspring. In this fashion, the ewes are self-selecting for successful maternal abilities; any ewe who fails to raise a lamb effectively culls herself and future offspring from the flock.

The breed differences resulting from such divergent selection over time are, as in many domesticated species, often quite sharp; making them a very useful tool for studying genetic components of various production traits, including behavior.

Dwyer (2005) reviewed comparisons of hill and lowland sheep breeds, noting physiological and behavioral adaptations that allow for hill breeds' maternal successes under extensive management in often harsh conditions, living a "semi-wild" existence for large parts of the year. Breeds included in this review as "highland" or "hill" breeds were Welsh Mountain, Cheviot, Scottish Blackface, Dalesbred, Swaledale, Pre Alps du Sud, and Romney sheep, while the "lowland" description most often referred to Suffolk sheep but also included Dormer and South African Merino, Border Leicester, Southdown, Jacob and Clun Forest sheep. Highland breeds were reported to have smaller litters (though more placental connections, or caruncles, per lamb), to have ewes that isolated themselves farther and longer from the flock at lambing, that experience shorter, easier labors (potentially related to pelvic width) and displayed variations in maternal behavior which could well affect lamb success. Suffolks, a lowland breed, were reported to show higher levels of aggression toward their own lambs, and were less cooperative toward their lambs' attempts at sucking compared to Blackface (highland) ewes. A battery of similar maternal measurements; including latency to groom lamb, time spent grooming, low bleat rate after birth, time spent with own lamb, and time spent allowing own lamb to nurse; were all significantly in favor of the maternal abilities of the highland breeds. Maternal behavior score showed no obvious difference between Suffolk and Blackface breeds. A comparison with Romanov ewes, known for high levels of maternal attention, revealed that they stood farther away form their lambs and received lower MBS scores than Lacaune ewes, a more intensively managed breed. Dwyer et al. (2008a) suggested that MBS really only measures emotivity, which is not necessarily correlated with maternal ability. This agrees with earlier results showing little effect of MBS on lamb survival (Dwyer and Lawrence, 2005).

Lamb behavior differences by breed may play as large a role in survival differences as do ewe behavioral differences. Highland lambs were reported to have lower latencies to stand, seek the udder, and suck. These lambs also appeared to be better at dam recognition, but this seems likely to be strongly influenced by dam behavior; embryo transfer resulted in lambs whose discriminatory ability was determined more by the breed of the mother to which they were born than by the genetic background of the lamb. This result extended to lamb vocal activity. Lambs were more vocal when raised by Suffolk dams than by Blackface dams, likely at least in part because Suffolk ewes tended at any given time to be farther from their lambs. While a high vocalization rate could be taken as a sign of vigilance and communication, vocalization by a lamb also makes it a target for predators. In extensive pasture or rangeland conditions, it is particularly disadvantageous for a lamb to announce its location to predators, so it would seem logical for highland ewe-lamb pairs to maintain contact spatially rather than vocally. Indeed, they are reported to maintain closer spatial relationships than lowland ewe-lamb pairs (Dwyer, 2008a). Non-behaviorally, but important to survival, highland breed lambs were reported to have average high mean rectal temperatures an hour after birth. This trait is likely almost purely genetic, controlled by the amount of brown adipose tissue deposited by the lamb during gestation (Dwyer and Lawrence, 2005). This long list of specific and useful adaptations favoring lamb survival, even under harsh conditions, makes a strong point of the genetic control over lamb survival and maternal behavior. Breeds that have been intensively managed for generations may have decreased maternal ability, often selected against by the use of management styles that relax selection for survival imposed under extensive conditions.

Chapter Three

Management

A variety of management tactics for sheep flocks are used across the globe. These systems vary from sprawling herds of thousands, left out on rangeland most of the year to systems housing lambs that may never leave the barn before slaughter, and every variation between. In many cases, these practices may be split into extensive and intensive systems. In an extensively managed flock, for parts of the year ewes are not closely monitored and are largely responsible for bonding to and raising their own offspring. Extensive flocks are generally grazed over large areas, and the farm may not even have a barn for housing. In contrast, an intensive system uses a greater amount of human labor, and will usually graze flocks in fenced paddocks of seeded, high-quality pasture (Dwyer and Lawrence, 2005). These systems tend to keep ewes indoors at lambing and until weaning, and will commonly feed the lambs concentrate diets in pens. Some farms will fall in-between management styles, perhaps only bringing ewes into the barn for a short period around lambing before returning them and their lambs to pasture, or only bringing pasture-born lambs into drylot pens after weaning, when a faster rate of gain is desired than can be achieved on grass (Rook et al., 2007).

Regions that have used extensive management systems for centuries traditionally are home to breeds that have been adapted to life in the region. These sheep are often not as highly productive as breeds selected for intensive systems, but require lower input and so can be kept in larger flocks that maintain a competitive bottom line. During the last century there has been a drive toward highly productive, prolific ewes, managed intensively. As labor costs rise, however, there has been a resurgence of interest in extensive management styles; it is no longer always more profitable to increase input in order to increase production values such as rate of gain or lambs raised per ewe lambing. One of the most labor-intensive periods is lambing time, particularly for an intensively managed farm, where ewes give birth in the barn and significant time can be put into caring for each ewe and ensuring that the mother-lamb bond is established (Dwyer and Lawrence, 2005; Dwyer, 2008b).

Lambing in a barn is preferable under some conditions, such as winter-lambing flocks. Timing the breeding of a flock so that ewes lamb in the winter can allow farmers to market lambs at a time when demand and prices are high, in time for spring holidays and before the market is flooded with spring-born lambs (Rook et al., 2007). Unfortunately, the high-density stocking that usually accompanies barn lambing is less than ideal for maternal bonding. When ewes give birth in close proximity to other late-parturient and lambing ewes, the chance of separation or lamb stealing by other ewes close to lambing is much greater than in a low-density situation, such as on pasture. Labor input is required to separate lambing ewes, allowing them time and privacy to form the exclusive maternal bond so vital to success in lamb-rearing.

A small number of studies have examined ways to improve the maternal bond under high-density stocking situations. Gonyou and Stookey (Gonyou and Stookey, 1985, 1983) examined the use of cubicles for in-barn lambing systems. Here, a cubicle is a claiming pen with an open entrance leading into the pen where lambing ewes are housed. As ewes are expected to seek privacy at parturition, it is expected that they will enter such pens and give birth in there. This was predicted by Gonyou and Stookey (1985, 1983) to improve maternal bonding, as ewes in claiming pens, even open-sided ones, would be less likely to have the bonding process interfered with by other ewes. Additionally, 0.25-meter-tall panels were placed over the entrances to the claiming pens. These panels were low enough that ewes could easily step over them, but newborn lambs could not, ensuring that lambs born in cubicles would stay there and not get mixed up with the main flock after birth.

The cubicles used in Gonyou and Stookey (1985, 1983) were 1 meter tall with a 0.6 meter entrance, placed at the outside of a large open pen in which ewes were housed. Corners of the pen were blocked off with panels to eliminate 90-degree corners other than those present in the cubicles. Gonyou and Stookey (1983) examined use rates of these cubicles over three trials, with comparisons between solid and open walls and ceilings, cubicle size, and use by primiparturient and multiparturient ewes. With stocking density maintained at 19.5 to 21.7 square feet per ewe, and cubicles accounting for 18% of pen area, multiparturient adult ewes utilized the cubicles for lambing at a rate of 42%, 25.6% and 46% for trials 1, 2, and 3, respectively. These percentages are all significantly higher than would be predicted by space alone. Ewes near or at lambing showed no preference for jute-covered walls or ceilings, nor for larger (1.8-by-1.8 meter) versus smaller (1.8-by-1.2 meter) cubicles. Non-parturient ewes preferred open-walled cubicles, but occupation of cubicles by non-lambing ewes was significantly lower than predicted by space alone, as 5.8% of non-lambing ewes were observed occupying cubicles at any given time. When cubicle use was compared between mature, multiparous ewes and yearling, primiparous ewes, 55% of mature ewes chose to lamb in cubicles, compared to

38% of yearling ewes, a significant difference. Additionally, ewes were significantly more likely to utilize cubicles farther away from trafficked areas such as work areas and alleyways.

In a follow-up experiment, Gonyou and Stookey (1985) compared the behavior of ewes and lambs in traditional pens and pens with cubicles provided. Only multiparous ewes were used, and some of the ewes had been exposed to cubicles previously. The breeds used were Suffolk, Targhee and crosses that were primarily Suffolk and Targhee but contained genetics from a number of other breeds including Barbados, Border Leicester, Finnsheep and Dorset. The behaviors of 54 ewes were analyzed from video recordings, including the following behaviors: lying, standing, moving, circling, standing nose-to-flank, number of birth sites investigated, cubicle use at parturition, interaction and interference with lambs by other ewes, distance traveled from the birth site, distance traveled by a ewe from her lambs, distance between lambs, and occurrences of lamb stealing or separation. 41% of ewes used cubicles, a number similar to that recorded in the 1985 study and noted as also similar to the percentage of ewes recorded seeking isolation of pasture in a previous study (Gonyou and Stookey, 1985, 1983).

Suffolk and Targhee ewes were significantly more likely to use cubicles than were crossbred ewes, a result that led the authors to propose a genetic component to cubicle use. This is reasonably surmised to be related to genetic differences in the desire for isolation at lambing. Other studies have documented differences in isolation-seeking behavior among breeds. For example, Scottish Blackface ewes (a highland breed with a history of extensive management) are more likely to separate themselves from the flock at lambing, and to remain isolated for longer periods, compared to Australian Merino ewes (a breed with a history of more intensive management, bred for production of fine wool) that show much less drive for isolation at lambing and rarely remain isolated for more than four hours after giving birth (Dwyer and Lawrence, 2005; Pollard, 2006).

Ewes that had been previously exposed to the cubicle system were significantly more likely to use cubicles than were ewes which had only lambed in traditional open pens (45% versus 23%). Interestingly, exposure to cubicles increased ewes' likelihood of using cubicles, but previously using a cubicle did not make a ewe more likely to use a cubicle in the future.

Behaviorally, there were no significant differences between ewes lambed in a traditional open pen and ewes lambed under a cubicle system, when all ewes in the cubicle system were analyzed as a whole (Gonyou and Stookey, 1985). However, when ewes that lambed in cubicles were compared to ewes that did not lamb in cubicles, behavioral differences became apparent and significant. Ewes that gave birth in cubicles spent more time in the cubicles, spent less time searching for a birth site, traveled less distance prior to parturition, and changed posture less frequently once settled into a birth site. This led Gonyou and Stookey (1985) to suggest that pen-lambing ewes were less satisfied with the available options, presumably for isolation, and so spent time searching for a better spot until shortly before parturition. After giving birth, ewes which utilized cubicles continued to show significant differences from ewes which lambed in the main pen: cubicle-using ewes remained closer to the birth site, their lambs were much less likely to be interfered with, separated or stolen by other ewes or rejected by their dams. In the control group, with no cubicles available, 73% of lambs were interfered with by ewes that were not their mothers. In the group which were given the option of cubicle use, 82%

of lambs born outside of cubicles were interfered with, while for lambs born in cubicles, the number dropped to only 17%. Of lambs born in the large pen areas, 3.1% of lambs were rejected by their dams, while no lambs born in cubicles were rejected. The authors concluded that lambing in a cubicle is advantageous for ewes and their lambs, though the possibility remains that better mothers are more likely to give birth in cubicles. The authors closed the discussion by suggesting that the next step would be to determine how to increase the percentage of ewes using cubicles.

It is widely accepted that the use of claiming pens improves a ewe's bond toward its lamb, preventing interference from other ewes and keeping the ewe and lambs in close proximity during the time period when selective bonds are being formed. Few studies have examined the role which claiming pens play in the lamb's development of discrimination and responsiveness toward its mother. Arnold and Morgan (1975) examined the role of social and spatial environment on a lamb's ability to identify its dam. For this study, ewes were placed in 2 x 1 meter pens prior to lambing, so no interference from outside ewes was possible. At 12 hours of age, lambs were given a two-choice test, with the opportunity to choose between their own dam and an alien ewe. Choice was measured as a "preference index" calculated from the amount of time a lamb spent in a contact zone near the pen containing each ewe. Lambs that failed to choose their own dam at 12 hours of age were retested at 24 hours of age. After birth, one group of lambs remained isolated in the claiming pens with their dams until testing. A second group spent 6 hours with only their dams, at which point one more ewe and her lambs were added and pen size was doubled; this was repeated at 12 hours, when 2 more ewes were added and pen size doubled again. A third group received the same increases in space without the addition of ewe-lamb sets, giving them the same spatial experience without the socially enriched aspects.

Lambs that were exposed to both increased space and social situations performed significantly better in the two-choice test. These lambs had lower latencies to reach their dams and spent more time near their dams than did lambs remaining in single claiming pens until testing. A high percentage of these socially enriched lambs also went directly to their dams, indicating use of distal cues that were not observed in isolated lambs. Lambs that had been housed in larger pens but without social enrichment were more likely to choose their own dam than were the lambs remaining in small pens, but Vallaillet and Nowak (2006) observed that these lambs did not appear to use distal cues and did not spend significantly more time near their own dam, rather moving between the two available ewes. In every group, some lambs clearly chose their own dams, some chose the alien dams, and others made no clear choice. This demonstrates the inherent variation between lambs at the young age of 12 hours. The authors suggested that the significant increase in recognition ability by lambs given increased social and spatial demands after 6 hours of age is an effect of learning; lambs in small pens never get a distant view of their dam and never have to practice reuniting after separation. Similarly, lambs given increased space but no social enrichment never experience rejection by other dams and are less likely to practice reuniting. It appears that lambs need a bit of challenge and experience to best learn to recognize their dams. These results suggest that an increase from smaller to gradually larger pens could help maximize lamb bonding in intensively managed farm-lambing systems.

Deaths in the first 3 days to a week of a lamb's life account for a very large percentage of losses and overall mortality in most commercial flocks. In an intensively managed barn-lambed flock, labor is used to ensure maternal bonding by the use of claiming pens and rejected lambs or lambs from dams with milk supply problems are cross-fostered or artificially reared. Maternal care early on is not left to the dam as much as it would be in an extensive system, and as such, fewer publications have examined maternal care in intensive systems than in extensive systems. The number of papers (reviewed in Chapter Two) examining maternal behavior score are an example of the focus on maternal behavior on pasture.

Large-scale examinations of lamb mortality generally identify hypothermia and starvation as the largest cause of early postnatal mortality, with other common causes being trauma due to dystocia, septicemia and other diseases, parasites (in older lambs) and on pasture, predation. In an extensively-managed pasture system, more pressure is put on ewes to be good mothers: to isolate enough from the flock so as to minimize interference and form a strong bond, to be vigilant, to keep track of her lambs. These skills are less important in a highly-monitored system where the lamb never has chance to get far from its dam, though the environment in a dense pen may be more challenging in some respects. Vallaillet and Nowak (2006) identify low milk production as a significant risk factor contributing to the high risk of hypothermia and starvation in intensive systems. This may also be a considerable factor in extensive systems, but has not been examined separately from other causes of lamb starvation on pasture.

As the combination of hypothermia and starvation play such a large role in lamb mortality, implementing management practices that minimize these issues should be a priority in any flock. Hypothermia and starvation are often difficult to separate and can work in a vicious circle, going either direction. A cold lamb will use all its brown fat energy reserves attempting to maintain homeostasis, and even if it has the energy or drive to stand and suck, may not be able to adequately metabolize the milk it has consumed. Of course, a lamb that does not eat enough in the first place will starve even in warm weather, and will use all its energy reserves and starve more quickly in colder weather (Pollard, 2006). Two elements come into consideration: nutrition and shelter. Milk production is one such factor with little behavioral component; others are lamb size and coat length. Once gross physiological factors are accounted for, there are some behavioral elements to be managed or manipulated. Adequate lamb nutrition requires a cooperative and attentive dam, both in the barn and in the field. Shelter in an intensive system is generally guaranteed, requiring little to no input from the ewe. In a pasture system, farmers must rely on the shelter-seeking behavior of ewes with lambs, and take into consideration these behaviors and needs when planning lambing season.

Extended cold weather is very dangerous to lambs, and so breeding times should be coordinated such that ewes will lamb after temperatures begin to rise and the ground warms to at least 5°C. In many climates, however, once the ground warms to this point, there can still be occasional bouts of poor weather, wind and rain. In these situations, appropriate and desirable shelters can increase lamb survival rates. Pollard (2006) examined effects of harsh weather and options for lambing shelter in New Zealand. The author notes a history of publications and interviews reporting greatly increased mortality in wind and rain, counteracted somewhat when shelter is available. This improved survival is particularly seen in multiple-reared lambs; an increased total survival of 8%

for singles and 22% for multiples was reported when Phalaris grass strips were provided for shelter.

Pollard (2006) cited numerous other studies, with survival rate improvements generally in a similar range (6 to 9% improvement) but with much variation (some farms reported only a 1% loss increase to poor weather, while others reported losing 91% of lambs born on bad-weather days). Various shelters, breed variations, and management styles contribute to variation in lamb survival. The type of shelters used ranged from topographical features such as hills, windbreaks made of plastic or formed by trees or shrubs, strategically placed hay bales and man-made shelters such as lean-tos and stells, round stone walls often found in Scotland. In general, shelter always was reported to improve survival rates, with only two publications reporting the same negative effect from providing shelter: increased rates of parasitic infection, due to repeated use of the same desirable areas. Pollard (2006) also noted that no field studies have examined "effective shelter from all avenues of heat loss;" that is, not only wind and rain, but also heat lost to the ground and to the open air.

Perhaps some of the most insightful discussion of pasture lambing management systems and techniques comes from unpublished sources and extension publications, designed for distribution to farmers and outside the peer-review process. Often these publications rely on small amounts of farmer-provided data, anecdotes and personal experience; sources not reputable or consistent enough for journal publication. Nonetheless, these are sources of information often available few other places outside of personal interview, and as such deserve consideration. Two papers fall into this category when considering pasture lambing management strategies: one, an extension publication, published online and distributed through extension channels, written by veterinarians associated with Michigan State's Extension program, and the other an unpublished paper written by the owner/manager of a very large and successful pasture-raised sheep farm.

Pollard (2006) described "drop lot," "pasture," and "winter" (barn) lambing systems. Mortality causes and rates, and management styles were compared among four farms practicing two of these three systems, drop-lot and pasture lambing. A drop-lot system is described as falling between pasture and barn lambing: ewes are confined in a claiming pen and then a group pen, each for 2 to 3 days, before being released to pasture with their offspring. This system results in the high density lambing area that is known to promote interference and lamb-stealing, but keeps ewes close to or in the barn during the most risk-filled days of a lamb's life (Rook et al., 2007).

Of the farms examined in an informal (cooperative extension) publication by Rook et al. (2007), the one utilizing a drop-lot system had the highest mortality rate (15% versus 5, 10.3 and 11% for the pasture systems), but this farm also was home to much more fecund ewes, with a 220% laming rate that, even with the increased mortality, resulted in the number of lambs weaned per ewe that was within the range of the pasture systems examined. Weaning percentages were 170% for drop-lot, and 176, 161 and 111% for pasture flocks. Indeed, one pasture flock reported much lower numbers than any other farm; this was due to severe coyote predation during the one season for which data were reported. As these numbers all come from a single season on individual farms, they cannot be taken as more than an indication of lambing success among systems, but it can at least be said that in some situations, pasture lambing ewes can do as well as or better than their more intensively-managed counterparts.

Specific tactics for successfully managing fecund or prolific ewes in a pasture system were described by the successful Midwestern producer Janet McNally in an unpublished manuscript (2008). McNally owns a large flock of ewes, many carrying the Booroola FecB gene, which results in a lambing rate of 2.4 to 2.8 lambs per ewe lambing. The flock was initially barn-lambed with an average mortality of 15%; after a transition to lambing on pasture, lamb mortality was decreased to between 3 and 6% in most years. This level of production is both admirable and profitable, and other sheep farmers could surely gain from the management practices used for this flock.

McNally described two classes of pasture lambing: In *set stock* lambing, ewes remain in one pasture or on one large range from before parturition generally until weaning. In *drift lambing* shepherds take advantage of the newly-lambed ewe's tendency to isolate and bed down. All pregnant ewes are moved to anew pasture or paddock as a flock every one to three days, leaving behind ewes that have given birth. This leaves young lambs and their dams in small groups containing lambs of the same age, ideal for developing distance recognition as shown in Gonyou and Stookey (1985) and for encouraging correct bonding due to low social density. Groups can later be combined as the lambs mature, for easier management.

Another management tactic McNally described to improve bonding on pasture is grazing management. Ewes should never have to travel far from their lambs to eat their fill. A well-managed pasture will keep a ewe fed without having to wander more than 9 meters from her lambs at any given time. McNally describes some lambs as "rendezvous" lambs, similar to the hiding behavior described in goat kids. Lambs are generally described as followers, staying near their dams while the dams graze, while goat does will plant their young in one location and return to them (Gonyou and Stookey, 1985). According to McNally's observations, some ewe-lamb pairs favor the "hider" strategy, choosing a rendezvous site and not remaining together while the ewe grazes. For this reason, she recommends that ewes with young lambs not be moved at all from their original paddock (McNally, 2008). Unfortunately this tactic can often be at odds with parasite management strategies, and individual farmers may choose to move at their own discretion. A different form of "drift" lambing, described by Rook et al. (2007), operates on a compromise: this system opens up new sections of pasture and allows the flock to naturally move forward into these sections, closing off previous areas after the sheep have moved forward without pressure. This eliminates any rousing of hidden lambs and could minimize confusion and lost lambs in the time period before distance recognition is firmly developed in young lambs.

Management decisions can often make the difference between profitable and unprofitable farms. While many of these strategies involve genetic improvement and farm labor practices, aspects of sheep behavior are important to decide which route is most efficient. This is particularly true at lambing time, when a ewe's innate maternal behaviors can so strongly influence the bottom line due both to labor required and overall lamb mortality. Choosing a management style that allows ewes to best express their own maternal behaviors and choosing to select for ewes that most effectively perform these behaviors is an important step forward when optimizing a commercial sheep flock.

Chapter Four

Evaluation of alternative strategies in lambing management

Management at lambing time is an important factor in the successful operation of a sheep farm. Most mortalities on sheep farms occur within the first three days of life, with the average flock experiencing between 5 and 15% lamb mortality, up to 30% in some flocks (Everett-Hincks and Dodds, 2008). Many farmers utilize intensive management systems, requiring large labor input, yet fail to reduce lamb mortality. For those farmers lambing in the winter in colder climates, an indoor system is the only option, but the amount of labor and high mortality rates can make it difficult for farmers to expand their flocks or even stay in the business at all (Binns et al., 2002; Dwyer and Lawrence, 2005). In some parts of the world, particularly New Zealand, Australia and Scotland, "easy care" systems or extensive management styles are popular. These systems encourage farmers to let ewes take more responsibility for the initiation of maternal bonding and care, while housing sheep outdoors in low-density pasture lots (Dwyer, 2008b; Everett-Hincks and Dodds, 2008). These systems, in moderate climates and in colder climates during warmer times of year, offer the ability for farmers to manage larger flocks than they could under intensive management.

The research reported here examines two strategies, one in-barn and one on pasture, for reducing labor at lambing time while maintaining or improving maternal care, and explores methods for the assessment of maternal bonding and ability in ewes.

The goal of experiment 1 was to evaluate cubicles as an alternative management tactic for ewes lambing in barn systems. Sheep in barns are generally kept at a much higher density than they would be on pasture, leaving little room for expression of natural pre-parturient isolation behavior. In a cubicle system (Gonyou and Stookey, 1985, 1983), ewes are given the option to enter small pens located off of the large main pen area. Ewes seek isolation so that selective bonding with their offspring can be maximally achieved, so it is predicted that ewes that give birth and bond in cubicles will as a group show improved maternal care as a result of better-formed maternal bonds.

In experiment 2, lambing on pasture was examined as an alternate management strategy for flocks that had previously only been lambed indoors under intensive management procedures. For many farmers utilizing intensive management practices, labor needs at lambing can be prohibitively taxing. This limits flock expansion and may even lead farmers to leave the sheep industry. In many parts of the world, particularly in New Zealand and Australia, sheep are extensively managed at lambing time, allowing for much larger numbers of ewes to lamb with much less labor. This is exemplified by the "easy-care" systems used on many New Zealand farms (Everett-Hincks and Dodds, 2008). However, the sheep in these systems have been self-selected for generations to lamb and raise their lambs on pasture. In contrast, sheep that have for generations been managed under traditional extensive systems have not been selected for such abilities. There has been speculation that such flocks may have been inadvertently selected for poor maternal behavior and difficult births, as such issues are dealt with by the increased labor inherent in intensive systems and do not act as natural culling forces as they would on pasture without close supervision.

The Cornell flock epitomizes such a lack of selection, as years of intensive management and dense stocking have meant that behaviors such as pre-parturition isolation serve no purpose. As such, it is an ideal subject flock in which to examine the ability of such unselected ewes to lamb and raise their lambs on pasture under more extensive situations than typically maintained. However, these ewes might be able to successfully lamb and raise lambs on pasture with minimal management, as the increased area available will encourage natural expression of maternal behaviors while limiting opportunities for interference from other ewes.

Materials and Methods

Late-pregnant Dorset, Finnsheep and their crosses belonging to the Cornell Sheep Farm were used for all experiments. Ewes in this flock are managed under the Cornell STAR system, an accelerated lambing system allowing 5 lambing periods each year with the potential for each ewe to lamb 5 times in 3 years. During 30-day lambing periods, ewes are housed in group pens, on bedded packs, until parturition. After giving birth, ewes with their lambs are moved to small claiming pens (approximately 1.5 x 1.5m), where they typically remain for 1 to 3 days. Once bonded, ewe-lamb sets are released into mixing pens with other sets from the same lambing period. These standard procedures served as the control condition for both experiments 1 and 2.

Experiment 1

Experiment 1 took place over a single lambing period in June and early July 2009. 42 ewes of both breeds and their crosses were housed in the sheep farm barn at a stocking density of 20 to 25 square feet per ewe. This stocking density was maintained over the course of the experiment by the addition of new ewes whenever one ewe was moved to the mixing pen with her offspring.

The experimental condition tested the use of "cubicles," bonding pens attached to the main lambing area by an open gate, to which pregnant ewes had open access. The cubicles used in this experiment were constructed of wire panels, 0.9 m tall with 10 x10 cm wire spacing, and wooden gates. The cubicles were 1.5 m wide and 2.4 m long, with a 0.75 m opening into the main pen area. Five of these cubicles were located in a row on the side of the lambing pen farthest from the alleyway and feed bunk, accounting for 26.6% of the entire lambing area. The layout of the lambing area is shown in Figure 3. Lambs and their dams were closed into these cubicles/pens after lambing, regardless of whether they chose the cubicle in which to lamb, and remained there for at least 4 hours and until processed (up to 12 hours.) Processing included ear-tagging and paint-marking, after which the ewes and their lambs were released into a "mixing" pen with other ewes and lambs of similar ages.

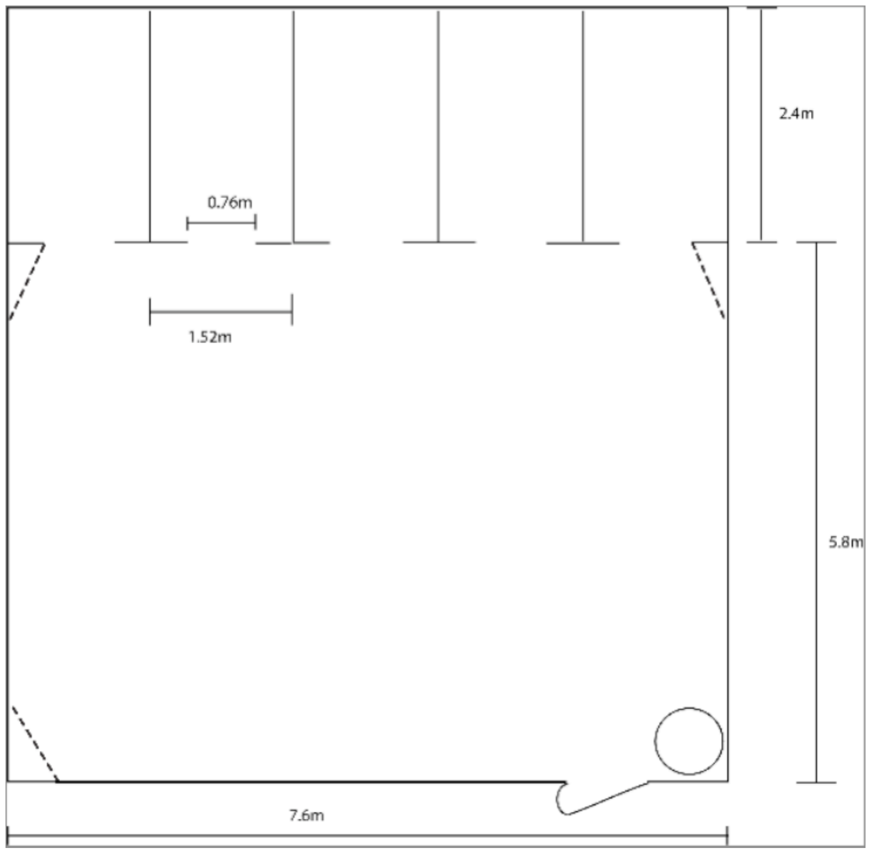

Figure 3. Diagram of the lambing pen in Experiment 1, with distances and cubicle locations shown.

The experimental lambing pen and cubicle areas were video-recorded digitally and stored for later analysis. Ez-Watch Pro surveillance software (Automated Video Systems, LLC, Salt Lake City, Utah) was used for all video recording and export. The cameras included infrared sensors for night-time recording. This video was used to determine where a ewe was located at time of lambing. If a ewe's location could not be determined using the video, she was excluded from analysis and not selected for behavioral testing (see below).

Approximately 3 weeks into the lambing period, an additional pen (3.6 x 7.6 m) was added, into which dams and their lambs were moved for approximately the first week after processing. After this, lambs and their dams were released into the main pen.

A second group of ewes, lambed under the typical Cornell Sheep Farm management procedures described above, were used as a control group in both tests. Ewes from this group to be tested were moved into the same claiming pen as experimental ewes to be tested four days prior to testing. Behavior tests were conducted in the area where the experimental group had lambed over the course of the prior month.

Behavioral Tests

Three groups of ewes were selected for two tests of maternal behavior: cubicle-lambing experimental ewes, pen-lambing experimental ewes, and control ewes (lambed and immediately confined to lambing jugs). All ewes from the experimental group that were known to have lambed in a cubicle were included (n = 6). Twelve ewes from the pen-lambing experimental group and 13 ewes from the control group were chosen for inclusion in the tests. Inclusion was decided pseudo-randomly by order of appearance at the gate when ewes were moved between pens.

The first test was a highly modified version of the "maternal behavior score" (MBS) used by O'Connor et al. (1996; 1985) The lambs were between 2 and 6 weeks of age when this test was conducted. The arena for this test was the lambing pen where the experimental ewes had lambed, set up just as it had been for the lambing period.

During the test, lambs were carried low to the ground by an experimenter while ewes followed from one open cubicle to another, through the empty main pen area. This mimics the way ewes and their lambs are often moved in a barn. An example path is shown in Figure 4. A score from 1 to 5, as shown in Table 1, was assigned to each ewe, reflecting how closely she followed her lamb and entered the claiming pen. These scores were analyzed by nominal logistic regression for differences between experimental group ewes lambing in cubicles, those not lambing in cubicles, and control group ewes.

Table 1. Rubric for Modified Maternal Behavior Score

Score	Description
1	Ewe is panicked, does not maintain interest in lambs and must be herded into small pen with difficulty
2	Ewe flees and gets distracted but returns to lambs, requires herding into small pen
3	Ewe maintains active interest in lambs but leaves and returns multiple times; requires coaxing into small pen
4	Ewe maintains strong interest in lambs, does not flee more than once, requi little coaxing into small pen
5	Ewe remains close to lamb and enters small pen easily

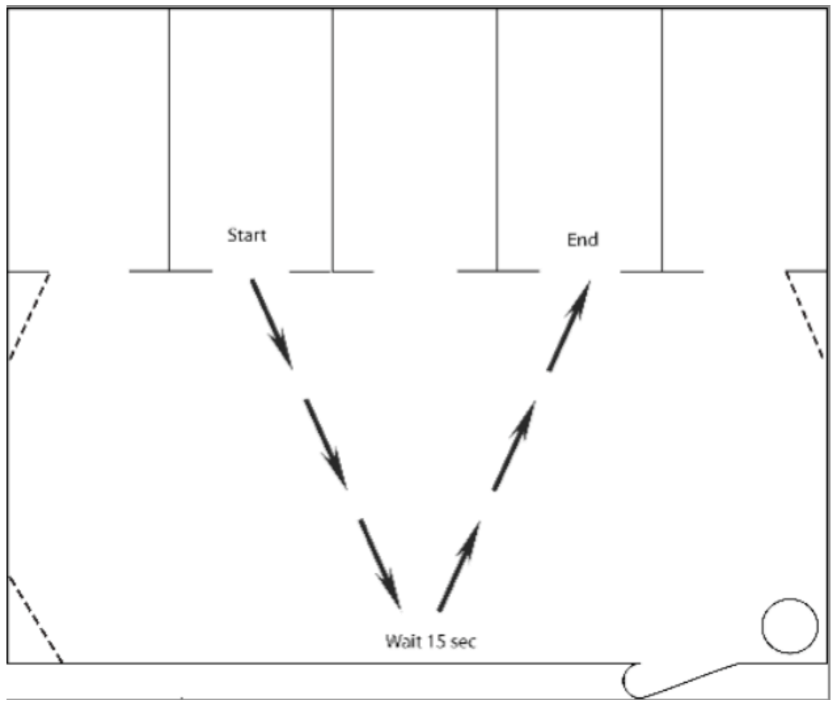

Figure 4. Example of a path taken (shown by the arrows) during the MMBS test.

The second test was conducted 10 days later when lambs were 3 to 7 weeks of age. This test presented ewes with a two-choice preference task. Ewes and their lambs were separated for an hour before testing to encourage desire for reunion.

The testing arena was created from a solid-sided 1.1 m tall aluminum chute system, with a guillotine gate at the end leading into an empty 2.4 x 3.0 m pen. On either side of this pen, smaller 2.4 x 1.5 m pens contained either the ewe's own lamb or lambs or alien lambs. The setup is shown in Figure 5. An equal set of alien lambs was used; if the ewe was raising a single lamb, one alien lamb was placed in the opposing pen. If the ewe was raising twins, both of her twins were placed in one pen and a pair of alien twins placed in the opposing pen. This test was also recorded digitally and analyzed from the recording. The amount of time each ewe spent facing her own lambs during the first 60 seconds after release was recorded and analyzed by ANOVA as a percentage of time spent. Additionally, weight per day of age was calculated from weaning weights (recorded as part of standard farm procedures) for comparison between control and experimental lambs.

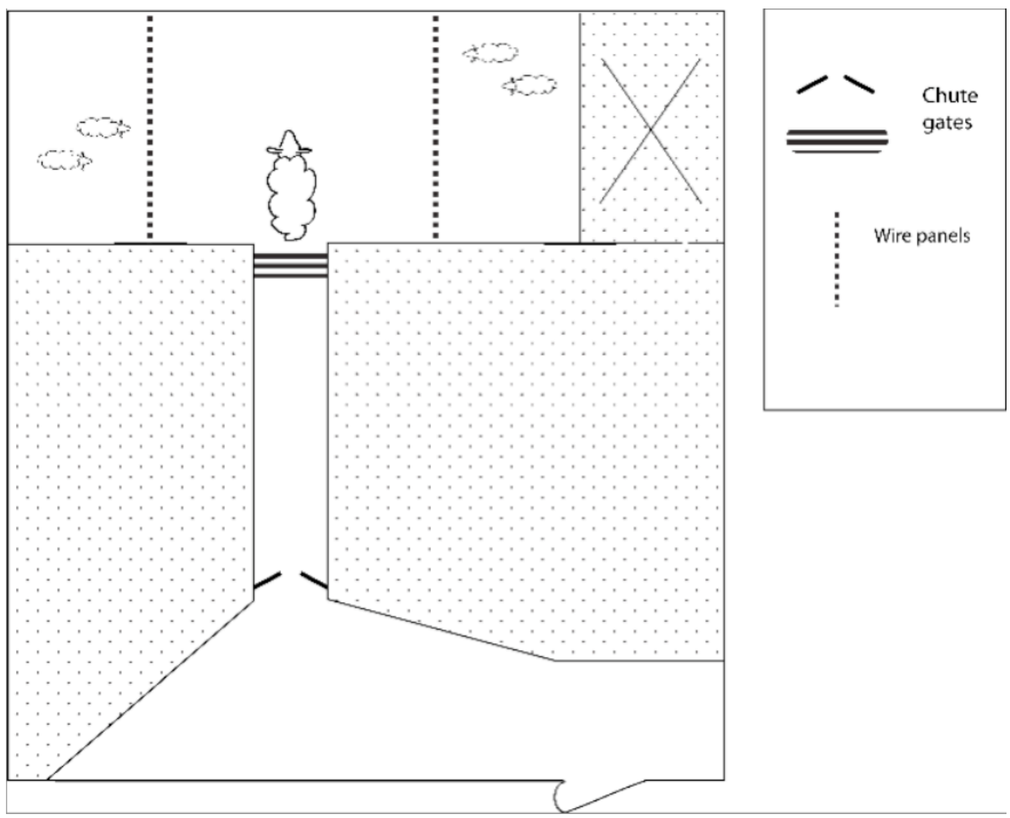

Figure 5. Diagram of the 2-choice testing setup, with a ewe shown as having entered the testing pen through a gated chute system.

Statistical analyses. A Fisher's exact test was used to compare predicted versus observed values in a contingency table comparing lambing locations for ewes offered cubicles. Weight per day of age (WPDA) at weaning was compared among lambing locations by one-way analysis of variance, as was the time a ewe spent facing her own lamb in the 2-choice test. The modified maternal behavior scores for ewes in each lambing location were analyzed by logistic nominal regression.

Experiment 2

Experiment 2 took place over two lambing periods in June through early September 2010. Twenty Dorset x Finnsheep ewes were individually paint-numbered and kept in an approximately 0.5 hectare pasture, subdivided once with electronet fencing which was moved to allow more grazing area as the season progressed. Data were collected over two lambing periods, in June and August of 2010.

The pasture was walked a minimum of twice per day, and lambs processed when first found. Processing included dipping navels of newborn lambs in 7% iodine solution, ear-tagging the lambs, and marking lambs with their dam's identifying number. For any ewe giving birth to triplets, the smallest or weakest-appearing lamb was removed to the barn and fostered or artificially raised.

At the same time, for both lambing seasons, the remainder of the late-pregnant ewes in the flock were lambed in the barn under standard management procedures, as described in experiment 1. A randomly chosen subset of these ewes served as a control group from which mortality rates and rate-of-gain data were drawn for comparison to the pasture-lambed ewes. The numbers of ewes included in each lambing type and season are shown in Table 2.

Table 2. Number of ewes in each category

Season	June				August			
Lambing Type	Pasture		Barn		Pasture		Barn	
Number of Lambs	One	Two	One	Two	One	Two	One	Two
N	5	8	7	8	8	6	4	9

At the time of processing, a maternal behavior score (MBS) was recorded. The MBS (O'Connor, 1996) assigns ewes a score of 1to 6, as shown in Table 3, based on the distance that they flee from their lambs during ear-tagging.

Table 3. Maternal Behavior Score Rubic, as used in Experiment 2 (O'Connor, 1996).

Score	
1	Ewe flees at approach of the observer, shows no interest in her lamb(s) and does not return when the observer leaves.
2	Ewe retreats further than 10 m but maintains an interest in her lamb(s) and comes back to them as the observer leaves them.
3	Ewe retreats to 5-10 m.
4	Ewe retreats but stays within 5 m.
5	Ewe stays close, within 1 m, to the observer during handling of her lamb(s).
6	Ewe makes physical contact with her lamb(s) while they are being held by the observer.

When lambs were between 4 and 6 weeks of age, one 15-minute set of focal behavioral observations were made for each ewe. One ewe was observed at a time, and the individual's behavior was recorded at 15-second intervals. The ethogram used is presented in Table 4. For analysis, specific behaviors were identified as "active," as indicators of attention paid by a ewe toward or in care of her lamb.

Table 4. Ethogram for focal observations of lactating ewes on pasture.

Classification	Behaviors	
Passive	• Cudding • Digging • Drinking • Grazing • Itching • Lying down	• Leaving lamb • Sniffing ground • Standing • Standing up • Urinating • Walking
Active	• Approach lamb • Head butt • Nursing	• Scanning • Sniff lamb • Vocalizing
Other	• Out of sight	

Statistical analyses. An equal number of barn-lambing ewes from each season were selected using a random number generator for comparison with the pasture-lambing ewes. Mortality rates at birth and from birth until weaning were compared by Chi-square analysis between control and experimental groups over each season. The weaning weights of each ewe's lambs were averaged and divided by age to compute average weight per day of age (WPDA) per lamb per ewe. The statistical model for WPDA included main effects of season (June or August), lambing type (Pasture or Barn), Litter size (1 or 2), and all two- and three-way interactions. The linear and quadratic effects of ewe age were included as covariates. Whether these covariates were affected significantly by main effects and interactions was also checked. Thus, the initial model included the following effects:

Table 5. Initial linear model used to quantify the effect of experimental variables on weight per day of age (WPDA).		
Minitab column	Minitab name	Real name
C22	SnEfct	Season (June or August)
C23	GrEfct	Lambing type (Barn or pasture)
C24	SxG	Season x Lambing type interaction
C25	NoL	Litter size (1 or 2)
C26	NoLxSn	Litter size x Season interaction
C27	NoLxG	Litter size x Lambing type interaction
C28	NoLxSnxG	Litter size x Lambing type x season interaction
C29	EA	Linear effect of Ewe age (covariate)
C30	EA^2	Quadratic effect of ewe age
C31	SxEA	Season x Ewe age (check for effect of Season on Ewe age covariate)
C32	SxEA2	Season x quadratic Ewe age (check for effect of Season on quadratic Ewe age covariate)
C33	GxEA	Lambing Type x Ewe age (check for effect of Lambing Type on Ewe age covariate)
C34	GxEA2	Lambing Type x quadratic Ewe age (check for effect of Lambing Type on quadratic Ewe age covariate)
C35	SxGxEA	Season x Lambing Type x Ewe age (check for effect of interaction on Ewe age covariate)
C36	SxGxEA2	Season x Lambing Type x quadratic Ewe age (check for effect of interaction on quadratic Ewe age covariate)
C37	NoLxEA	Litter size x Ewe age (check for effect of Litter size on Ewe age covariate)
C38	NoLxEA2	Litter size x quadratic Ewe age (check for effect of Litter size on quadratic Ewe age covariate)
C39	NxSxEA	Litter size x Season x Ewe age (check for effect of interaction on Ewe age covariate)
C40	NxSxEA2	Litter size x Season x quadratic Ewe age (check for effect of interaction on quadratic Ewe age covariate)
C41	NxSxGxEA	Litter size x Season x Lambing Type x Ewe age (check for effect of interaction on Ewe age covariate)
C42	NxSxGxEA2	Litter size x Season x Lambing Type x quadratic Ewe age (check for effect of interaction on quadratic Ewe age covariate)

Many of the Ewe age covariate effects were correlated. Therefore, beginning with the highest order covariates, those that were not significant ($P < 0.05$) were removed from the model until only significant covariate effects were left.

Results

Experiment 1

Of the 29 ewes whose lambing locations were observed in the cubicle management system, 6, or 20.7% lambed in cubicles. The entire lambing area measured 44 m^2, of which 19 m^2, or 29.6%, consisted of space in cubicles. This rate of use was not significant as analyzed by Fisher's exact test ($p = 0.45$) shown in Table 6. Neither did lambs differ in rate of gain, measured by weight per day of age, between cubicle and control lambing locations ($p = 0.52$, data not shown) nor among lambs born in cubicles, in the main pen, or whose dams were in the control condition and were given no choice (Table 7, $p = 0.88$).

Table 6. Cubicle use and area in experiment 1.

Item	Cubicles	Main pen	Total
Lambings	6	23	29
Area (m^2)	19	44	63
Total	26	67	92
Fisher's exact test		P = 0.45	

Table 7. Effect of lambing location on weight per day of age (WPDA), modified maternal behavior score (MMBS), and percentage of time (Time) spent by the ewes facing their own lambs in a two-choice test.

Lambing location	N	WPDA[a], g/d	MMBS[b], 1 to 5	Time[a], Percent
Cubicle system- in cubicle	5	281	4.3	63.3
Cubicle system – not in cubicle	12	290	3.8	60.8
Traditional system	13	275	3.8	62.4
Standard Error		23.8	0.48	4.52
P-value		0.78	0.125	0.89

[a]Analyzed by analysis of variance.
[b]Analyzed by logistic regression.

Measures of maternal bonding also showed no significant difference between cubicle and traditional Lambing Types. Modified maternal behavior score (MMBS) values were slightly but non-significantly higher in cubicle-using ewes (Table 1). As seen in Figure 6, MMBS distribution was skewed toward the right, with animals in all lambing locations receiving scores of 5 most often, and no scores of 1 being given. A histogram of MMBS distribution by lambing location (Figure 6) (cubicle, pen, or traditional management) showed that all cubicle-lambing ewes received scores of 4 or 5; however the percentage of ewes using cubicles was very low and logistic nominal regression determined the distribution of MMBS to not be significantly correlated with lambing location ($P = 0.125$).

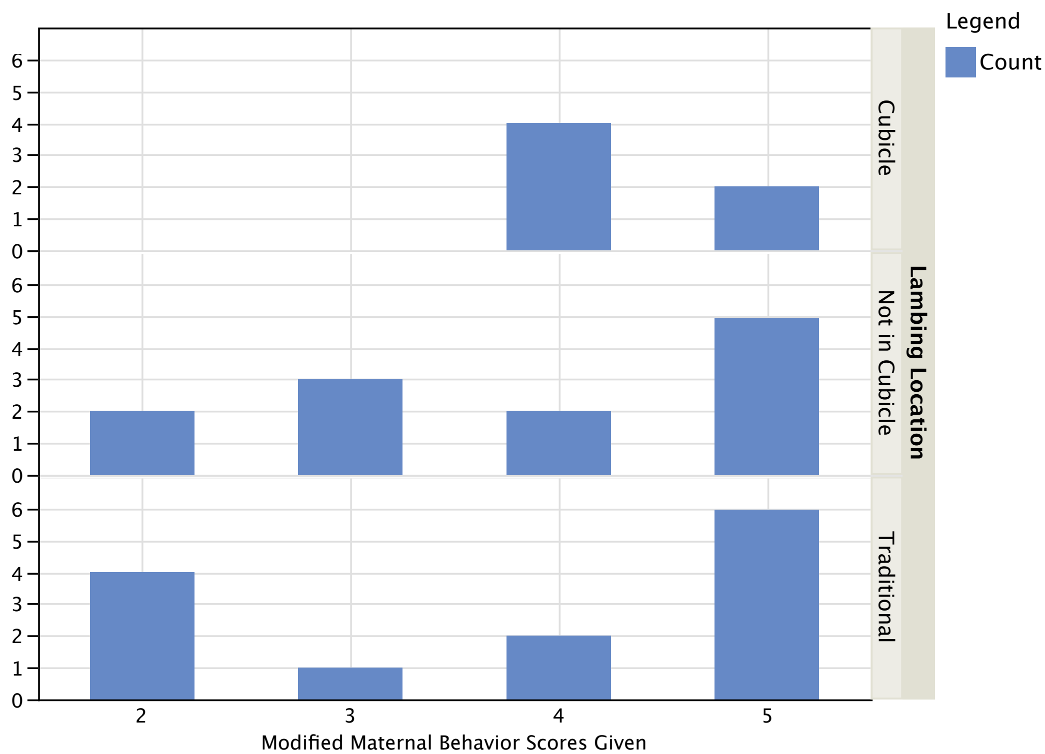

Figure 6. Distribution of modified maternal behavioral scores by lambing location

There was little difference between lambing locations in the 2-choice test. Ewes lambing in cubicles spent slightly more time facing their own offspring ($p = 0.85$). Within ewes offered cubicles, those lambing in cubicles spent slightly more time oriented toward their offspring in the 2-choice test, but this was not significant ($p = 0.63$).

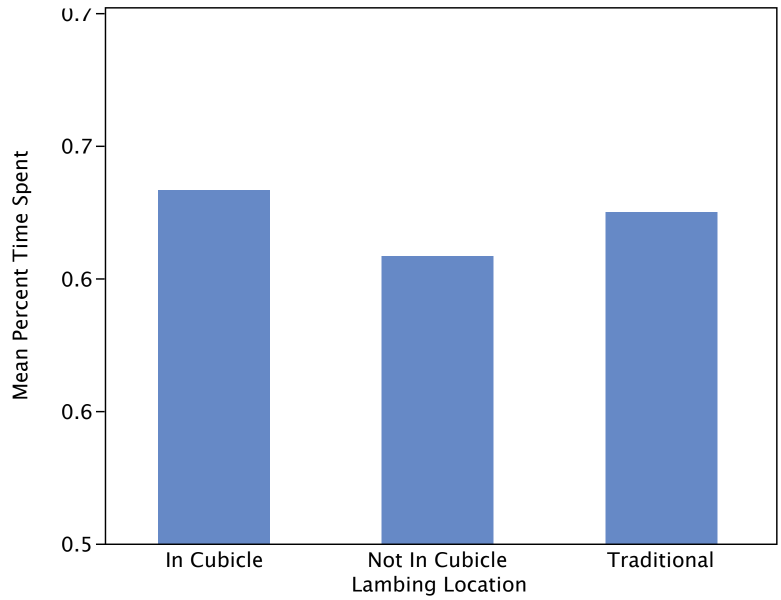

Figure 7. Mean percent of time spent oriented to offspring in the two choice test.

Experiment 2

Comparisons of mortality between pasture-born (experimental) and control lambs showed no significant differences between either stillborn rates (total lambs born compared to lambs born alive for each season, chi-square P = 0.913) or between total mortality rates of lambs raised to weaning (chi-square P = 0.933, Table 8).

Table 8. Numbers of lambs for various categories.

Item	June		August	
Lambing type:	Barn	Pasture	Barn	Pasture
Ewes	17	17	18	18
Lambs delivered	41	34	33	34
Born alive[a]	37	31	28	31
	(90.2%)	(91.2%)	(84.9%)	(91.2%)
Total lambs raised	26	22	28	27
Weaned (of raised)[b]	24	21	24	20
	(92.3%)	(95.5%)	(85.7%)	(74.1%)

[a] Chi square P-value was 0.91 for lambs born alive compared to lambs delivered.
[b] Chi square P-value was 0.93 for lambs weaned compared to lambs raised by the ewes.

Maternal Behavior Score was not correlated with weight per day of age (WPDA) (P = 0.13), nor was the proportion of behavioral observations during which pasture-lambed ewes were seen performing "active" behaviors (P = 0.26). These two measures were however correlated with each other (P = 0.005).

No significant difference was found between pasture and control ewes for WPDA (Figure 8), though other measured variables did appear to contribute to this measure of gain rate. The mean WPDA values for lambing types and seasons are shown in Table 9. August lambs tended to have lower WPDA than did June lambs, and Pasture (Experimental) lambs tended toward lower WPDA than did Barn-raised (Control group) lambs, but these differences were only significant in the interaction of Season and LambingType. This was reflected in the lower WPDA for August pasture lambs.

Table 9. Effect of lambing type, season, and litter size on grams of weight per day of age (WPDA)[a].

	June		August	
Lambing type	Single	Twin	Single	Twin
Barn	309	320	377	293
Pasture	388	278	292	268

[a]SE = 26.3

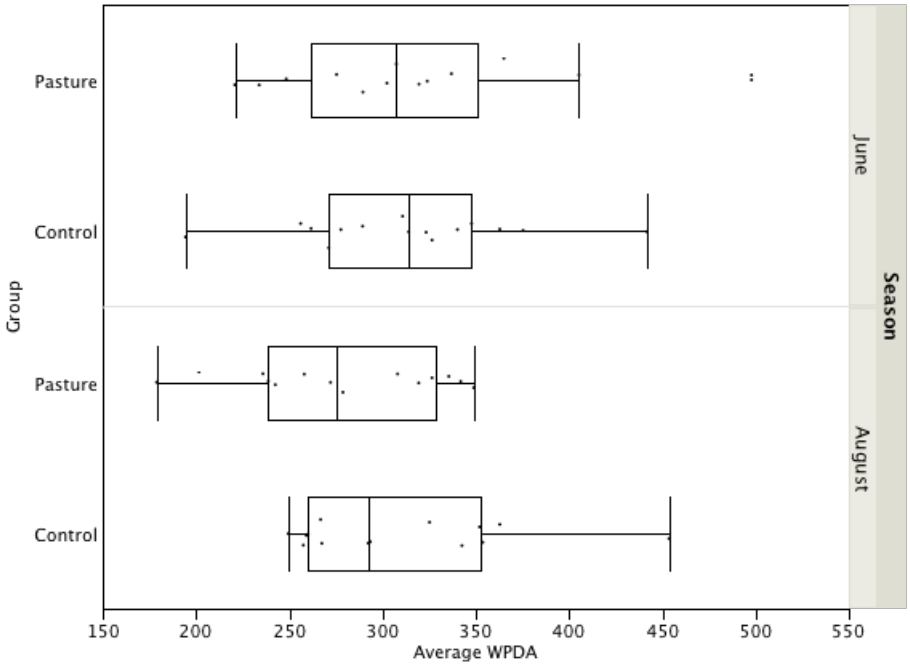

Figure 8. Box plots for weight per day of age for lambs in lambing groups and seasons.

P-values for main effects and significant covariates in the model are shown in Table 10. WPDA was affected by Litter Size, Ewe Age, interactions between Season and Lambing Type (as mentioned above), between Lambing Type and Ewe Age Squared, Season, Lambing Type, and Litter Size (Table 10). Trends between WPDA and Ewe Age can be seen in Figure 9, where regression shows a strong increase in WPDA with Ewe Age for lambs reared in the barn, while lamb WPDA on pasture shows no such pattern, increasing slightly until ewes are around 4 years of age, then decreasing again with age.

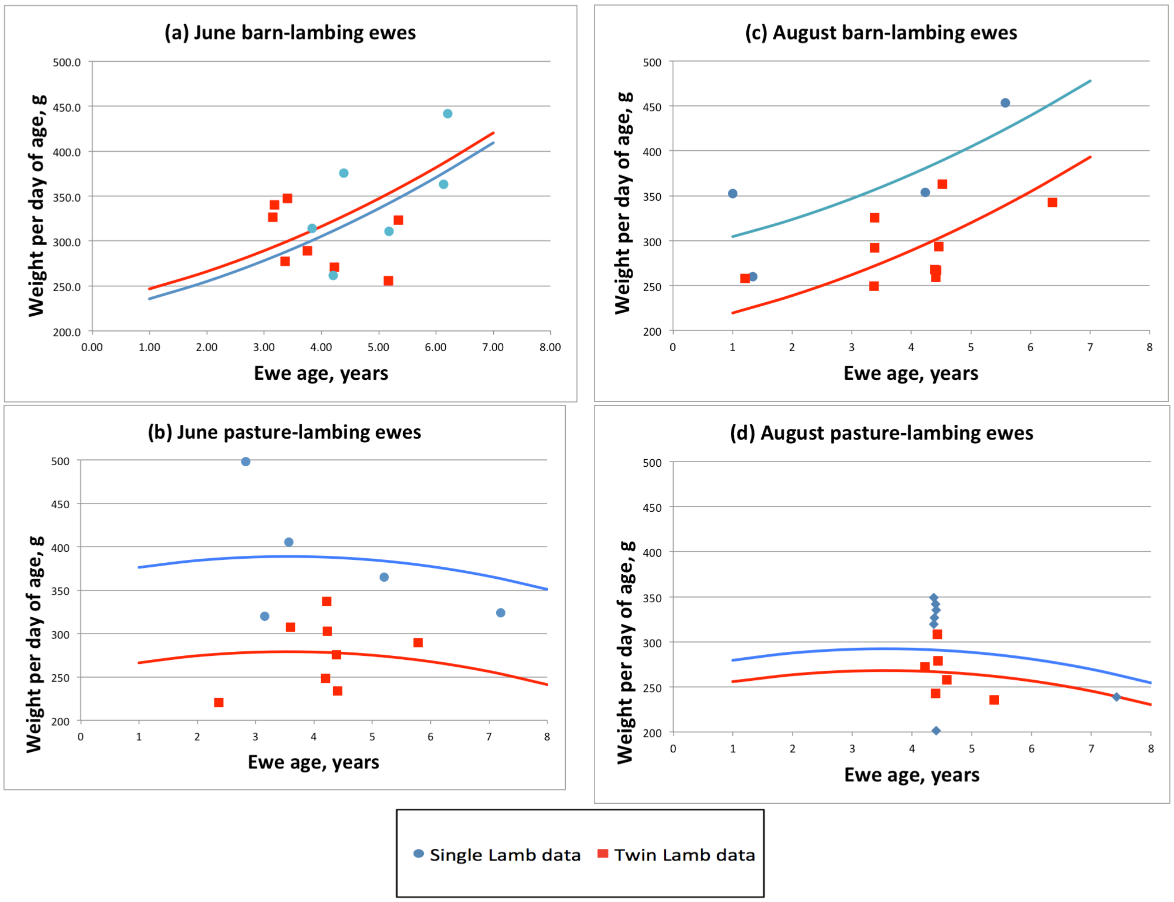

Figure 9. WPDA for each group, by ewe age

Table 10. Analysis of variance for weight per day of age (WPDA).

Source	DF	SS	MS	F	P
Season	1	3435	3435	1.47	0.232
LambingType	1	7163	7163	3.06	0.087
Season x LambingType	1	17218	17218	7.35	0.009
LitterSize	1	34399	34399	14.68	0.000
Season x LitterSize	1	80	80	0.03	0.854
LambingType x LitterSize	1	2866	2866	1.22	0.275
Season x LambingType x LitterSize	1	25225	25225	10.77	0.002
EweAge	1	17137	17137	7.31	0.010
LambingType x $EweAge^2$	1	23001	23001	9.82	0.003
Error	45	105428	2343		
Total	54				

Discussion

In experiment one, when ewes were provided the opportunity to use cubicles, they did not reliably choose to do so. Use rates were not significantly different than would be predicted by chance alone. Overall, the percentage of ewes choosing to lamb in the cubicles was lower than the percentage of pen space consisting of cubicles. This is in contrast to the results reported by Gonyou and Stookey (1985, 1983), in which ewes lambed in cubicles at rates significantly higher than would be predicted by available space alone; in all their experiments, the percentage of ewes lambing in cubicles was much higher than the percentage of pen space composed of cubicles. Gonyou and Stookey (1985) suggested that the ewes in their flock that did not choose to use cubicles may have done so because of innate difference in temperament. This could perhaps be extended to the Cornell flock; there is a chance that the behaviors of Cornell ewes differ significantly in respect to their isolation-seeking behavior, which is known to differ among breeds (Vallaillet and Nowak, 2006). The sheep used in Gonyou and Stookey's experiment were either unidentified cross-breds (1983) or primarily Suffolk, Targhee and their crosses (1985). As the Cornell flock is primarily Dorset, Finnsheep and their crosses, it is quite likely that the temperaments would differ between flocks.

Because such a small number of ewes offered cubicles chose to lamb in them, it is difficult to make any conclusions regarding the maternal success of cubicle-using ewes. There were no distinguishable differences between control and cubicle-offered ewes for any measurement. Comparing ewes that did use cubicles to those that had the option to but did not, it appears that those ewes lambing in cubicles may have had stronger maternal responses, but no responses that I measured reach statistical significance.

However, no cubicle-lambing ewe received less than 4 out of 5 for Modified Maternal Behavior Score, while some ewes in all other groups did receive lower scores. Additionally, cubicle-using ewes on average spent more time than control ewes facing their own offspring during the 2-choice test, while non-cubicle-using ewes on average spent less time facing their own offspring. Since the pen-lambing (non-cubicle-using) ewes had the same overall experience as control ewes, giving birth in a crowded area before being moved with their lambs to claiming pens, it is possible that the ewes that did chose to lamb in cubicles were by nature better mothers. In this case, any higher maternal performance seen by cubicle-lambing ewes may not be a result of better bonding from the isolation provided by cubicle privacy, but a result of ewes with stronger maternal drive being more likely to isolate themselves in cubicles.

That ewes did not preferentially utilize cubicles may not inherently promote the use of a cubicle-based in-barn lambing management system, but at the same time, there are few obvious detriments to such a system if a producer's barn is set up to allow for gates to be easily moved to and from the claiming pens. For the few ewes that do use the cubicles, not having to move them and their lambs into claiming pens saves a a few minutes. Of course, if this is negated by the time required to move gates to close off the cubicles, then it is not an optimal management system; these small decisions will often depend on the barn setup within which any individual farmer is working.

In experiment 2, no overall significant differences were found for ewes giving birth to and raising their lambs on pasture when compared to ewes managed in the barn under traditional intensive procedures. Mortality rates at birth (due to stillbirth or dystocia) were no higher, and neither were mortality rates from birth until weaning.

Neither did rate of gain by itself, measured as weight per day of age (WPDA) at weaning, differ significantly between Lambing Type (pasture or barn), without other factors taken into consideration. Factors that were found to correlate with rate of gain were litter size and ewe age. These also significantly interacted with lambing type to influence WPDA. Litter size is unsurprising, as it requires more energy for a ewe to raise multiple lambs, which often begin life at lighter weights than singletons, and then face competition for milk supply. As a result it is not uncommon for twin or triplet lambs to be smaller than singletons at any given age.

Ewe age has also been reported as a factor in successful lamb rearing, with younger and much older ewes generally making worse mothers, and maternal ability peaking around 4 years of age (Everett-Hincks and Cullen, 2009). This was observed in the current experiment, particularly in the pasture-lambing ewes, with the modification that older ewes fared better in the barn than on pasture. This is likely related to the same factor that led to the overall trend for lighter weights in August compared to June: very hot weather occurred during this lambing period, acting as a stressor for all sheep. It may have been more difficult for older ewes to manage the heat stress on pasture than in the barn. Unfortunately, the distribution of ewe age in pasture-lambing August ewes makes it difficult to make any conclusions about aged ewes raising lambs in late-summer heat; only two ewes over the age of 5 were included in each group (though the lambs raised by these older ewes performed much more poorly in the pasture group.)

Another potential reason behind the strong effect of ewe age on maternal success is the bias imparted by the culling process. In a typical flock, and at the Cornell Sheep Farm, ewes failing to successfully rear lambs during their first few years of life are very often culled from the flock. As a result, only ewes having at least moderate maternal ability remain in the flock to an older age.

While lambing types on the whole did not result in significant differences, pasture lambs had lighter average weaning weights and rates of gain compared to those born and raised in the barn and there were significant interactions with season, ewe age and litter size. There are a number of factors that could contribute to this, including the above-mentioned factor of weather. During poor weather, lamb mortality is known to rise. June and August lambing periods were chosen as to minimize the chance of exposure to chilling weather, though several days in the June lambing season were wet and below 10°C, a dangerous combination for newborn lambs. The worst impact of weather seemed to be due to heat stress. Temperatures were high in August and all lambs in this season grew more slowly. It is well documented that heat reduces milk production (Fuquay, 1981) and so is reasonable to suggest that the lower rates of gain may be in part from lower milk availability. Lambs in the barn had access to "creep" areas, where feeders provided supplemental concentrate feed; this alone could lead to higher in-barn rates of gain, and particularly so if ewes were under-producing milk. On pasture, lambs graze with their dams and so receive additional nutrition. Any pre-existing inequality in energy intake between barn-fed concentrate and pasture grazing was likely exaggerated by the heat, as pastures were not in the best condition with grasses succumbing to heat stress as well. Supplemental feed was provided on pasture in the form of hay, but overall August forage conditions were poor.

One further potential influence on lamb rate of gain on pasture was parasite exposure. For these seasons, preventative rotational pasture management tactics were not implemented, in favor of allowing lambs to remain on the same familiar terrain until weaning. The poor forage quality also is likely to have aggravated any parasite issues. As sheep graze closer to the ground they are more likely to encounter and ingest worm larvae.

In general, raising lambs on pasture appears to be more challenging for ewes than raising lambs in the barn, and lambs are less likely to gain weight at as high a rate if their ewes are faced with stressors. These may be the same stressors that influence ewes under any management system, such as the nutritional pressure from lactating to feed multiple offspring, but on pasture the repercussions in lamb weight gain are more severe. The effect of this cumulative stress is possibly why significant interactions were detected for season and lambing type (heat stress), and season by lambing type by litter size (the combination of heat stress and raising twins.)

Future pasture work is set to examine several of these factors. While heat stress is difficult to counter, variety in shelter options can be explored. Moving ewes and their lambs on a regular basis (such as weekly) will prevent much of the exposure to worms that may have caused weight gain issues in the current study. Worm egg counts in fecal samples can provide data on parasite loads. Preliminary data from June 2011 indicate moderate loads of *Strongyloides* and *Strongylidae* species in pasture-raised lambs rotated to new pasture approximately every 2 weeks. A structured pasture management plan and deworrming protocol is highly recommended to counter this issue.

To increase nutritional status of pasture lambs, availability of creep feed is an option, but preliminary observations from August 2011 suggest that pasture lambs do not choose to eat much of this feed, possibly due to learning by imitation from dams observed grazing. However, in-barn lambs certainly do utilize creep feeders, which ewes cannot gain access to, so the low apparent use on pasture may also just be due to a preference for grazing, which barn-raised lambs do not have as an available option.

One oft-cited concern of farmers regarding pasture lambing is predation, but this was not encountered during any pasture lambing trial. Observations from August 2010 and 2011 indicate that birds, likely raptors such as hawks and possibly owls, and/or also vultures did consume lambs, but any lambs that were intact enough for necropsy were determined to have been stillborn, so it remains unknown whether birds were the cause of death for any lambs. It is more likely that these birds merely scavenged already-dead lambs and that true predation was not an issue. The use of electrically-charged net fencing has proven an able deterrent against ground predators such as coyotes and stray dogs. In general predation by these animals (to non-lambing flocks outside the realm of this experiment) has only been noted when this fencing has been knocked over, does not make full contact with the ground along the bottom wire, or is uncharged.

Two measures proposed as predictors of maternal behavior in pasture-managed lactating ewes were examined in experiment 2. The purpose of these measures, if reliable, would be to provide farmers a way to predict success in lamb-rearing and potentially to aid in culling decisions, where poor mothers are removed from the flock and their offspring not kept as replacement animals. The behavioral observation of “active” behaviors was similar to that used by O’Connor (1996), where positive but non-significant correlations were found between “head-up” posture and lamb weight gain, as well as between ewe vocalizations and lamb weight gain, while significant correlations were found between these vigilance behaviors and MBS. The results from Experiment 2 mirrored those from O'Connor (1996), as neither "Active" behaviors nor MBS were correlated with rate of gain, while they were correlated with each other. This supports the conclusions of more recent studies (Everett-Hincks and Cullen, 2009; Everett-Hincks et al., 2005; Lambe et al., 2001) reporting low correlation of MBS with maternal or production success.

If MBS is not a reliable predictor of maternal success, then the factor it measures, ewe temperament, also should not be correlated with maternal success. MBS and vigilance postures can both be taken as evidence of emotional reactivity in sheep; overall these appear not to reflect maternal ability. Yet maternal bonding and skill requires a strong behavioral component, so it is reasonable to keep searching for a behavioral measurement that will correlate with such ability. One approach with substantial potential is the test of arena behavior, in which a sheep's reaction to separation and exposure to a strange human is measured in terms of distance traveled and emotional reactions such as rearing and vocalizing. This test also measures emotional reactivity, but appears more able to predict maternal success than MBS or active/vigilance behaviors. The most reliable predictors in arena tests appear not to be locomotion, but fear displays, suggesting that a bold ewe may make a better mother.

CONCLUSIONS

Predicting ewe maternal success and measuring maternal bond strength remain, to an extent, topics of mystery. The optimization of management strategies will always be an important goal for any livestock farmer. Optimizing maternal success at lambing time is an essential point of focus for any farmer hoping to profit from his or her flock of sheep. As more is understood about the behavioral tendencies related to maternal success, management systems will be tailored to lower labor requirements, making sheep farming less stressful for those involved and encouraging the growth of the sheep industry. Any tactic that can work toward the goals of decreased labor and increased production, while preserving or enhancing animal welfare, should continue to be thoroughly explored. Allowing for and encouraging the natural expression of innate behaviors to achieve these goals, particularly including maternal behavior, will remain an important area of focus if we are to keep sheep production viable.

WORKS CITED

Arnold, G. W., and P. D. Morgan. 1975. Behaviour of the ewe and lamb at lambing and its relationship to lamb mortality. Applied Animal Ethology 2: 25-46.

Beausoleil, N., D. Blache, K. Stafford, D. Mellor, and a. Noble. 2008. Exploring the basis of divergent selection for temperament in domestic sheep. Applied Animal Behaviour Science 109: 261-274.

Bickell, S. et al. 2009a. Genotype rather than non-genetic behavioural transmission determines the temperament of Merino lambs. Animal Welfare 18: 459-466.

Bickell, S. et al. 2010a. Maternal behaviour and peripartum levels of oestradiol and progesterone show little difference in Merino ewes selected for calm or nervous temperament under indoor housing conditions. Animal 5: 608-614.

Bickell, S. L., R. Nowak, P. Poindron, and D. Ferguson. 2010b. Maternal behaviour at parturition in outdoor conditions differs only moderately between single-bearing ewes selected for their calm or nervous temperament. Animal Production 50: 675-682.

Bickell, S. L. et al. 2009b. Temperament does not affect the overall establishment of mutual preference between the mother and her young in sheep measured in a choice test. Developmental psychobiology 51: 429-438.

Binns, S. H., I. J. Cox, S. Rizvi, and L. E. Green. 2002. Risk factors for lamb mortality on UK sheep farms. Preventive veterinary medicine 52: 287-303.

Blache, D., and S. L. Bickell. 2010. Temperament and reproductive biology: emotional reactivity and reproduction in sheep. Revista Brasileira de Zootecnia 39: 401-408.

Boissy, A. et al. 2007. Assessment of positive emotions in animals to improve their welfare. Physiology & behavior 92: 375-397.

Dwyer, C. 2008a. The welfare of the neonatal lamb. Small Ruminant Research 76: 31-41.

Dwyer, C., and a. Lawrence. 2005. A review of the behavioural and physiological adaptations of hill and lowland breeds of sheep that favour lamb survival. Applied Animal Behaviour Science 92: 235-260.

Dwyer, C. M. 2008b. Genetic and physiological determinants of maternal behavior and lamb survival: Implications for low-input sheep management. Journal of Animal Science 86: E246-E246.

Everett-Hincks, J. M., and N. G. Cullen. 2009. Genetic parameters for ewe rearing performance. Journal of animal science 87: 2753-2758.

Everett-Hincks, J. M., and K. G. Dodds. 2008. Management of maternal-offspring behavior to improve lamb survival in easy care sheep systems. Journal of Animal Science 86: E259-270.

Everett-Hincks, J. M., N. Lopez-Villalobos, H. T. Blair, and K. J. Stafford. 2005. The effect of ewe maternal behaviour score on lamb and litter survival. Livestock Production Science 93: 51-61.

Ferreira, G. et al. 2000. Learning of olfactory cues is not necessary for early lamb recognition by the mother. Physiology & behavior 69: 405-412.

Fuquay, J. W. 1981. Heat Stress as it Affects Animal Production. Journal of Animal Science 52: 164-164.

Gonyou, H. W., and J. M. Stookey. 1983. Use of lambing cubicles and the behavior of ewes at parturition. Journal of animal science 56: 787-791.

Gonyou, H. W., and J. M. Stookey. 1985. Behavior of parturient ewes in group-lambing pens with and without cubicles. Applied Animal Behaviour Science 14: 163-171.

Hatcher, S., K. D. Atkins, and E. Safari. 2009. Phenotypic aspects of lamb survival in Australian Merino sheep. Journal of animal science 87: 2781-2790.

Hatcher, S., K. D. Atkins, and E. Safari. 2010. Lamb survival in Australian Merino sheep: a genetic analysis. Journal of animal science 88: 3198-3205.

Keller, M. et al. 2003. Maternal experience influences the establishment of visual/auditory, but not olfactory recognition of the newborn lamb by ewes at parturition. Developmental psychobiology 43: 167-176.

Kendrick, K. 1996. Are faces special for sheep? Evidence from facial and object discrimination learning tests showing effects of inversion and social familiarity. Behavioural Processes 38: 19-35.

Kendrick, K. 2000. Oxytocin, motherhood and bonding. Experimental physiology 85: 111s-124s.

Kendrick, K. M., a. P. da Costa, a. E. Leigh, M. R. Hinton, and J. W. Peirce. 2001. Sheep don't forget a face. Nature 414: 165-166.

Kendrick, K. M., and E. B. Keverne. 1991. Importance of progesterone and estrogen priming for the induction of maternal behavior by vaginocervical stimulation in sheep: effects of maternal experience. Physiology & behavior 49: 745-750.

Kilgour, R. J. 1998. Arena behavior is a possible selection criterion for lamb-rearing ability; it can be measured in young rams and ewes. Applied animal behaviour science 57: 81-90.

Lambe, N. R., J. Conington, S. C. Bishop, A. Waterhouse, and G. Simm. 2001. A genetic analysis of maternal behaviour score in Scottish Blackface sheep. British Society of Animal Science 72: 415-425.

Levy, F. 2008. Neural substrates involves in the onset of maternal responsiveness and selectivity in sheep. p 23-37.

Levy, F., K. M. Kendrick, E. B. Keverne, V. Piketty, and P. Poindron. 1992. Intracerebral Oxytocin Is Important for the Onset of Maternal Behavior in Inexperienced Ewes Delivered Under Peridural Anesthesia. Behavioral Neuroscience 106: 427-432.

Lindsay, D. R., and I. C. Fletcher. 1968. Sensory involvement in the recognition of lambs by their dams. Animal behaviour 16: 415-417.

McNally, J. W. 2008. A pasture system for prolific sheep. p 1-11.

Nash, M. L., L. L. Hungerford, T. G. Nash, and G. M. Zinn. 1996. Risk factors for perinatal and postnatal mortality in lambs. The Veterinary record 139: 64-67.

O'Connor, C. E. 1996. Ewe maternal behaviour score and lamb growth: Ten years on. Proceedings of the New Zealand Society of Animal Production 56: 107-109.

O'Connor, C. E., N. P. Jay, A. M. Nicol, and P. R. Beatson. 1985. Ewe maternal behavior score and lamb survival. Proceedings of the New Zealand Society of Animal Production 45: 159-162.

Poindron, P., F. L√©vy, and M. Keller. 2007a. Maternal responsiveness and maternal selectivity in domestic sheep and goats: the two facets of maternal attachment. Developmental Psychobiology 49: 54-70.

Poindron, P., A. l. Terrazas, M. a. D. L. L. N. Montes de Oca, N. Seraf√≠n, and H. Hern√°ndez. 2007b. Sensory and physiological determinants of maternal behavior in the goat (Capra hircus). Hormones and behavior 52: 99-105.

Pollard, J. C. 2006. Shelter for lambing sheep in New Zealand: a review. New Zealand Journal of Agricultural Research 49: 395-395.

Porter, R. H. et al. 1991. Individual olfactory signatures as major determinants of early maternal discrimination in sheep. Developmental psychobiology 24: 151-158.

Rook, J., M. Kopcha, and B. Bartlett. 2007. Pasture Lambing - A Viable Alternative for Midwester Producers? No. 00. p 1-9.

Sawalha, R. M., J. Conington, S. Brotherstone, and B. Villanueva. 2007. Analyses of lamb survival of Scottish Blackface sheep. Animal 1: 151-151.

Sébe, F., J. Duboscq, T. Aubin, S. Ligout, and P. Poindron. 2010. Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations. Animal Behaviour 79: 1055-1066.

Sébe, F., R. Nowak, P. Poindron, and T. Aubin. 2007. Establishment of vocal communication and discrimination between ewes and their lamb in the first two days after parturition. Developmental psychobiology 49: 375-386.

Shayit, M., R. Nowak, M. Keller, and a. Weller. 2003. Establishment of a preference by the newborn lamb for its mother: The role of opioids. Behavioral Neuroscience 117: 446-454.

Terrazas, A. et al. 2002. Twenty-four-hour-old lambs rely more on maternal behavior than on the learning of individual characteristics to discriminate between their own and an alien mother. Developmental psychobiology 40: 408-418.

Torriani, M. V. G., E. Vannoni, and A. G. McElligott. 2006. Mother-young recognition in an ungulate hider species: a unidirectional process. The American naturalist 168: 412-420.

Vallaillet, D., and R. Nowak. 2006. Socio-spatial criteria are important for the establishment of maternal preference in lambs. Applied Animal Behaviour Science 96: 269-280.

Vierin, M. 2002. Influence of maternal experience on fear reactions in ewes. Applied Animal Behaviour Science 75: 307-315.

Vierin, M., and M. F. Bouissou. 2001. Pregnancy is associated with low fear reactions in ewes. Physiology & behavior 72: 579-587.

Vince, M. A. 1993. Newborn lambs and their dams: the interaction that leads to sucking. Advances in the Study of Behavior 22: 239-268.

Vince, M. A., and T. M. Ward. 1984. The responsiveness of newly born Clun Forest lambs to odour sources in the ewe. Behaviour 89: 117-127.