MOTHER-OFFSPRING RELATIONSHIPS IN SCOTTISH BLACKFACE SHEEP

by

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This thesis has been composed by me and is a record of my own work
ABSTRACT

This thesis gives a complete description of the changes in the ewe-lamb relationship from birth to weaning, and determines those ewe behaviours of greatest importance to lamb survival and growth.

Detailed observations on the grooming behaviour of 50 Scottish Blackface ewes illustrated the extent to which grooming behaviour in twin bearing ewes is affected by the birth of the second lamb. Although previous experience does not affect grooming behaviour specifically it does affect the ability of primiparous ewes to cope initially with grooming twin lambs. Previous experience does however, strongly affect ewes responses to active lambs, shown in uncooperative movement by primiparous ewes as lambs attempt to suckle. It was also found, using crossbreeding, that although a lamb, such as the Mule, may have a high birthweight and also stand quickly after birth this does not necessarily mean it will also suckle quickly and effectively. The Mule lambs which were intended to be inactive relative to pure Blackface lambs, were not in the event inactive but failed to show appropriate udder-seeking behaviour. It would appear that the initiation of grooming is genetically controlled and that lamb behaviour, particularly lamb activity may influence the further development of grooming.

Longer term observations on 73 Scottish Blackface ewes and lambs outdoors in two years showed that the major changes in the ewe-lamb relationship occur at 3 weeks of age. This corresponds to the time of commencement of weaning, or a new phase in the ewe-lamb relationship and is determined by the willingness of the ewe to allow suckling and the subsequent ability of the lamb to adjust its behaviour. The lamb has to learn that it will only be allowed to suckle when the ewe communicates her willingness by a headup or call signal. These results are discussed in relation to current literature on parent-offspring conflict and weaning theories.

Ewe behavioural measures were also shown to influence lamb growth. Estimations of the quality of the ewe-lamb relationship, using measurements such as headup and call frequencies, appear most likely to have an influence on lamb survival and growth. The influence of ewe behaviour, on the lamb and the ewe-lamb relationship, may well be best investigated in the future through the use of an individual ewe 'character' description.
ACKNOWLEDGEMENTS

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Finally, my very special thanks to Roger for .................. everything.
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CHAPTER 1

GENERAL INTRODUCTION
Maternal behaviour occupies a central position in the lives of the mother and the offspring in both social organisation and preservation of the species (Rheingold, 1963). For the mother, parturition is an event of considerable biological importance, which signals maturity (Rheingold, 1963) and represents a means of investing in her fitness (Gonyou and Stookey, 1987). For the offspring, the behaviour of the mother is crucial not only for life itself but for its own subsequent adjustment to the environment (Rheingold, 1963) and presumably to aid the young in growth and development, both physically and behaviourally (Rosenblatt, 1987).

Domestic species are required to bear and care for their young in a wide variety of environments (Gonyou, 1987). Domestic sheep (*Ovis aries*) of all farmed livestock species are required to inhabit a very broad range of extensive and intensive environments. The present day domestic sheep originated from wild species present in Southwest Asia 8000 to 10000 years ago (Zeuner, 1963). The Scottish Blackface sheep, the breed observed in this study, is the most numerous breed in the British Isles (M.L.C., 1988). Despite the lack of records, it is generally accepted that the predecessors of the Blackface spread up the Pennine Chain and established themselves in the Southern Uplands of Scotland (Parnell, 1950). In the middle of the eighteenth century, they spread west and northwards and displaced, or interbred, with the native small, white- and dun-faced breed (Parnell, 1939, 1950). Both the breeding and management of a typical Blackface flock is less controlled than any other British breed. Under such extensive conditions, the behaviour of the ewe can be expected to have an even greater significance on production than in more intensive systems, in which the behaviour of the animal is under greater management control (Lawrence, 1984). A good description of maternal behaviour and the ewe-lamb relationship under natural, or non-intrusive, conditions can also provide important information with which to examine the effects on animals kept under more intensive conditions.
High perinatal mortality in sheep flocks world-wide remains a major economic and welfare issue in sheep production. In Britain, for example, between 5% and 40% of all lambs born die before weaning every year (Eales et al., 1983). In lamb mortality studies the cause of lamb deaths is classified by post-mortem and shepherding notes. Although there is always a large number of undiagnosed deaths, many studies have found that dystocia and starvation/exposure are the main causes of death (Hight and Jury, 1970; Meyer and Clarke, 1978; Dalton et al., 1980).

Many variables influence lamb survival, and extensive studies have been done on many of these (Alexander et al., 1959; Hight and Jury, 1970; Purser and Young, 1974; Dalton et al., 1980; Hinch et al., 1983). Lamb birthweight is considered to be the key factor in lamb survival (Hight and Jury, 1970; Dalton, 1980; Dalton et al., 1980; Hinch et al., 1983; Owens et al., 1985a). The highest survival rate occurs within the birthweight range of 3.5-5.5 kg (Dalton et al., 1980), with weights above this causing problems with dystocia, particularly in singles. Starvation/exposure on the other hand, occurs predominantly with multiple-born lambs and has a negative relationship with birthweight (Dalton, 1980). Birthweight influences all the other major factors involved in lamb survival but to varying degrees, even between studies. The most important factors are breed, season, age of dam, sex and litter size (Hight and Jury, 1970; Dalton, 1980; Dalton et al., 1980; Hinch et al., 1983).

Despite all these studies, few have considered the effect of the ewe’s behaviour on lamb survival, in any detail. Although many workers have made statements on maternal behaviour similar to Bareham (1976) that "it is clear that the chance of survival of some lambs is reduced by inadequate maternal behaviour", there has been little evidence to substantiate this.

Recently O’Connor et al. (1985) have quantified for the first time, the potential influence of maternal behaviour on lamb survival and growth. They established a
positive relationship between a Maternal Behaviour Score (MBS) and lamb survival and growth. The MBS was recorded on a 5-point scale based on the response of the ewe to handling and tagging of her lambs by a shepherd within 24 hours of birth. A trend for lamb survival to improve with increasing MBS over a range of litter sizes (Figure 1.1) was found. With an increase in MBS from 2 to 5, lamb survival (number of lambs weaned/number of lambs born) increased by 10% and with an additional increase in weaning weight, total ewe productivity increased by 20% over this range.

Having established this relationship to a score, it was now necessary to explore what specific aspects of the ewe's behaviour are important. It is important to investigate which behaviours are involved as causal factors in lamb survival and to see which behaviours are exhibited by those ewes which have a high mothering ability. This is then the rationale behind this study, which aimed to give a complete description of maternal behaviour from birth to weaning and to thus determine
those ewe behaviours of greatest importance to the lamb.

Shillito-Walser (1977) has described maternal behaviour in terms of three phases: preparatory, lactation and weaning. Initially, there is the pre-parturient phase, when the female becomes physiologically and behaviourally primed to respond to the newborn young. In this phase some mammals such as pigs (Suidae) build nests in which the young can be born (Wood-Gush et al., 1986). Most ungulates at this stage show a tendency to move away from the other members of their group (Lent, 1974).

The onset of maternal behaviour in the ewe is closely associated with parturition (Poindron and Le Neindre, 1980), suggesting that the hormonal changes occurring in the ewe just before lambing are involved in the onset of maternal responsiveness (Poindron and Le Neindre, 1980). Firstly there are the sex steroid hormones, particularly oestrogen (Poindron and Le Neindre, 1979) which although lacking any specific 'coding' for maternal behaviour in the brain are essential as a general stimulus to 'prime' the noradrenergic system (Keverne, 1988). The onset of maternal behaviour can be induced in non-pregnant multiparous ewes by injection of oestrogens (Poindron and Le Neindre, 1980), although it is not always possible to obtain induction of maternal behaviour with this manipulation. This is because both the patterning of several hormones and the delivery experience itself are important aspects, as is exemplified by the need for the complete process to occur in primiparous ewes before maternal behaviour is shown (Poindron et al., 1980). The temporary maternal interest in the neonate, which is elicited through hormonal facilitation, and the birth process itself, ensures the establishment of the initial contact between the ewe and the lamb (Poindron et al., 1980; Keverne et al., 1983). After this the lamb plays an increasingly important role in the further development of maternal behaviour.
In the formation of any mother-young relationship, two factors must be considered, one inherent in the mother (maternal responsiveness) and the other inherent in the young (newborn attractiveness). At parturition, both maternal responsiveness or sensitivity (interest in any young) and lamb attractiveness are maximal. Poindron and Le Neindre (1979) found that the decline in maternal responsiveness showed large individual variation, but was most marked in the first 12 hours following parturition indicating that this is the probable limit of the sensitive period in the ewe. It has also been found that injection of oestrogen lengthens this sensitive period, suggesting that oestrogen is involved in the control of maternal responsiveness, both in the appearance of maternal behaviour and its reduction after parturition (Poindron and Le Neindre, 1979).

More specifically though, oxytocin levels are significantly increased following parturition, or vaginal stimulation (Keverne, 1988). An injection of oxytocin induces the rapid onset of maternal behaviour but this declines after one hour, which is a similar response to that found in ewes who have had their lambs removed (Poindron and Le Neindre, 1980). More recent work has indicated that oestrogen is not the direct initiator which acts on the brain, but that its role is to activate the noradrenergic system (Keverne, 1988). The noradrenergic synchronization of other neural events, particularly the effects of oxytocin, are essential for complete maternal behaviour and appear to be acting on restricted areas of the brain specific to maternal behaviour, once the system is 'primed' (Keverne, 1988). It must be emphasised however that none of these neurochemical manipulations have yet fully explained the process, as the quality of the behaviour still does not compare with that of the post-parturient ewe.

After initial manifestation of maternal behaviour, the lamb enables the ewe to adjust her maternal behaviour and therefore to display appropriate responses at any moment in time (Poindron et al., 1980). This role of the young has already been well
demonstrated in the laboratory rat (Rosenblatt and Lehrman, 1963). A detailed description of ewe and lamb behaviour at parturition is given in Chapters 3 and 4. Chapter 4 considers, in particular, the effect of the lamb on ewe behaviour and the development of the ewe-lamb relationship at this time.

The second and major phase of maternal behaviour is lactation, when the young is for the most part dependent on the mother for nourishment (Shillito-Walser, 1977). In this phase of maternal behaviour, a series of behaviour patterns which are elicited by the different stages of the developing young can be seen. One of the most important behaviour patterns is suckling, though it is not the only part to the relationship at this time. Lactation was formerly thought to be the basis for maternal behaviour as it was believed that the internal pressure created by accumulated milk motivated the mother to nurse and exhibit all other maternal activities (Rosenblatt, 1987). The modern view is however, that lactation is dependant on maternal behaviour, rather than the reverse (Rosenblatt, 1987).

The variety of patterns of maternal behaviour occurring at this time are primarily determined by the nature of the young at birth and their rate of development. Altricial young, which are helpless and naked infants, elicit the mother to retrieve them and to nest build, and are cleaned and cared for by the female (Shillito-Walser, 1977; Rosenblatt, 1987). This group of mammals includes rats and mice (Murinae), cats (Felis catus) and dogs (Canis lupus). Young of many primates can be considered as semi-altricial, as they have poor locomotion and are relatively helpless at birth though they are fur-covered and can cling to their mothers (Rosenblatt, 1987). They are however entirely dependant on their mother for locomotion and food.

The other large group of mammals, including most ungulates, such as sheep, goats, cows, deer and horses, give birth to precocial young. In this group, the
mother will not care for other young once the sensitive or 'critical' period has passed (Lent, 1974). With sheep, a very rapid bond is formed at birth and unless elaborate fostering techniques are used, all other young will be rejected with violence (Kilgour, 1972). In ungulates, the young can stand and walk at birth, and as such signals for communication and behaviour patterns which maintain the young and parent in close proximity are of great importance (Shillito-Walser, 1977; Rosenblatt, 1987). The changing ewe-lamb relationship from birth to 14 weeks of life is considered in Chapter 5 and ewe-lamb communication during this period in Chapter 6.

The third phase of maternal behaviour is weaning, when the young becomes independent of the mother (Shillito-Walser, 1977). In some animals, such as mice (Murinae) weaning occurs quickly and the young disperse, or they may stay and become incorporated into the family (e.g. wolves, Canis lupus) or a larger group (e.g. sheep), (Shillito-Walser, 1977; Rosenblatt, 1987). The course of weaning in the cat has been divided into three phases (Rosenblatt, 1987). Initially the mother takes the initiative in approaching the kittens, then the young take the initiative to approach and suckle. Lastly, the mother begins to actively avoid the kittens (Deag et al., 1988). Weaning is therefore a gradual process during which the rate of maternal investment falls sharply and the young move rapidly towards independence (Martin, 1984). In chapter 5 this aspect of three stages in the weaning process are considered for the ewe-lamb relationship.

Chapter 7 considers the effect of maternal behaviour on sheep production. There has been little application of behaviour studies to agriculture at the present time. The influences that the differences in ewe behaviour and those processes involved in the changing ewe-lamb relationship have on lamb growth and survival have not been considered in any detail before.
The importance of parity and litter size effects will also be considered throughout the thesis. Both these variables have already been discussed above in terms of their influence on lamb survival. Many primiparous ewes, in particular, show aberrant behaviours when first faced with a newborn lamb (Alexander, 1960; Shelley, 1970; Sharafeldin and Kandeel, 1971; Arnold and Morgan, 1975; Poindron and Le Neindre, 1983), but how great an effect these types of maternal behaviour have on the young and growing lamb is not known. There are no indications if further differences in behaviour are displayed by primiparous ewes beyond the parturient period.

Similarly, some ewes appear unable to care for more than one lamb adequately (Stevens et al., 1982) but why some ewes and even some breeds (Alexander et al., 1983a,b) are better at adapting their behaviour to accommodate a second lamb is, again, unknown. This study will investigate the different specific behaviours of ewes rearing twins and singles. Differing aspects of the ewe-lamb relationship will also be considered with particular emphasis on what alterations in behaviour the ewe needs to care for twins, and whether it is the ewe or lamb that has to adapt to these changes.
CHAPTER 2

GENERAL METHODS
Location

The study site for the duration of my field observations (1987-1988) was a field (St. Catherines) located on Castlelaw Farm in the Pentland hills, Midlothian. St. Catherines is a 6.5 ha drained hill park on the lower south-facing slopes of Castlelaw hill which runs down to the Glencorse Reservoir (Figure 2.1). The southern boundary is formed by the road running along the reservoir and the northern by a farm track. Both the east and west fences separate the field from shelter belts and then further fields.

Figure 2.2 shows the general vegetation pattern of St Catherines. The vegetation is predominantly semi-permanent pasture, composed of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) mixture including some timothy (*Phleum pratense*). Wet areas in the field are covered in reeds (*Phragmites communis*) and other weeds, particularly nettles (*Urtica spp.*), are also present. The south-east corner of the field is scrub, mainly gorse (*Ulex europaeus*).

The housed accommodation used in 1989 (see Chapter 4) was an open-ended wooden barn, within the farm buildings complex at Castlelaw, typical of the type used for housing hill sheep.

Animals

A core flock of 60 primiparous Scottish Blackface ewes, was established in 1987. They were chosen after pregnancy diagnosis, such that the flock contained 30 primiparous ewes bearing singles and 30 bearing twins. In addition 20 multiparous ewes, third and fourth parity, were included and maintained with the primiparous ewes, as one flock, for the duration of the study. In 1988, after pregnancy diagnosis, 53 of the original 'core flock' ewes were observed in their second parity along with 20 new primiparous ewes. Losses from the study, due to barren ewes and the
FIGURE 2.1  MAP OF THE STUDY SITE

CASTLELAW HILL

WEST PARK

SHELTER BELT

ST. CATHERINES

FIRING RANGE

GLENCOUSE RESERVOIR

TURNHOUSE HILL

Far Front Greens

Drawn from: OS sheet NT 26 SW
Scale: 1:10 000
Figure 2.2  VEGETATION MAP

Legend:
- Reeds
- Scrub
- Pasture
- Drains

Figure 2.3  GRID SQUARE PLAN
requirement for miscellaneous specialised treatment for either ewe or lamb, meant that actual numbers observed were less than the total flock size (Table 2.1). Additionally in 1989 all third parity ewes on the farm were observed indoors, and this included 46 of the core flock ewes.

Table 2.1. Ewe numbers observed

<table>
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<th>Season 1987</th>
<th>Season 1988</th>
<th>1989</th>
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<tr>
<td>Primiparous Ewes</td>
<td>57</td>
<td>19</td>
<td>-</td>
</tr>
<tr>
<td>Multiparous Ewes</td>
<td>19</td>
<td>52</td>
<td>67</td>
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(46 Core Flock)

Although all ewes were ear-tagged it was essential they could be individually recognized at a distance beyond which the ear-tags could be easily read. The ewes were therefore marked with coloured insulation tape wrapped around their horns. Each individual was marked with a unique combination of 1 to 3 bands of different coloured tape duplicated on each horn. Beyond the first week it was possible to recognize individually all ewes in the flock from their face markings. Again at the start of the 1988 season it was only necessary to tape the new primiparous ewes as it was possible to identify all other individual ewes from the previous season by their facial markings.

All lambs also required to be individually identifiable, but due to the large number of them it was not possible to use facial patterns for recognition. The day after birth all lambs were ear-tagged and to assist in field recognition a number was sprayed on their body on both sides, using blue for singles and red for twins. These numbers had faded considerably within six weeks and photographs were therefore taken of all lambs at this stage, to enable individual recognition for the later fourteenth week observations.
Management

Table 2.2 illustrates the calendar of management procedures. Tups were put out to the Castlelaw ewes in the last week of November for two cycles (six weeks). All Castlelaw ewes were then pregnancy tested by ultrascan in the last week of February, with all twin bearing ewes being marked. The ewes for the study were then selected from the three different hefts running on Castlelaw and to balance for litter size (see above).

Table 2.2. Management Calendar

<table>
<thead>
<tr>
<th>Date 1987/1988</th>
<th>Procedure</th>
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<tr>
<td>November 23</td>
<td>Tups out with ewes</td>
</tr>
<tr>
<td>December 15</td>
<td>Start of second cycle</td>
</tr>
<tr>
<td>January 3</td>
<td>Tups removed</td>
</tr>
<tr>
<td>February 2</td>
<td>Ewes pregnancy tested</td>
</tr>
<tr>
<td>March 20 (April 4)</td>
<td>Ewes weighed, condition scored, anthelmintic dose and copper injection</td>
</tr>
<tr>
<td>March 20-April 11 (1987 only)</td>
<td>Habituation period</td>
</tr>
<tr>
<td>April 12 (April 4)</td>
<td>Ewes in St. Catherines</td>
</tr>
<tr>
<td>April 15-May 19</td>
<td>Lambing</td>
</tr>
<tr>
<td>May 12 (May 19)</td>
<td>Lambs weighed</td>
</tr>
<tr>
<td>May 26 (June 2)</td>
<td>Ewes and lambs weighed, Lambs: Cu injection, anthelmintic dose, tails trimmed and males castrated</td>
</tr>
<tr>
<td>June 9 (1987 only)</td>
<td>Lamb weighed</td>
</tr>
<tr>
<td>June 23</td>
<td>Lamb weighed</td>
</tr>
<tr>
<td>July 5 (July 8)</td>
<td>Ewes and lambs weighed</td>
</tr>
<tr>
<td>July 14</td>
<td>Study ended at this point in 1988</td>
</tr>
<tr>
<td>July 16</td>
<td>Ewes shorn</td>
</tr>
<tr>
<td>July 24</td>
<td>Lambs weighed</td>
</tr>
<tr>
<td>August 4</td>
<td>Lambs weighed</td>
</tr>
<tr>
<td>August 18</td>
<td>Lambs weighed and weaned</td>
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() - signifies dates in 1988

A 'heft' is a term that describes both the area of ground and the flock of sheep that
graze it (Lawrence, 1984). There are two main hefts on Castlelaw, the 'Front' which is the south facing area of the hill above St. Catherines and 'Heft' ewes which run on the north of the hill. A third small heft, 'Howgate', grazed the lower slopes of the hill on the north in an area called 'The Wilderness'. Two weeks before the beginning of lambing all ewes were weighed, condition scored, given a Copper injection, and anthelmintic dose and in 1988 put directly into St. Catherines. In 1987, the study ewes were sorted two weeks earlier to allow time for them to become habituated to my presence in the field. All ewe and lamb weights were measured, to the nearest 0.5 kg. The body condition of ewes was assessed by condition scoring (Speedy, 1980), by the same person on all occasions. The technique is to feel the backbone and lumbar processes of the ewe with the fingers and to then assess the sharpness of the bones, thickness of the muscle and degree of fat cover in the loin area. Scores range from 1 (lean) to 5 (fat) and include quarter intervals.

Lambing began on 15th April in both years and ended on 19th May, except for one late ewe in 1988 which lambed on 25th May, with the peak occurring over the 10 day period 20th-30th April. Throughout the lambing period and until the spring grass growth was well underway ewes were given supplementary feeding, in the form of sheep pellets, every morning at day break.

The day after birth all lambs were caught (twins together), ear-tagged, marked and the date of birth, sex, position in the field, birthweight and Maternal Behaviour Score (O'Connor et al., 1985 - see chapter 7) all recorded. The field was divided into 8 areas (Figure 2.3) based on easily identifiable landmarks. The 8 grid squares were four approximately equal areas across the top and bottom of the field, separated on the basis of topography, and the position of drains and power poles. All ewes and lambs were therefore allocated to a grid square whenever they were observed. Once the majority of ewes had lambed, 12th May 1987 and 19th May 1988, all ewes
and lambs were brought into pens in the field on a fortnightly basis and lamb weights were recorded. On the second weighing date, when lambs were on average 28 days old, all lambs received a copper bullet and anthelmintic dose. They also had their tails trimmed and males were castrated. Ewes were also given an anthelmintic dose, weighed and condition scored at this time. Ewe weights and condition scores were also recorded at the beginning of July, and in 1987 at the final weighing in August.

Ewes were shorn on 14th July and the ewes and lambs were all dipped on 16th July. At the end of observations in 1987, 18th August, all castrated male lambs and non-replacement ewe lambs were weaned. Those ewe-lambs that were to act as replacements to older ewes remained with their mothers and were released onto Castlelaw Hill. In 1988, at the end of observations all ewes and single lambs were released onto the hill and those with twins remained with the main twin flock in in-bye fields.

Sampling Methods

Most of the behavioural observations in this study were based on focal-animal sampling (Lehner, 1979; Martin and Bateson, 1986), in which an individual is observed for a specified amount of time and all instances of its behaviour, including interactions with other individuals, are recorded. At parturition, focal animal samples on ewe grooming behaviour and related ewe and lamb activities (Chapters 3 and 4) were taken. In addition further records were taken of the time of occurrence of periparturient events at this time. Appendix 1 shows an example of the record sheet used in both 1987 and 1988. A more detailed set of records was used in 1989, of which an example is given in Chapter 4.

Focal animal sampling was also used for the longitudinal study on the ewe and
lamb relationship (Chapters 5 and 6). Three minute scan samples were also taken in this study, concurrent with the fifteen minute focal observations. The ethogram of ewe behaviours used for both methods is shown in Appendix 2.

At commencement of all observations the date, time, grid square (see above), week and session of observation were recorded. The choice of focal animals on any one day was at random except to ensure each ewe was not observed at the same time of day within any week's observations. All ewes quickly became habituated to my presence and although observation at relatively close distances was possible I tried to stay at such a distance to not cause any effect on their behaviour but to still clearly see all relevant behaviours (usually a distance of 20-30 metres). This was possible due to clear visibility over one, two or even three grid squares from single positions in the field. All data was collected by myself alone and as such required over 1000 hours in the field over the two seasons (1987 and 1988).

All observations were tape-recorded in the field and then later transcribed onto computer in real time using Key Behaviour (Deag, 1988). This program provides frequency and time budget data which was then analysed further through use of computer statistical packages. In this study Minitab release 6.1.1 (Ryan et al., 1985), SPSS-X version 3.0 (SPSS-X, 1985) and Genstat 4.04B (Genstat, 1977) were all used at different times. Additional details of methods and analysis techniques are given in the appropriate chapters.
CHAPTER 3

INFLUENCE OF PARITY AND LITTER SIZE ON MATERNAL BEHAVIOUR AT PARTURITION
INTRODUCTION

The neonatal period accounts for two thirds of lamb deaths (McMillan, 1983). It has been shown (Alexander et al., 1959; Alexander and Peterson, 1961) however, that lamb mortality can be virtually eliminated when ewes are provided with early assistance and lambs are adequately fed and kept warm. This indicates the importance of behavioural factors which encourage short labour, and drying and feeding of the lamb.

Ewe grooming of the newborn lamb is often considered to play several important roles, both in drying and warming the lamb and also in providing tactile stimulation to the lamb (McGlone and Stobart, 1986). In most mammals, the consumption of amniotic fluids and licking of the neonate are characteristic behaviour patterns of the parturient female (Rosenblatt and Lehrman, 1963; Schneirla et al., 1963), the exception being camelids (Lent, 1974). This is particularly true in ungulates, especially sheep in which this short term attraction for amniotic fluid plays a role in the development of maternal behaviour and the establishment of the ewe-lamb attachment (Levy and Poindron, 1987). Hence, although there has been a number of studies giving general descriptions of both ewe and lamb behaviour at birth, the aim of this study was to analyse ewe behaviour, particularly grooming behaviour, in detail.

Most ewes stand and commence grooming their lamb within 2 minutes of birth (Alexander, 1950; Alexander and Peterson, 1961; Owens et al., 1985a). Qualitative descriptions describe how the ewe most frequently starts grooming the head and front of the body, working gradually over the body until the newborn lamb is completely dry and free of birth membranes (Hersher et al., 1963; Shillito and Hoyland, 1971; Bareham, 1976; McGlone and Stobart, 1986). In cattle, the predominant activity during the first hour after birth is also licking of the calf
(Edwards and Broom, 1982; Lidfors and Jensen, 1988). Cows however, begin grooming at the belly and flank area of the calves paying particular attention to the broken umbilical cord (Owens et al., 1985b). Poindron et al. (1980) support Hulet et al. (1975) in suggesting that besides the presence of the birth fluids, the relative immobility of the newborn is part of its attractiveness to the ewe. In contrast, Owens et al. (1985a) reported that, the lamb’s attempts to commence breathing were generally associated with vigourous head shaking, and ewes appeared to groom the most actively moving part of the lamb.

Lambs attempt to stand within a few minutes of birth and normally succeed within 30 minutes (Wallace, 1949; Arnold and Morgan, 1975; Bareham, 1976). Once the lamb is standing the ewe’s subsequent concentration of grooming is to the perianal region of their lambs. This is critical in the establishment of the discriminatory ewe-lamb bond and also helps to orientate the lamb towards the udder region (Alexander and Williams, 1964). Ewes with strong maternal responses arch their back, tilting out the teats slightly, thus helping the lamb to locate them (Kilgour and Dalton, 1984). Although all these maternal actions facilitate teat-seeking in the lamb they are not essential for the newborn lamb to find the teats, as lambs have an inherent teat-seeking tendency (Alexander and Williams, 1966). Soon after standing the lamb attempts to find and suck the udder, usually succeeding in 30-45 minutes and invariably within 90 minutes of birth (Arnold and Morgan, 1975; Owens et al., 1985a).

Despite the obvious importance of behavioural events at parturition to lamb survival, particularly grooming, there has been little quantitative study of ewe behaviour at this time. In particular, there has been no indication of how factors such as litter size or parity influence grooming behaviour. In some species, such as red deer (Clutton-Brock and Guiness, 1975) and rhesus monkey (Seay, 1966) the behaviour of primiparous mothers differs little from that of experienced mothers. In other species
however, experience may have an effect on maternal behaviour at parturition. In the longer term, primiparous bison for example, show differences in nursing behaviour (Green, 1986), by nursing for shorter durations and ending more suckling bouts than older bison cows. Edwards and Broom (1982) also found in cattle that failure to groom the calf was only found in heifers. They studied grooming in detail and found that heifers licked their calves less in the first hours post-partum and, at least initially, were tentative with their grooming.

Poor maternal behaviour in primiparous ewes is often considered a possible cause of lamb deaths (Alexander, 1960; Alexander and Peterson, 1961; Shelley, 1970; Arnold and Morgan, 1975; Hewson and Verkaik, 1981; McMillan, 1983). The pain of a longer labour in primiparous ewes (Alexander, 1960; Sharafeldin and Kandeel, 1971) may inhibit their maternal instincts. Aberrant behaviours in primiparous ewes such as failure to stand immediately after delivery, delay or failure to groom the lamb, and uncooperative responses to teat-seeking at parturition have been reported (Alexander, 1960; Shelley, 1970; Sharafeldin and Kandeel, 1971; Arnold and Morgan, 1975; Holmes, 1976; Poindron and Le Neindre, 1980, 1983; Owens et al., 1985a). In the extreme, aggressive behaviour and ewe desertions can occur.

These studies only considered the percentage occurrence of these behaviours, and to date a more quantitative analysis of the differences between primiparous and multiparous ewes and the consequences of these behaviour differences has not been considered. The principal aims of this study were to describe ewe grooming behaviour, and analyse how it is affected by litter size and parity. The effect of litter size and parity on other aspects of ewe behaviour were also considered, as were the relationship between ewe grooming behaviour and lamb behaviour.
MATERIALS AND METHODS

Detailed observations were made at parturition on 25 ewes in each of the 1987 and 1988 lambing seasons. A number of factors, but in particular the non-random lambing pattern, meant that only a third of the flock were observed at parturition.

The data that forms the basis of this chapter were from focal animal observations on the ewes' grooming behaviour. The observations, of the ewe grooming any of three regions of the lambs body; head (head and neck), trunk (main body between and including the front and hind legs) or tail (rump and perianal region), were recorded on an individual lamb basis. A continuous record of lamb posture and any sucking attempts were made and also any ewe movement (forward, backward or circling) when a lamb attempted to suck.

Each observation lasted for 10 minutes and, for singles, commenced at parturition and were subsequently taken at 30 and 90 minute intervals after birth. The first-born twin (Twin 1) was also observed at parturition, but the timing of subsequent observations was dependant on the time of birth of the second lamb. On average the second lamb (Twin 2) was born 34±5.54 (n=32) minutes after Twin 1, at which time a 10 minute observation was taken. Observations followed 30 and 90 minutes later. This was on average 61 and 121 minutes, respectively, after the birth of Twin 1.

Season was found to have no effect on a variety of non-behaviour parameters (lamb sex, birthweight, lambing date, ewe condition score, ewe weight, Maternal Behaviour Score or litter size), and so ewes from both seasons were treated as a single population. Data were transformed by arcsin, for proportions, or log, for frequencies to make the distribution of the data closer to normal, and analysed by analysis of variance (ANOVA). The model included the main effects of litter size, parity and sex of lamb and the covariate birthweight, with all two factor interactions
included. Each paired combination of Single, Twin 1 or Twin 2 was tested at comparable times. For example, singles for the first ten minutes of life versus Twin 2 in the first ten minutes of life, or Twin 1 versus Twin 2 in their final observation (120 versus 90 minutes). Means from the ANOVA are presented with the appropriate, between litter, standard errors.
RESULTS

The proportion of time spent grooming by ewes is shown in Figure 3.1. Singles and first-born twins (Twin 1) received the same amount of grooming when born. Second-born twins (Twin 2) however, received significantly less ($F=20.26; \text{df}=1,45; P<0.001$) grooming in the first ten minutes after birth than either Twin 1 or singles. Furthermore when Twin 2 was born the amount of grooming Twin 1 received was dramatically reduced.

![Figure 3.1](image)(Proportion of time spent grooming)

The interval between the birth of twin lambs was less than thirty minutes in 64% of cases and less than one hour in 79% of parturitions. In the few cases where Twin 2 was born more than 40 minutes after Twin 1 ($n=6$) there was still a significant decrease ($F=5.35; \text{df}=1,18; P<0.05$) in the proportion of grooming, that those first-born twins alone at 30 minutes received compared to singles. Within 30 minutes after birth of the second lamb there was no significant difference between the first and second-born in amount of grooming received.
The percentage of grooming received to each of the body areas is shown in Table 3.1. The trunk received the greatest overall attention decreasing from 70% in the first 10 minutes to 50% in later observations. The head also received its greatest attention in the first 10 minutes and then, in both singles and Twin 2, declined. In Twin 1 there was little decline in grooming of the head throughout the observation period. Grooming of the tail region increased over time from 10-16% initially to 42-46% by 90 minutes after parturition.

Table 3.1. Percentage grooming to each of three body regions

<table>
<thead>
<tr>
<th>Minutes since parturition</th>
<th>0</th>
<th>30</th>
<th>34</th>
<th>61</th>
<th>90</th>
<th>121</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Single</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>11</td>
<td>6</td>
<td>-</td>
<td>-</td>
<td>8</td>
<td>-</td>
</tr>
<tr>
<td>Trunk</td>
<td>73</td>
<td>53</td>
<td>-</td>
<td>-</td>
<td>46</td>
<td>-</td>
</tr>
<tr>
<td>Tail</td>
<td>16</td>
<td>41</td>
<td>-</td>
<td>-</td>
<td>46</td>
<td>-</td>
</tr>
<tr>
<td><strong>Twin 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>17</td>
<td>-</td>
<td>17</td>
<td>16</td>
<td>-</td>
<td>15</td>
</tr>
<tr>
<td>Trunk</td>
<td>69</td>
<td>-</td>
<td>59</td>
<td>48</td>
<td>-</td>
<td>46</td>
</tr>
<tr>
<td>Tail</td>
<td>14</td>
<td>-</td>
<td>24</td>
<td>36</td>
<td>-</td>
<td>38</td>
</tr>
<tr>
<td><strong>Twin 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>-</td>
<td>-</td>
<td>18</td>
<td>11</td>
<td>-</td>
<td>8</td>
</tr>
<tr>
<td>Trunk</td>
<td>-</td>
<td>-</td>
<td>72</td>
<td>57</td>
<td>-</td>
<td>50</td>
</tr>
<tr>
<td>Tail</td>
<td>-</td>
<td>-</td>
<td>10</td>
<td>32</td>
<td>-</td>
<td>42</td>
</tr>
</tbody>
</table>

Differences in grooming of the trunk appears to be the major contributor to the overall treatment differences (e.g. Twin 1 vs Twin 2 in the first 10 minutes: $F=8.98$; $df=1,45$; $P<0.01$). There were also similar significant differences for litter size in grooming of the tail.

Analysis of the total time spent grooming showed a similar pattern to the proportion of time, for the litter size effects, when considering the individual lamb (Figure 3.2).
For example there was again a significant difference ($F=8.63; df=1,39; P<0.01$) in the time spent grooming singles compared to Twin 2 in the first ten minutes after birth. This measure shows that there was some enhancement of grooming activity in ewes with twins (Figure 3.2), both in the total grooming performed by a ewe at any one time and also in the increased length of time grooming continues for. Neither sex of lamb nor birthweight had any influence on ewe grooming behaviour.

![Figure 3.2](image)

There were no differences between multiparous and primiparous ewes in their grooming of singles. With twins, however, there was a significant interaction effect ($F=7.33; df=1,56; P<0.01$) at the birth of the second lamb. Newborn, second lambs of multiparous ewes received more grooming attention than those from primiparous ewes (Figure 3.3). Conversely, first-born twins of primiparous ewes received more grooming at this time than their counterparts born to multiparous ewes.

There were very large parity effects on ewe movement in response to a lamb's
sucking attempts. Primiparous ewes with either singles or twins moved significantly more, during the whole observation period, than multiparous ewes. With singles (Figure 3.4), for example, the largest effect was at 30 minutes ($F=14.06; \text{df}=1,46; P<0.001$). By 90 minutes there was already much less ewe movement, but a significant difference remained ($F=7.14; \text{df}=1,4; P<0.05$) between primiparous and multiparous ewes.

The distribution of the different types of ewe movements is shown in Figure 3.5. Primiparous ewes showed significantly more circling ($F=11.72; \text{df}=1,46; P<0.01$) and backing movement than multiparous ewes. Noticeably, on no occasion did multiparous ewes show any backing movements. The majority of movement shown by primiparous ewes was circling around the lamb.
Figure 3.4
Effect of Parity on Ewe Movement
(Single-bearing ewes)

Moves per 10 mins

Time Since Parturition (min)

Figure 3.5
Description of ewe movements
(Single-bearing ewes)

Moves per 10 mins

Minutes Since Parturition
Analysis of the lamb's behaviour during this time showed that singles tended to be more active. Again there was no effect of either sex of lamb or birthweight on lamb activity. Singles spent less time lying than twins, an effect that reached significance at 90 minutes (F=4.82; df=1,43; P<0.05; Figure 3.6). There were no apparent differences between twins in general activity. Singles also had significantly more (F=4.70; df=1,43; P<0.05) sucking attempts at 90 minutes than either Twin 1 or Twin 2 (Figure 3.7). There was very little difference between the twin pair in sucking attempts, but at the final observation period there was again a significant interaction between litter size and parity (F=4.80; df=1,60; P<0.05) with second-born lambs of multiparous ewes having more sucking attempts than second-born lambs of primiparous ewes.

**Figure 3.6**
Proportion of time spent lying by lambs

![Proportion of time spent lying by lambs](image.png)
Figure 3.7
Attempted suckings by lambs

Frequency per 10 mins

Minutes Since Parturition
DISCUSSION

This study has illustrated the strong effect that litter size has on the distribution of the ewe’s grooming behaviour, particularly the extent to which grooming behaviour in twin-bearing ewes is affected by the birth of the second lamb. Specifically, first-born twins suffer a dramatic loss of grooming when the second lamb is born, as the ewe shows compensation in grooming activity towards the newborn lamb. In fact there are indications that grooming behaviour was disrupted before the actual birth of the second lamb as a ewe starts into her second labour, with a decrease in grooming of Twin 1 compared to singles when they were both still alone 30 minutes after birth. Despite this shift of attention second-born lambs did not receive as much grooming as first-born twins or singles at birth. Although there was an overall increase in grooming activity by ewes with twins, it is not twice that for singles and so twin lambs individually received less grooming than singles.

This study can explain the conflicting views of Owens et al. (1985a) whose Booroola ewes distribute their grooming attention to all lambs regardless of birth order, and that of Holmes (1976) and Atroshi and Osterberg (1979) who found in Finnsheep, that there is a progressive reduction in time spent grooming for each successive lamb in the litter and an apparent favouritism for grooming the first born. The Blackface ewes in this study did show compensatory grooming towards a newborn second-born lamb as reported by Owens et al. (1985a). A second-born lamb however does not receive as much grooming as any lamb on its own, as reported by Holmes (1976) and Atroshi and Osterberg (1979), as a ewe continues to distribute her grooming attention to each lamb in the litter. None of the previous studies presented quantified grooming data and did not describe the complete grooming process but reported only on 'the duration of the first intensive licking'. There is no indication from any of the studies on the length of the time periods considered. Whether it was the first seconds, minutes, or even hours would have
greatly influenced the type of behaviour patterns observed.

Although in the first few seconds of a lamb's life the ewe may concentrate on grooming its head, as previously reported (Hersher et al., 1963; Owens et al., 1985a), this study found that the ewes grooming moved rapidly, to being directed to the trunk. It would be expected that whilst grooming the head maybe important in removing of membranes to permit breathing, grooming of the trunk may stimulate the heart and respiratory centre in the first minutes of life. As with other workers (Hersher et al., 1963; Bareham, 1976) this study showed a much increased concentration of grooming to the perianal region as a lamb initially stands and then as it searches for the udder.

Although many authors (Sharafeldin and Kandeel, 1971; Poindron and Le Neindre, 1983; Owens et al., 1985a) have reported delays in initiating grooming in primiparous ewes, this was not seen here. This is the first time a complete description of grooming behaviour has been considered and there was in general very little effect of parity. Previous experience did however, affect the ability of ewes initially to cope with grooming of twin lambs. Multiparous ewes switched more completely to grooming the second lamb when it was born than inexperienced ewes, which were slower to switch their grooming attention from the first-born to the newborn lamb.

The lack of parity effects indicates that grooming has a considerable genetic component. Grooming is however also open to influence by both experience and litter size. For example an increase in litter size causes an enhancement of grooming activity by the ewe. This would suggest that the initiation of grooming is genetically controlled and that it is the further development of the grooming pattern that is influenced by environmental factors.

The largest differences in ewe behaviour due to parity are seen in the ewes'
responses to an active lamb. The inappropriate movements by primiparous ewes, as a lamb moves along her side in an attempt to find the udder, appear to attempt to maintain the lamb's position directly in front of the ewe. This results in some backing away movements but particularly a circling motion, where the ewe moves her back legs, particularly, around and away from the teat-seeking lamb. Failure of primiparous ewes to stand still during sucking attempts have been reported by other authors (Alexander, 1960; Shelley, 1970; Sharafeldin and Kandeel, 1971; Arnold and Morgan, 1975; Holmes, 1976; Poindron and Le Neindre, 1980, 1983) but details of these movements and their consequences have not been considered. The improvement in co-operative teat-seeking behaviour (standing still and assisting the lamb to reach the udder) by primiparous ewes by 90 minutes, supports the view of Poindron and Le Neindre (1980) that contact with the newborn lamb facilitates the development of proper maternal behaviour in inexperienced ewes. It would therefore appear, that the poor maternal behaviour previously reported (Alexander, 1960; Shelley, 1970) in primiparous ewes is primarily manifested in inappropriate ewe movement delaying the lamb from sucking, rather than in inadequate grooming behaviour.

Single lambs which received greater grooming attention are also more active than twins. In cattle however, Edwards and Broom (1982) found that although licking appeared to stimulate a standing bout in single-born calves, there was no correlation between total grooming received and time spent standing. Single lambs also had an increased number of sucking attempts compared to twins. Similarly second-born twins of multiparous ewes which received more immediate grooming attention at birth than those of primiparous ewes show a small but significant increase in sucking drive.

Lamb birthweight had no effect on general lamb activity in this study though previous authors have considered it to have a major effect on lamb behaviour.
(Bareham, 1976; Owens et al., 1985a). In both these studies there were however larger differences in birthweight, due to larger litter sizes. Also, the time to first successfully stand and suck were the behaviours measured, as opposed to the continuous record of lamb activity and sucking attempts used in this study.

The present results suggest that ewe grooming behaviour influences lamb behaviour at parturition, particularly lamb activity and sucking behaviour. It may be through this route, that maternal behaviour most directly influences lamb survival and initial growth.
SUMMARY

Focal animal observations were made at parturition on ewe grooming behaviour on 50 primiparous and multiparous single and twin bearing ewes. This chapter illustrated the extent to which grooming behaviour in twin bearing ewes is affected by the birth of the second lamb. Although previous experience did not effect grooming behaviour specifically, it does affect the ability of primiparous ewes initially to cope with grooming twin lambs. Previous experience did strongly effect ewes' responses to active lambs, shown in uncooperative movement as lambs attempted to suckle.

There are indications that these maternal effects influence lamb behaviour. Equally it may well be lamb behaviour influencing grooming behaviour. Although the initiation of grooming behaviour appears to be genetically controlled certain aspects of the lamb, besides litter size, may also influence it. The relative influence that the ewe and lamb have on each other will be considered in Chapter 4.
CHAPTER 4

RELATIONSHIP BETWEEN LAMB VIGOUR AND EWE BEHAVIOUR ON SUCKING SUCCESS AT PARTURITION
INTRODUCTION

The unique behaviour associated with the birth and care of the young is essential for the survival of the species (Gonyou and Stookey, 1987). In mammals, only the females feed the young, due to their ability to produce milk. Even with an optimal structure, function and development of the mammary glands, lactation is of no significance without the appropriate behaviour from the mother, which allows suckling to take place. Similarly, the behaviour of the young is also important, with the behaviour patterns of the two having to combine effectively before the offspring of any mammal can be nourished (Shillito-Walser, 1977). In domestic animals failure of the maternal and neonatal behaviours to interact properly can result in death of the offspring, loss of a reproductive season for the dam and a reduction of profit to the producer.

In order to survive, a newborn lamb should stand and suck from its mother as soon as possible after birth. Once the lamb is standing, normal 'teat-seeking' behaviour is elicited by a variety of sensory stimuli provided by the ewe (Vince et al., 1985). Vince et al. (1987) suggest that visual stimuli are most important in the initiation of lamb approach and contact with the ewe. Once the lamb has made contact, the normal teat-seeking behaviours, such as vigourous forward and upward head movement and oral activities, are encouraged by tactile stimulation of the head and face (Vince et al., 1985) and a warm (Billing and Vince, 1987a), smooth and yielding surface (Billing and Vince, 1987b). Other cues, such as olfaction and inguinal wax, also play a part in teat location (Vince and Ward, 1984).

Although studies, especially those concerned with lamb survival, have considered the time taken from birth to stand and suck (Alexander, 1958; Alexander, 1960; Shelley, 1970; Sharafeldin and Kandeel, 1971; Arnold and Morgan, 1975; Owens et al., 1985a), there have been no quantitative studies on the relative importance of ewe or lamb behaviour on these events. Previous work with Blackface ewes and
lambs outdoors (Chapter 3 of this thesis) has indicated that ewe grooming behaviour may influence lamb behaviour at parturition. Cattle studies (Edwards and Broom, 1982; Lidfor and Jensen, 1988) have also shown that the predominant cow activity for the first hour after birth is licking of the calf. If ewes are prevented from grooming and orientating towards their lambs it results in a significant delay in the lamb putting on weight (Alexander and Williams, 1964), indicating a delay in the time from birth to first successful suckle. Other studies (Alexander, 1960; Sharafeldin and Kandeel, 1971; Poindron and Le Neindre, 1983) have considered that not licking of the lamb has detrimental consequences, but Alexander and Williams (1964) found that neither grooming nor lack of orientation had significant effects on time to first suck successfully, when considered separately. All studies to date (Arnold and Morgan, 1975; Bareham, 1976; Owens et al., 1980) which have considered ewe grooming behaviour, have only compared it to the discrete times of lamb behaviour events occurring, such as time to first stand.

It is clearly important to include more quantified descriptions of lamb behaviour in order to assess which behaviours are critical to lamb survival. Various aspects of lamb behaviours need to be considered, as subjective descriptions of lamb vigour have been found to be totally inadequate (Owens et al., 1985a).

There are large differences between breeds in lamb survival (Hight and Jury, 1970; Dalton et al., 1980) which are not fully explained by birthweight differences. Sheep breeds have each been subjected to different selection pressures, but few behavioural studies have taken breed effects into consideration. One exception being Slee and Springbett's (1986) study on 10 different lamb breeds, in which significant breed differences in lamb behaviour were found, based on times to stand and reach the udder.

There has been no further quantification of breed differences in lamb behaviour and few attempts to explore the effect that these differences have on the ewe. Various
forms of reproductive manipulation can be used to investigate the separate influences of ewe and lamb on each others' behaviour. Previous work has used cross fostering (Key and Maclver, 1980) to investigate long term maternal influences on the lambs' grazing, resting and courtship behaviour, although the use of this technique is limited by the disturbance it causes at birth. The technique of embryo transplantation is now well developed in sheep although it has been used very little in behavioural studies. Shillito et al. (1982) used embryo transplantation to test differences in maternal vocal recognition between breeds, as it was considered essential to have a strong, natural ewe-lamb bond when investigating ewe-lamb recognition. The advantage of embryo transplantation is that the bond is formed at birth and is not broken and reformed as in cross fostering. The third technique is cross breeding which again allows formation of a natural ewe-lamb bond at birth.

The present chapter describes an experiment that uses cross-breeding to investigate the relationship between lamb vigour and maternal behaviour at birth. In recent years, there has been an increase in the number of hill ewes being crossed to longwool sire breeds, particularly Bluefaced Leicester. Although there is no quantified information on the viability of these cross lambs there are suggestions that they lack vitality at birth. It was hoped therefore, to establish how maternal behaviour is affected by the vigour of the lamb by comparing the effect on Scottish Blackface ewe behaviour, of pure Scottish Blackface lambs with Mule (Bluefaced Leicester X Scottish Blackface) lambs. This study also planned to extend the study of breed differences in lamb vigour by using more complete lamb behaviour descriptions than have previously been provided.
MATERIALS AND METHODS

Forty, third parity, Scottish Blackface ewes were mated with a Bluefaced Leicester tup in December 1988, and then managed with the rest of the Castlelaw flock until one week prior to lambing (12th April). These forty ewes crossed to the Bluefaced Leicester tup were randomly mixed with forty, third parity, ewes crossed to a Blackface tup and kept in two indoor 6 metre by 6 metre pens for lambing. Similarly, single- and twin-bearing ewes, as determined by ultrascan in February, were mixed and allocated to both pens.

Hay and water were available ad libitum and concentrates were fed every morning at first light. All ewes remained in the large pens during lambing, where all observations were made. After observations were completed they were removed to individual pens with their lambs, until they were released back into the field the day after they had lambed. While indoors, these animals were kept under daily surveillance from dawn (5:45 am) until early evening (5:30 pm).

Data on 32 of these third parity single and twin-bearing ewes were collected by focal animal observations. As in chapter 3 attention was focused on the ewes grooming behaviour and observations included details of the time spent grooming specific areas of the lambs body (head, trunk or tail) along with general activity and udder-seeking behaviour of the lambs. Each observation lasted 10 minutes and, for singles, were taken at parturition and then at 30 and 90 minute intervals. The first born twin (Twin 1) was observed at parturition and then on average 23, 53 and 113 minutes later, concurrently with the 0, 30 and 90 minute observations on the second-born twin (Twin 2).

To make the distribution closer to normal the data were transformed, by arcsin or logarithm, before analysis by analysis of variance. The ANOVA model included litter size, breed and sex as the main factors and the co-variate birthweight along with all
two-factor interactions. Each paired combination of single Twin 1 or Twin 2 was tested at comparable times, as described in Chapter 3.

In addition, the first occurrence of various lamb activities from birth were recorded to the nearest second by a digital stop-watch. These observations taken from the birth of the lamb were: the time the ewe first stood; ewe first commenced grooming; lamb first bleated; lamb first shook head; lamb first rose onto knees; lamb first attempted to stand fully; lamb first stood successfully; lamb first nudged ewe; lamb first nudged ewe in udder region and lamb first successfully sucked. Due to the non-normal distribution of these data, analysis of the differences between litter size or breed groups, were performed by the Wilcoxon-Mann-Whitney test (Siegel and Castellan, 1988).
RESULTS

All significant effects discussed are true for all time periods and litter size comparisons unless otherwise stated. There were no sex or birthweight effects on any aspect of ewe or lamb behaviour studied. As with Blackface ewes lambing outdoors (Chapter 3), there was a strong effect of litter size on proportion of time spent grooming (Figure 4.1).

![Figure 4.1: Effect of Litter size on Grooming](image)

Again, the birth of the second lamb was found to markedly disrupt the grooming of the first born lamb as the ewe switched attention to the newborn, second lamb. Twin 2 however, still received significantly less grooming in the first ten minutes of life ($F=11.44; df=1,31; P<0.01$) than Twin 1 or singles. Within 30 minutes of the birth of the second lamb, both twins in this study received exactly the same amount of grooming. The total amount of grooming by twin bearing ewes again suggests that increased litter size enhances grooming behaviour.

An effect of lamb breed on the proportion of time spent grooming was only found
during the final observation period. At this time, Blackface lambs received significantly more grooming than Mule lambs (F=9.07; df=1,34; P<0.01; Table 4.1).

Table 4.1. Proportion of time spent grooming singles

<table>
<thead>
<tr>
<th>Time since parturition (mins)</th>
<th>0</th>
<th>30</th>
<th>90</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blackface</td>
<td>0.88±0.06</td>
<td>0.75±0.05</td>
<td>0.42±0.04</td>
</tr>
<tr>
<td>Mule</td>
<td>0.84±0.09</td>
<td>0.82±0.08</td>
<td>0.29±0.06</td>
</tr>
</tbody>
</table>

Spearman rank correlations of the times to first attempt and successfully stand and suck, with the amount of grooming received in the first 10 minutes showed only a significant correlation for attempt to stand (r=0.725; n=32; P<0.01; Table 4.2). Correlations of these events with amount of grooming received at 30 minutes and a combination of both time periods (10 and 30 minutes) showed a similar pattern to that for 10 minutes only.

Table 4.2. Correlations between grooming attention and lamb behaviour

<table>
<thead>
<tr>
<th>Attempt to Stand</th>
<th>Successfully Stand</th>
<th>Attempt to Suck</th>
<th>Successfully Suck</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.725 P&lt;0.01</td>
<td>0.435 NS</td>
<td>0.245 NS</td>
<td>-0.331 NS</td>
</tr>
</tbody>
</table>

Analysis of lamb behaviour showed that neither breed nor litter size had an effect on the proportion of time spent lying by lambs (Figure 4.2).
There was also no significant breed effect on time to first stand successfully. The median time to first stand was 12 minutes for Blackface compared to 10 minutes for Mule lambs. However the inter-quartile range for these times was larger (6-20 minutes) for Blackface compared to Mule (8-13 minutes) lambs.

Despite the lack of breed effect on parameters of general lamb activity there were large breed effects on the number of lamb sucking attempts. Single Mule lambs failed to show any sucking attempts until the final, 90 minute, observation and then the average was only 1 attempt in 10 minutes, which was still significantly less than that for Blackface lambs ($F=13.29$; $df=1,28$; $P<0.01$; Figure 4.3).

Twin Blackface lambs also made significantly more sucking attempts than Mule lambs ($F=16.09$; $df=1,28$; $P<0.001$; Figure 4.4). A similar pattern was found for the number of successful suckings.
Figure 4.3
Lamb Sucking Attempt Frequency
(Singles)

Figure 4.4
Lamb Sucking Attempt Frequency
(Second-born twins)
In addition to the breed effect on the number of sucking attempts there was also a significant effect of breed on time to first suck successfully. When considered within litter size however, the effect was only significant for singles ($W_X = 48; P < 0.05$). The median time to first suck successfully, for singles, was 28 minutes for Blackface compared to 55 minutes after birth for Mules (Figure 4.5). The trend was the same for both twins (Twin 1 and Twin 2) but failed to reach significance.

![Figure 4.5](image.png)

Two examples taken from the parturition record sheets, of the relative time of events for a Blackface and Mule lamb are shown in Table 4.3. These examples clearly show that the early lamb movements occur at similar times for both lamb breeds, but once standing there is a marked difference in the behaviour of the two breeds. Blackface lambs stayed by the ewe and attempted to suckle whereas Mule lambs showed a tendency to move away from the ewe, and despite attempts by the ewe to follow her lamb there was a resultant delay in suckling. The behaviour patterns
seen indoors were mainly the same as those previously seen outdoors, but lambs were quicker to stand and particularly quicker to first suck when indoors.

Although there was no significant birthweight differences between breeds in this study, there was a tendency for Mule lambs to be heavier, as can be seen in Table 4.4. There were also large individual differences in birthweight within both breeds.

Table 4.3. Parturition Records

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Times Since Birth (Seconds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ewe first stands</td>
<td>0</td>
</tr>
<tr>
<td>Ewe commences grooming</td>
<td>5</td>
</tr>
<tr>
<td>Lamb first bleats</td>
<td></td>
</tr>
<tr>
<td>Lamb first head shake</td>
<td>25</td>
</tr>
<tr>
<td>Lamb first rises to knees</td>
<td>336</td>
</tr>
<tr>
<td>Lamb first stands on two legs</td>
<td>553</td>
</tr>
<tr>
<td>Lamb first stands successfully</td>
<td>641</td>
</tr>
<tr>
<td>Lamb first nudges ewe</td>
<td>766</td>
</tr>
<tr>
<td>Lamb first nudges udder</td>
<td>1412</td>
</tr>
<tr>
<td>Lamb first sucks successfully</td>
<td>1828</td>
</tr>
</tbody>
</table>

Table 4.4. Birthweight Medians

<table>
<thead>
<tr>
<th>Breed</th>
<th>Litter Size</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Single</td>
<td>First-born Twin</td>
<td>Second-born Twin</td>
</tr>
<tr>
<td>Blackface</td>
<td>4.75</td>
<td>3.85</td>
<td>3.50</td>
</tr>
<tr>
<td>Mule</td>
<td>6.30</td>
<td>4.15</td>
<td>4.175</td>
</tr>
</tbody>
</table>
DISCUSSION

The effects of litter size shown in chapter 3 for ewes and lambs outdoors were also found again in this indoor trial. In particular, the grooming behaviour of twin-bearing ewes was markedly affected by the birth of the second lamb.

Studies of the longer term ewe-lamb relationship have shown differences between animals kept indoors compared to outdoors. Horrell (1988) found suckling at two and five weeks was more often disturbed in ewes indoors. Similarly it has been found that ewes and lambs kept indoors were less able to select their partners at a distance (Poindron and Schmidt, 1985). Although the results of this, and the previous chapter suggest no difference in the behavioural repertoire of ewes and lambs at parturition whether indoors or outdoors, lambs were quicker to stand when born indoors. Even more marked was the fact that, the majority of both twin and single, lambs observed indoors had suckled by 100 minutes after birth. Most Blackface lambs born outdoors however, had not suckled by 100 minutes and the few who had took longer than the average for lambs indoors.

Results in Chapter 3 had suggested a relationship between ewe grooming behaviour and lamb activity, however against expectations, ewe grooming behaviour in the present experiment did not correlate with general lamb activity. The amount of grooming singles received in the first 10 minutes after birth was however correlated with time to first attempt to stand. This supports previous suggestions (McGlone and Stobart, 1986) that grooming is important in drying and initial stimulation of the newborn lamb. The present study however found no correlation to first stand successfully or later behavioural events, once the lamb was dry and active. Similarly in cattle, Edwards and Broom (1982) found no correlation between total time licking and calf standing time, although the authors commented that licking appeared to initiate or prolong a standing bout. There may however, be an effect of grooming on lamb activity when conditions are less ideal than in this study,
especially outdoors. Particularly as drying of the lamb is likely to be more vital under cold, wet and windy conditions (Hersher et al., 1963). The ability of a newborn lamb to maintain its body temperature is likely to be of major importance in determining its survival, or death, in the field (Alexander and McAnce, 1958). Rate of heat loss is principally a function of the ambient air temperature, wind velocity, humidity and wetness of coat (McDonald, 1962). Possible interactions between the environment and effects of grooming behaviour on lamb activity should be considered in future research.

Although ewe grooming behaviour did not seem to strongly influence lamb behaviour in this study, Vince et al. (1985) have shown that the mere presence of the ewe can act as a composite stimulus to the lamb. Three aspects of the parturient ewe which they have shown to stimulate the lamb are the ewe as a large visual object, movement by the ewe and also the ewe providing tactile stimulation.

Ewe grooming behaviour was found to be largely unaffected by lamb breed. Where there was a breed effect this appears to have been the result of Mule lambs distancing themselves from the ewe and inevitably making themselves unavailable for grooming. Holmes, 1976 found no breed differences in licking attention of Finnsheep compared to Clun Forest ewes. Vince et al. (1987) however, found differences in ewe attention, as measured by grooming activity, in Merino compared to crossbred (Dorset Horn X Corriedale) ewes. They also comment that this was linked to abnormal behaviour, specifically inactivity, in some Merino lambs. In the present study although the two lamb breeds behaved differently they did not differ in terms of their general activity, and it may be activity level which has the greatest impact on any observed differences in ewe grooming behaviour. Again however, there appears to be breed differences in the ewes ability to compensate for an inactive lamb, as lamb inactivity did not reduce ewe attention in crossbred ewes, as it did in Merino ewes (Vince et al., 1987). Hence it still remains unclear the extent to
which aspects of the lambs' behaviour influences ewe responsiveness in the first hours post-partum.

Neither ewe grooming behaviour nor general lamb activity were directly related to lamb sucking success. Failure of a lamb to suck can either be attributed to the lamb itself or poor ewe maternal behaviour. It seems that the reason Mule lambs did not suck successfully, was not because they were less active or received less maternal attention, but because they failed to show proper udder-directed behaviour.

There is no clear reason as to why Mule lambs fail to show effective udder-seeking behaviour. It would seem to be a specific characteristic of this breed, but whether it results from a lack of visual or olfactory perception, or other more general factors such as a greater sensitivity to disturbance, has yet to be determined. What ever the reason it would appear to be the result of a correlated response during artificial selection, which may also occur in other lamb breeds. These results are in agreement with the breed differences Slee and Springbett (1986) obtained, from which they suggest that udder-seeking and early sucking behaviour may be genetically influenced.

As a result of genetic selection, man has succeeded in changing the morphology and physiology of the ancestral wild sheep into many distinct breeds differing in terms of fecundity, wool type, growth rate and mature size (Key and Maclver, 1980). The extent to which selection for these various characteristics has resulted in genetically correlated changes in behaviour is unclear. Under natural conditions successful sucking is essential for lamb survival, and in breeds adapted to extensive conditions, such as the Scottish Blackface, there would be selection pressure in favour of efficient udder-finding.

Ineffective udder-seeking behaviour, as displayed by the Mule lambs, has been
shown to be associated with poor resistance to hypothermia and thus high perinatal mortality (Slee and Springbett, 1986). Mule lambs, therefore, are likely to have a lower survival rate than Blackface lambs, particularly when under more extensive conditions than in this study. Under more severe climatic conditions the energy reserves of a lamb that has not sucked (1700-4200 kJ), would soon be exhausted (Alexander, 1962b). The rate at which energy reserves are exhausted depends on the climatic demands on heat production, which can vary between 33-250 kJ/hour or more (Alexander, 1962a). This means that death can occur from 16 hours and certainly within 3 days.

Descriptions on the effect of lamb 'vigour' (Alexander et al., 1959; Alexander and Peterson, 1961; Shelley, 1970; Arnold and Morgan, 1975; Atroshi and Osterberg, 1979; Stevens et al., 1982) or calf 'vigour' (Edwards, 1982) are often made with no data to substantiate them. Even when some kind of definition of this term is given (Owens et al., 1985a) it is usually a subjective description (e.g. good, fair or poor), based on size and activity of the lamb. One study, which did give a description of their use of the term 'lamb vigour', was Vince et al. (1987) who equated lamb vigour to lamb activity. Slee and Springbett (1986) refrain from using the term 'lamb vigour' completely, and relate their discussion to the physiological measures and behaviour they observed. In future discussions, statements on 'lamb vigour' should only be considered of any worth when they are defined by quantitative descriptions of lamb behaviour.
SUMMARY

To investigate the relationship between lamb vigour and maternal behaviour this chapter reported on an experiment that compared the behaviour of pure Scottish Blackface lambs with Mule (Bluefaced Leicester X Blackface) lambs, all born indoors. Observations on the grooming behaviour of 32 single or twin-bearing ewes, and on the general activity and udder-seeking behaviour of their lambs were made at parturition.

This chapter has shown that, although a lamb such as the Mule, may have a high birthweight and also stand quickly, this does not necessarily mean it will also suck quickly or be more likely to survive. Neither ewe grooming behaviour nor general lamb activity were directly related to lamb sucking success. It seems that Mule lambs failed to suck successfully by failing to show proper udder-directed behaviour and this is most likely to cause poorer survival in this breed.

The relative influence which the ewe and lamb have on each other at parturition still remains unclear but the differences between Blackface and Mule lamb behaviour may well affect the formation of the ewe-lamb bond. Long term effects of the differing behaviours of the two lamb breeds was not considered but a basis for future investigations in this area is given in Chapter 5, through a detailed description of the ewe-lamb relationship in Blackface ewes and lambs outdoors.
CHAPTER 5

EWE-LAMB SPATIAL RELATIONSHIP
INTRODUCTION

Most of our current detailed knowledge of mother-offspring relations comes from primate studies. The dramatic change in the relationship between a rhesus monkey infant and its mother throughout the first year of life have been much studied, and even become a model for the study of changes in any dyadic relationship (Hinde and Spencer-Booth, 1967a; Hinde and Atkinson, 1970; Simpson et al. 1986). In terms of this model, one can ascribe primary responsibility for an age-related change by considering together changes in a number of measures of the relationship to form a single index, such as a proximity or contact index. Simpson et al. (1986) found that much of the complexity of the changes was oversimplified by using a single index and suggested that one should always consider a single index along with further descriptions of the behaviours occurring at that time. They found, that whilst maternal rejection behaviour may have been primarily responsible for initial changes in time spent apart, at six weeks rhesus monkey infants were actively seeking social interactions with others and they themselves were less willing to make contact with their mother.

Most of the work with rhesus monkeys has been carried out on small captive groups. Altmann (1980) undertook one of the first in an increasing number of quantitative studies on primate mothers and infants to be done in their natural habitat. She also found, that the infant must adjust its behaviour to that of its mother. The young infant learns that it can be out of contact with its mother only at particular times which are determined by the mothers activity. The first indication of infant 'weaning' or distress behaviour seems to involve the reversal in these contact contingencies. In early life, a mothers' rest time could be used by the infant for play and exploration. At 4-6 months of age however, an infant must learn to take advantage of this rest time for any contact they may want with their mother, and to not interfere with her activities at other times. This conflict is but one example of
those which will occur, as a baboon mother ceases to provide all the infants nutritional and other needs. As the infant grows and becomes more active there will be several mother-infant conflicts (Trivers, 1974, 1985), as the infant is gradually forced to become self-sufficient in any of those areas formerly provided by the mother. To obtain this detailed information on the complexity of the mother-infant spatial relationship in primates, comprehensive data on the time and identity of the individual which effected each change in the mother-infant spatial state (i.e. movement towards or away from each other) were collected.

These discussions on mother-young conflicts have been stimulated by theories put forward by Trivers (1972, 1974). Unlike classical evolutionary theory, which only considers unilateral parental investment, Trivers (1974) regards the offspring to be an active member of the interaction. In this model, parent and offspring are expected to "disagree" on how long parental investment should last and over the amount to be given. In general, parent-offspring conflict is expected to increase during the period of parental care, and offspring are expected to employ psychological weapons in order to compete with their parents. These conflicts are progressively resolved through many behavioural adjustments by both the mother and, particularly, the young.

In ungulates there has been little study of the development of the mother-young relationship. In cattle, within a few weeks after birth, calves are increasingly attracted to other calves and spend most their time in groups together, possibly facilitating normal social development (Price et al., 1985). In sheep, however, the lamb is a strong follower (Lent, 1974), so ewes and lambs are rarely separated by large distances for any great length of time during the early weeks of life.

Work on the ewe-lamb bond has concentrated on its formation at birth. Most studies, which have looked at the changes as the lamb grows, have employed recognition choice tests or measurement of ewe-lamb distances. The maintenance
of the ewe-lamb bond involves a slowly changing pattern of behaviour. In the first few days of the lambs' life, the bond is the responsibility of the ewe alone (Kilgour, 1972), since the lamb is unable to discriminate the ewe initially. When 4-6 days old, the lamb can recognize its own mother (Arnold et al., 1975; Shillito and Alexander, 1975) mutual recognition occurs and bond maintenance then becomes increasingly dependant on the lamb (Morgan and Arnold, 1974).

Ewe-lamb distance data has been used to support the recognition work in describing the changing role of the ewe and lamb. Morgan and Arnold (1974) found, that the ewe and lamb maintained close contact during the first four weeks after birth, staying within 10 metres of each other 56% of the time observed and were only rarely more than 50 metres apart (6% of the time). The lamb’s growing independence of the ewe is shown by the formation of peer groups, increased play, decreased suckling and increased grazing; all at greater distances from the grazing ewe (Arnold and Pahl, 1974; Morgan and Arnold, 1974; Hewson and Verkaik, 1981). Throughout this time though, the lamb continues to express dependant forms of behaviour such that the lamb will walk and lie synchronously with the ewe and maintain a constant distance to her (Morgan and Arnold, 1974).

Hinch et al. (1987) suggest that the gradual increase in ewe-lamb distance during this first month occurs, as the maternal role in maintaining the mother-lamb attachment becomes less. After this time the ewe-lamb distance declines again (Arnold and Grassia, 1985; Hinch et al., 1987), as the lamb’s role in the maintenance of attachment increases. Although there is a long-lasting ewe-lamb attachment in hill sheep it is not a permanent one (Lawrence, 1990). In feral populations, weaning occurs at approximately 6 months in Mountain Bighorn Sheep (Geist, 1971; Berger, 1979a) and slightly earlier in Desert Bighorn (Berger, 1979a). Even if a lamb is not obtaining milk (i.e. is nutritionally weaned), Arnold and Pahl (1974) have reported that lambs of four different breeds will continue to
maintain contact with the ewe, and can be found in association with her up to 12 months of age, and the same has been reported in Soay sheep (Grubb, 1974). Nutritional weaning, therefore, cannot be considered as the end of the ewe-lamb relationship. As with primates, a ewe may provide more than just nutrition to a lamb and a continued association may be essential for development of social relationships and home ranges (Shackleton and Shank, 1984; Lawrence and Wood-Gush, 1988).

Previous work describing the weakening of the ewe-lamb bond or attachment, is based only on the observations that ewes and lambs spend less time together and are found at greater distances apart (Morgan and Arnold, 1974; Arnold and Pahl, 1974; Arnold and Grássia, 1985; Hinch et al., 1987). Beyond the very close ewe-lamb relationship (or 'bond') observed in the first few weeks of life, there may however, continue to be other phases in the relationship which develop over time. This chapter reports on the changes in the ewe-lamb spatial relationship from birth to enforced weaning. As well as considering the classical measurements of changes in ewe-lamb distance and behaviours over time, a more comprehensive investigation will be undertaken by applying techniques previously used by primatologists. This approach quantifies the development of the changing ewe-lamb relationship over time. According to Martin (1984), the concept of weaning is of central importance in the study of behavioural development. The complex and gradual process of weaning in mammals involves, not only a progressive reduction in the rate of milk transfer between mother and young, but also profound behavioural changes in the parent-offspring relationship (Martin, 1984). Weaning conflict has been suggested as the major influence on changes in the ewe-lamb relationship (Arnold et al., 1979). Hence, I will also emphasise the importance of weaning as a process, not an event, influencing the changes in the ewe-lamb relationship.
MATERIALS AND METHODS

Data for this longitudinal study were obtained from focal animal observations concurrent with scan samples. Both these methods give unbiased estimates of time budgets, and focal-animal samples produce data for frequencies and bout durations (Altmann, 1980). Many behavioural comparisons of frequency differences are actually statements about rates (Altmann, 1974), but because the observation times in this study were identical for all individuals, it is justifiable to compare frequencies directly.

In 1987, individual ewes were observed for fifteen minutes on three separate days, within each of weeks 1, 3, 6 and 14 after parturition. A similar procedure was followed in 1988, except the fourteenth week observations were excluded and a more detailed observation scheme used in week 1. In 1987, the medians for the days of observation in week 1 were days 2, 5 and 7. In 1988, observations were taken on days 1, 2, 3 and either 6 or 7 after birth. The observation protocol assured that within a week, each observation was made at a different time of day (6am to 9am; 9:01am to 12pm; 12:01pm to 3pm; 3:01pm to 6pm).

It proved impractical to keep a complete record on both the ewe and her lamb(s), given their often large spatial separation. However, by concentrating on the ewe’s behaviour it was possible to also record all interactions with her lamb(s). As part of the focal-animal observations, records were taken of whether a ewe or lamb elicited spatial change by:

- Approaching to within 1 metre
- Leaving to beyond 1 metre
- Partially approaching by moving directly towards the other member(s) of the family group, but not to within 1 metre of the individual(s).
All occurrences of suckling, and ewes preventing suckling were also recorded.

Throughout these focal observations, scan samples were also taken at 3 minute intervals. Scan sampling is instantaneous sampling on a group (Altmann, 1974), which in this study was the ewe and her lamb(s). Every attempt was made to keep the complete scan times as brief as possible (5 to 7 seconds). Hence for each ewe on a particular observation day there were six records of ewe behaviour, lamb(s) behaviour and ewe-lamb(s) distance. The distance between ewe and lamb was estimated, by eye, into nine classes (contact with ewe, < 1 metre, 1-5 metres, 5-10 metres, 10-15 metres, 15-20 metres, 20-25 metres, 25-30 metres, > 30 metres). During the habituation period, before lambing, distances between features in the field were estimated by eye and then measured to ensure consistency and reasonable accuracy in later distance estimates.

All observations were tape-recorded in the field and later transferred (in real time) onto computer using 'Key Behaviour' (Deag, 1988), a data collection package. Each year's observations were treated as a separate data set because the majority of the ewes were present in both years.

Two variables from the scan data, ewe-lamb distance and lamb behaviour, were analysed by analysis of variance. The analysis was blocked for ewe with the main effects being week, litter size, and parity, including all two-factor interactions between these factors. An average ewe-lamb distance from a session was used for the analysis, giving three values per ewe for each week. Similarly, the percentage occurrence of a particular behaviour within a session was calculated for the lamb behaviour analysis.

Data from the focal-animal observations (being primarily frequencies) were very skewed towards zero and were therefore analysed using non-parametric statistics. The effect of week was tested by Friedman Two-way Analysis of Variance (Siegel
and Castellan, 1988). When using non-parametric analysis of variance, such as the Friedman test, it is not possible to test for interaction effects (Siegel and Castellan, 1988). As such, interactions between week and the factors litter size and parity are described by the use of plots of means with standard errors. All frequencies discussed relate to the number of occurrences in a fifteen minute period.

Further investigation of the changes in tendencies of both the ewe and lamb to be together or apart, was determined by calculating a single index of responsibility for proximity. This Proximity Index, as described by Simpson et al. (1986) is the percentage of total approaches by both the ewe and lamb which were made by the lamb, minus the percentage of all leaves by either the ewe or lamb which were made by the lamb.

\[
\text{Proximity Index} = \left( \frac{L_A - L_L}{L_A + E_A + L_L + E_L} \right) \times 100
\]

where \( L_A \) = Number of approaches made by lamb  
\( E_A \) = Number of approaches made by ewe  
\( L_L \) = Number of leaves made by lamb  
\( E_L \) = Number of leaves made by ewe

Individual values for days in week 1, may be illustrated in the results, if there is a significant session effect. There were no session effects within any other week, therefore the mean for three observations from the remaining weeks will be shown. All significant effects discussed are true for both years, 1987 and 1988, unless otherwise stated. Most frequently, 1987 will be used to illustrate the effects because of the inclusion of observations in week 14. Twin A and Twin B are used here to distinguish between the lambs in a twin pair but without implying birth order, as in Chapters 3 and 4, where Twin 1 and Twin 2 are used.
RESULTS

Ewe-lamb distances over developmental age for both observation seasons are shown in Table 5.1.

Table 5.1. Mean ewe-lamb distances (m)

<table>
<thead>
<tr>
<th>Season</th>
<th>1</th>
<th>3</th>
<th>Week 6</th>
<th>14</th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1987</td>
<td>8.59</td>
<td>15.84</td>
<td>15.47</td>
<td>15.02</td>
<td>0.91</td>
</tr>
<tr>
<td>1988</td>
<td>9.59</td>
<td>15.84</td>
<td>15.35</td>
<td>-</td>
<td>0.93</td>
</tr>
</tbody>
</table>

The significant week effect ($F=31.27; \ df=3,837; \ P<0.001$) in both years is mainly due to the increase in distance from 8-9 metres in week 1, to 15 metres in subsequent weeks. This pattern of increasing ewe-lamb distance begun in the first few days of the lamb's life, as seen in Figure 5.1, with a significant effect of day within week 1 ($F=20.52; \ df=3,252; \ P<0.001$).

There was a significantly different pattern over time for singles compared to twins, as shown by the significant interaction between week and litter size ($F=4.83; \ df=3,791; \ P<0.01$; Figure 5.1). The peak distance of 17-18 metres was reached in week 3 for singles as opposed to week 6 for twins, before both declined to an overall 15 metres standard at week 14. Parity also had a small significant effect on ewe-lamb distance over time. As Figure 5.2 shows, multiparous ewes tended to be a greater distance from their lambs in 1987, reaching significance by week 14 ($F=2.92; \ df=3,791; \ P<0.05$). In 1988, multiparous ewes were also found further apart from their lambs in week 1 but showed a significant decrease ($F=7.61; \ df=2,636; \ P<0.01$) in ewe-lamb distance at the sixth week, compared to primiparous ewes (Figure 5.3).
Both ewe and lamb activity effected ewe-lamb distance. The predominant ewe behaviour was grazing, which occurred in more than 90% of all observations (Table 5.2).

The changing pattern of ewe-lamb distance over time was therefore primarily the pattern for when the ewe was grazing. The behaviours which were most prominent in the remaining 10% of observations were lying/ruminating, walking and headup, and they all occurred at closer ewe-lamb distances than when a ewe was grazing (Table 5.2). The only difference between singles (shown in Table 5.2) and twins was that in the fourteenth week ewes with singles were observed lying 5% of the time compared to only 0.4% for ewes with twins. Ewes with twins grazed for the extra 4.5% of time.
Figure 5.2
Parity effect on ewe-lamb distance -1987

Figure 5.3
Parity effect on ewe-lamb distance -1988
Due to the large amount of time the ewe spent grazing the majority of lamb activities were observed during this time (Table 5.3). Over the weeks, the time the lamb spent lying and standing were increasingly replaced by grazing and, to a lesser extent, lying/ruminating. Play behaviour only occurred in weeks 1 and 3. Ewe-lamb distances for all lamb behaviours increased from weeks 1 to 3 but thereafter lying, standing and walking remained similar, and grazing and lying/ruminating continued to increase until week 6 before declining again in the final week of observations.

Table 5.2. Ewe behaviour (proportion of observations) and ewe-lamb distances (m) - 1987 (Values for ewes with singles)

<table>
<thead>
<tr>
<th>Week</th>
<th>Grazing</th>
<th>Headup</th>
<th>Lying/ Ruminating</th>
<th>Walking</th>
<th>Lying</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.90</td>
<td>0.02</td>
<td>0.04</td>
<td>0.02</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>8.7</td>
<td>0.7</td>
<td>6.2</td>
<td>4.2</td>
<td>3.0</td>
</tr>
<tr>
<td>3</td>
<td>0.94</td>
<td>0.01</td>
<td>0.03</td>
<td>0.007</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>17.6</td>
<td>2.1</td>
<td>3.5</td>
<td>21.0</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>0.94</td>
<td>0.009</td>
<td>0.02</td>
<td>0.01</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>14.2</td>
<td>3.3</td>
<td>8.9</td>
<td>9.11</td>
<td>-</td>
</tr>
<tr>
<td>14</td>
<td>0.91</td>
<td>0.007</td>
<td>0.02</td>
<td>0.01</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>15.1</td>
<td>22.0</td>
<td>7.9</td>
<td>26.1</td>
<td>14.7</td>
</tr>
</tbody>
</table>

Table 5.3. Lamb behaviour (B) (proportion of observations) and ewe-lamb distances (D) (m) when the ewe is grazing - 1987 (Values for twins)

<table>
<thead>
<tr>
<th>Week</th>
<th>Playing</th>
<th>Lying</th>
<th>Standing</th>
<th>Grazing</th>
<th>Lying/ Ruminating</th>
<th>Walking</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 B</td>
<td>0.02</td>
<td>0.69</td>
<td>0.27</td>
<td>-</td>
<td>-</td>
<td>0.008</td>
</tr>
<tr>
<td>D</td>
<td>8.6</td>
<td>10.2</td>
<td>7.8</td>
<td>-</td>
<td>-</td>
<td>3.4</td>
</tr>
<tr>
<td>3 B</td>
<td>0.05</td>
<td>0.46</td>
<td>0.15</td>
<td>0.27</td>
<td>-</td>
<td>0.03</td>
</tr>
<tr>
<td>D</td>
<td>21.7</td>
<td>17.0</td>
<td>12.4</td>
<td>10.7</td>
<td>-</td>
<td>13.9</td>
</tr>
<tr>
<td>6 B</td>
<td>0.001</td>
<td>0.21</td>
<td>0.03</td>
<td>0.55</td>
<td>0.11</td>
<td>0.02</td>
</tr>
<tr>
<td>D</td>
<td>10.0</td>
<td>20.0</td>
<td>11.0</td>
<td>14.4</td>
<td>26.7</td>
<td>13.2</td>
</tr>
<tr>
<td>14 B</td>
<td>-</td>
<td>0.02</td>
<td>0.02</td>
<td>0.68</td>
<td>0.06</td>
<td>0.008</td>
</tr>
<tr>
<td>D</td>
<td>-</td>
<td>19.6</td>
<td>10.1</td>
<td>9.8</td>
<td>16.3</td>
<td>11.0</td>
</tr>
</tbody>
</table>

Suckling tended to only occur when the ewe had her head up. The other lamb
behaviours which occurred when the ewe had her headup were lying and standing in week 1 and then in later weeks predominantly grazing (Table 5.4), with all these lamb behaviours occurring within 5 metres of the ewe. Lambs were less than 10 metres from the ewe when she was lying/ruminating, and they were predominantly lying (and in later weeks ruminating) or grazing. Ewe-lamb distance was greater than 10 metres when the ewe was walking, except if the lamb was also walking, which was the predominant lamb behaviour (Table 5.4), and then they remained closer together. There were no litter size effects in the development of behaviours over time.

Although the focal-animal observations allowed for several possible combinations of ewe and lamb behaviour to be recorded as 'eliciting spatial change', over 98% of all these transitions (approaches or leaves) were effected by either the ewe or her lamb(s) acting alone. Only in week 3 were there a few ewe-initiated mutual approaches. No lamb-initiated mutual approaches were recorded.

Table 5.4. Lamb behaviour (proportion of observations) concurrent with 3 ewe activities - 1987 (Values for singles)

<table>
<thead>
<tr>
<th>Week</th>
<th>Suckling</th>
<th>Lying</th>
<th>Standing</th>
<th>Grazing</th>
<th>Lying/ Ruminating</th>
<th>Walking</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ewe Headup</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.21</td>
<td>0.14</td>
<td>0.5</td>
<td>-</td>
<td>-</td>
<td>0.14</td>
</tr>
<tr>
<td>3</td>
<td>0.57</td>
<td>-</td>
<td>-</td>
<td>0.14</td>
<td>-</td>
<td>0.14</td>
</tr>
<tr>
<td>6</td>
<td>0.33</td>
<td>-</td>
<td>-</td>
<td>0.67</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>14</td>
<td>0.20</td>
<td>-</td>
<td>-</td>
<td>0.20</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ewe Lying/ruminating</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>-</td>
<td>0.93</td>
<td>0.07</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>-</td>
<td>0.62</td>
<td>0.38</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>-</td>
<td>0.46</td>
<td>-</td>
<td>0.31</td>
<td>0.23</td>
<td>-</td>
</tr>
<tr>
<td>14</td>
<td>-</td>
<td>0.27</td>
<td>-</td>
<td>0.55</td>
<td>0.18</td>
<td>-</td>
</tr>
<tr>
<td>Ewe Walking</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>(Play 0.21)</td>
<td>-</td>
<td>0.07</td>
<td>-</td>
<td>-</td>
<td>0.71</td>
</tr>
<tr>
<td>3</td>
<td>-</td>
<td>0.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.4</td>
</tr>
<tr>
<td>6</td>
<td>-</td>
<td>0.22</td>
<td>-</td>
<td>0.11</td>
<td>-</td>
<td>0.67</td>
</tr>
<tr>
<td>14</td>
<td>-</td>
<td>-</td>
<td>0.11</td>
<td>-</td>
<td>-</td>
<td>0.44</td>
</tr>
</tbody>
</table>
Figure 5.4 shows the time dependant changes in the proximity index. Even in week 1 the index is strongly positive. A closer examination of the variables used in calculating the index shows a lamb would leave its mother less than 40% of the time in the first three weeks, but by six weeks of age the ewe or lamb were equally likely to move away (Figure 5.5). The lamb already made 50% of all approaches by 2 days old, and by the end of week 1 and beyond was responsible for over 80% of approaches.

Figure 5.4  
Proximity Index - 1987

Figure 5.6 confirms that ewes rapidly ceased to approach lambs, as ewe approaches were highest in week 1 (0.68 per 15 minutes), rapidly declining to 0.19 per 15 minutes in week 3 and showing little change beyond this stage ($X^2=15.24$; df=3; $P<0.001$).
In contrast, lamb approaches showed a tendency to increase from a frequency of 1.39 in week 1 to 1.74 in week 3, before declining again to a constant level at 1.1-1.2
(Figure 5.7). This overall week effect did not however, reach significance. A similar pattern was seen in the frequency of ewe not allowing suckling (Figure 5.8). There was a marked increase from 0.12 in week 1 to 0.37 in week 3 before declining again quite steeply to week 6 and more gradually to week 14 ($X^2=10.48; \text{df}=3; P<0.01$). Lamb suckling frequency decreased over time ($X^2=44.26; \text{df}=3; P<0.001$) from 0.89 in week 1 to 0.11 in week 14 (Figure 5.9). Partial approaches by lambs (Figure 5.10) however, increased throughout the observation period from a frequency of 0.13 in week 1 to 1.06 in week 14 ($X^2=40.96; \text{df}=3; P<0.001$). All these significant week effects were also found in 1988.

![Figure 5.7](image)

**Figure 5.7**

*Frequency of Lamb Approaches - 1987*

There was little evidence of litter size effects interacting with the time dependant changes. Figure 5.5 shows a typical effect of litter size, with twins responsible for approaching and leaving in total at only a slightly higher level than singles. There are two exceptions to this, firstly, twins initially had a higher suckling frequency than singles, but the decline in suckling frequency over the first six weeks was far greater
Figure 5.8
Frequency of Ewe Not Allowing Suckling
1987

Suckling refusals/15 minutes

0.5 |
0.4 |
0.3 |
0.2 |
0.1 |
0 |
0   2   4   6   8   10   12   14
Weeks since birth

Figure 5.9
Suckling Frequency - 1987

Sucklings/15 minutes

1 |
0.8 |
0.6 |
0.4 |
0.2 |
0 |
0   2   4   6   8   10   12   14
Weeks since birth
in twins (Figure 5.11). By 6 weeks, singles had a higher sucking frequency. Secondly, twin lambs had a greater number of sucklings refused during the first 3 weeks than singles, whilst ewe’s raising a single lamb maintain the level of refusals over weeks 3 to 6 (Figure 5.12). Figure 5.12 also demonstrates the similarity observed between the twin pair in these variables.

![Figure 5.10](image)

**Figure 5.10**
**Frequency of Lamb Partial Approaches**
**1987**

Generally there appeared to be very little effect of parity on these parameters, with the exception of week 6, where a relative increase in the frequency of leaves which a lamb effects in primiparous ewes compared to multiparous ewes, was found (Figure 5.13). In 1988 only, there was an increase in the incidence of primiparous ewes not allowing suckling at week 3 relative to multiparous ewes (Figure 5.14).
Figure 5.11
Effect of Litter on Suckling Frequency
1987

Figure 5.12
Effect of litter on frequency of ewes
not allowing suckling - 1987
Figure 5.13
Parity effect on frequency of lamb leaves - 1987

Lamb leaves/15 minutes

- Primiparous ewes
- Multiparous ewes

Weeks since birth

Figure 5.14
Effect of parity on frequency of ewes not allowing suckling - 1988

Suckling refusals/15 minutes

- Primiparous ewes
- Multiparous ewes

Weeks since birth
DISCUSSION

Investigations of the ewe-lamb relationship have traditionally been based on ewe-lamb distance information. This study has found that ewe-lamb distance increased during the first week after birth, but there is very little change after this, with the distance thereafter averaging 15 metres. These results are in agreement with those found in Merinos by Morgan and Arnold (1974), although their use of a "weighted mean score for distance" only indicated a range of 11-25 metres after the first week.

In another study with Scottish Blackface ewes and lambs (Hewson and Verkaik, 1981) very similar distances to the present study were found. As with this study, Morgan and Arnold (1974) also showed that the distance between ewes and lambs is dependant on both the ewe and lamb activities.

Morgan and Arnold (1974) only considered the first month of a lamb's life, but work by Arnold and Grassia (1985) on general flock associations and nearest neighbour data showed an initial high peer group association amongst lambs, which gradually declined. This was the result of lambs spending progressively more time grazing and, as they did so, being closer to the ewe. The present study found similar results with a maximum ewe-lamb distance of 22 metres at 3 weeks when lambs were playing, but as the lamb began to spend increasingly more time grazing, the distance declined from 15 to 10 metres in weeks 6 and 14 respectively.

These results are all in contradiction to Hinch et al. (1987) and Hinch (1989), who found only very small ewe-lamb distances, less than 6 metres over 10 weeks. There is no indication of field size in Hinch's 1987 study, but one might presume it was less than in the previous studies discussed, resulting in closer association between the ewe and lamb. In Hinch's 1989 study, the field was rather small (2.2 ha), and another confounding factor may be the use of very high litter sizes in this study, or a breed effect, as breed differences in spatial associations have been shown (Arnold and Pahl, 1974). Other work, with Bighorn sheep in three different environments,
has demonstrated that the social environment (group size and composition) affects both spatial association (Berger, 1979a) and behavioural repertoire (Berger, 1979b). Ewes with lambs have been found to be much less gregarious in summer than in winter (Lawrence and Wood-Gush, 1985) and in fact individual sheep vary in their gregariousness (Arnold and Grassia, 1985). Such influences on distances between ewes may also be expected to have some effect on ewe-lamb distances.

Despite all the previous attention on ewe-lamb distance, this discussion has shown how there are too many other influences on spacing behaviour to be able to fully understand the implications on the ewe-lamb relationship from this single approach. Hence a more detailed description on different facets of the development of the relationship was undertaken. The proximity index has been widely used in other species, particularly primates, but has never been considered in ungulates before. The present study suggests that the lamb becomes responsible for maintaining contact with the ewe much earlier in life than previously thought, with the proximity index strongly positive from the first week of life. In comparison to the precocial lamb, the proximity index seen in an altricial animal such as the kitten is initially zero (Figure 5.15).

It takes about four weeks from birth for a kitten’s motor and sensory abilities to develop (Martin, 1982), and for the kitten to become responsible for initiating close contact. The pattern in later weeks resembles that of the lamb. In the more socially complex primates, with their longer developmental period, the proximity index shows the greatest changes. In the early weeks of life, the index is negative with the mother playing the greater role in maintaining proximity, but after several weeks the infant begins to have a greater role (Figure 5.15).
The proximity index appears fairly robust towards changes in the environment, as shown by the comparison between captive and free-range monkeys (Figure 5.15). The general course of mother-infant relationships among free-ranging rhesus monkeys is remarkably similar both qualitatively and quantitatively to that observed in a "socially living" captive colony (Berman, 1980). Nevertheless there are differences, particularly between mothers rather than infants, in the two environments. Captive mothers are less responsible for maintaining proximity initially, being primarily responsible only in weeks 2 and 4 compared to weeks 8-10 in free-ranging rhesus mothers. By week 16 however, free-ranging mothers are much less responsible for proximity relative to captive mothers (Simpson et al., 1986), showing a very similar pattern by this stage to that of sheep (Figure 5.15).

Moreover, there have been changes in mother-infant interactions in the captive colony over the 10 years they have been studied.

The work comparing proximity in free and captive rhesus monkeys has illustrated
the many factors, physical and social, influencing mother-young relationships. Under the most extreme of social conditions studied, using isolated mother-infant pairs, mothers were less restrictive during the first six months than mothers in a group, due to the lack of aunts in the isolated pairs (Hinde and Spencer-Booth, 1967b). However, in the following six months the lack of play companions resulted in infants approaching their mother more often, resulting in a greater proportion of rejections by the isolated mothers (Hinde and Spencer-Booth, 1967b). When first studied, before 1968, the 'socially living' captive infants didn't play a primary role in maintaining proximity until at least 12 weeks, but by 1974 they had become more similar to their free-ranging counterparts (Berman, 1980). This change over the years is most likely to be due to captive mothers having been allowed to raise their infants in the presence of kin (Berman, 1980). By 1977 however, captive infants were even more responsible for maintaining proximity in early weeks than the free-ranging infants (Simpson et al., 1986). This may be due to the larger predation risks faced in the free-ranging environment. Free-range mothers therefore, are more likely to stay closer to their young infants to be able to react quickly to any immediate danger.

These examples give an indication of the relative complexity of the primate relationship. In sheep there is much less social complexity and variability is less likely compared to primates. One would therefore expect similar proximity indices for sheep breeds across environments, with perhaps a more rapid increase to early lamb responsibility in harsher environments. Desert Bighorn sheep inhabit a very harsh environment and their lambs tend to spend more time alone (Berger, 1979a), be more independent (Berger, 1979b) and are weaned earlier (Berger, 1979c) than their Mountain relations. This indicates the likelihood of a very early lamb responsibility for maintaining proximity with the ewe in Desert Bighorn.

A single index such as the Proximity Index does not, however, give a complete
picture of the changing ewe-lamb relationship. Examination of the percentage of
transitions made by either the ewe or lamb shows that ewe approaches only
contribute to the relationship, to any degree, in the very early stages of the lambs
life. The ewe does however, remain equally responsible for breaking contact
throughout the fourteen week period. The pattern of approaches and leaves in week
1 shows that the lamb, even at this early stage, is required to actively maintain
contact. When only a day old, a lamb spends a lot of its time lying, often sleeping,
and at this time the ewe is also most attentive and will approach the lamb, nose it
and then continue grazing or ruminating. As with the first weeks of life in primates
(Altmann, 1980), the ewe may restrict how far her lamb can explore in the first days,
and will continually approach to maintain contact. Within the first week, the lamb is
already very active and it is very likely to explore its surroundings moving in close
proximity to the ewe. From personal observation the ewe will still, at this stage,
move towards her lying lamb or even follow a lamb that has wandered away. By
three weeks of age, the lamb is primarily responsible for maintaining contact, with a
dramatic decrease in the number of ewe approaches from that of the first week.

At 3 weeks of age as the lamb is making an increased number of approaches, the
present results show the ewe starting to prevent the lamb suckling. Until the lamb is
3 weeks old, this study and others (Munro, 1956; Ewbank 1964, 1967) have found,
that the ewe apparently places little restriction on access to the udder. Hence, the
major determinant of changes in the ewe-lamb relationship at this time, appears to
be the willingness of the ewe to allow suckling and the subsequent ability of the
lamb to adapt its behaviour to these changes in ewe behaviour. These parent-
offspring conflicts are predicted by Trivers (1974, 1985) as he states, that there will
be continual conflict throughout the period of parental investment in how much care
should be given. Weaning remains a poorly defined term with a range of definitions
(when any are given), used by workers in the field. In one respect there is 'classical'
weaning (nutritional self-sufficiency) which is the relatively brief period when the offspring switches from milk to solid food for nutrition. In the broad sense though, weaning includes all behavioural, nutritional, morphological and physiological changes which occur in the transition to an independent adult life (Martin, 1984). Martin (1984) suggests, that the point where the rate of parental investment drops most sharply corresponds to commencement of weaning. Given this, the present findings suggest, that weaning in hill sheep commences at 3 weeks or earlier with a dramatic reduction in maternal investment and subsequent changes in the ewe-lamb relationship. The process of weaning then continues with a less dramatic, but progressive, reduction in the rate of maternal care until the point of "classical" weaning, and lamb independence.

Weaning has long been considered a gradual process (Hersher et al. 1963; Berger, 1979a; Altmann, 1980) and although of potential importance in farming, very little attention has been paid, until very recently, to the process of weaning in farmed ungulates (Wood-Gush et al., 1986). Mother-young interactions in pigs in a semi-natural enclosure show that the most dynamic changes occur, as in sheep, during 1-4 weeks post-partum (Jensen, 1988). As long-lasting family bonds are maintained long after this time, this again suggests, that weaning commences at 1-4 weeks with a gradual decline to classical weaning at 16 weeks. In the case of pigs, the weaning process did not seem to include aggressive rejection behaviour by the sow. Similarly, Gauthier and Barrette (1985) proposed, that in both white-tailed and fallow deer, weaning is a slow process, taking months to be completed entirely, but starts as early as the second or third week of a fawn’s life with changes in suckling behaviours.

With the changes in the level of maternal care occurring at 3 weeks, a new stage in the ewe-lamb relationship is established. By week 6 there is a marked decrease in refusals of suckling and in the frequency of complete approaches made by the
lamb, although lamb approaches still represent over 80% of all approaches made. This situation remains stable through to the fourteenth week. Part of this new relationship is based on the continual alertness by the lamb of the ewes position and behaviour, as shown by the continued increase in lamb partial approaches, and the increase in time that the ewe and lamb spend grazing together.

This finding is also consistent with Trivers (1974) model, in which, as the interests of the mother and offspring diverge, the offspring must assume a greater role in inducing whatever parental investment is forthcoming. As lactation constitutes the major component of parental investment in mammals, Martin (1984) considers rate of milk transfer to be an ideal indicator for assessing the boundaries of weaning. Although no milk yield data was collected in this study, such data from Arnold et al. (1979) shows a very similar time scale for weaning as that indicated by the dynamics of the social relationship in this study. This is even more surprising when one considers that two different breeds, Merino and Dorset Horn, and the environmental conditions used, differ between the two studies. Nonetheless, the milk yield data followed Martin’s (1984) generalised prediction, with a dramatic reduction of milk yield, and thus the onset of weaning at 2-3 weeks of age. This study (Arnold et al., 1979) was primarily concerned with classical weaning or the end of the weaning period. This was determined by the behavioural response of both the ewe and lamb, when reunited after 4 hours separation. After a prolonged and gradual decline in milk yield, weaning (classified as the period when the ewe did not allow suckling) occurred at 100-150 days, a time also seen in wild Bighorn (Berger, 1979a) and Mountain sheep (Geist, 1971). Arnold et al. (1979) concluded, that milk yield was the major determinant of the strength of the ewe-lamb bond, and that weaning occurs when milk yield is below a threshold level.

Both Arnold et al. (1979) and Berger (1979a) have indicated that breed, nutrition and environment can all effect time of weaning. In particular Berger’s (1979a) data
suggested that Desert Bighorn ewes invested a far greater amount, through milk production, in their lambs when they were young, but they were then weaned more abruptly and earlier than their Mountain counterparts. Long weaning periods are also seen in baboons (Altmann, 1980), in which maternal rejection and punishment at 4-6 months of age results at first in dramatic tantrums by the infants. A new relationship is then established, through which the infant learns to obtain care from its mother, for a further 18 months, without interfering in certain of her activities.

In sheep, the development of a new phase in the ewe-lamb relationship is to some extent also influenced by litter size. In general terms, the development of behaviours and distance from the ewe over time were the same for either litter size, unlike a few unexplained differences noted by Morgan and Arnold (1974). There were never any differences within the twin pair, and in the field they would spend a large part of their time together and often be seen performing the same behaviours at any particular instant in time. The first and strongest association of all lambs is with their mothers, but in twins there is a second close association between siblings (Shillito-Walser et al., 1981). Twin lambs can recognize their sibling and in choice tests have been shown to prefer each others company rather than that of an alien lamb (Shillito-Walser et al., 1983).

In the present study there was, however, a distinctive peak in the ewe refusing suckling in twin lambs compared to singles, which may well be a milk yield factor. Unfortunately, there are no milk yield data nor any indication of whether twins are more likely to graze more at an earlier age. A lack of milk supply, to support all lambs, in ewes with higher litter sizes has been shown by Hinch (1989). Suckling behaviour in the present study suggests, that initially there was no restriction on milk supply with twins having a higher suckling frequency than singles, as has been seen in most previous studies (Munro, 1956; Ewbank 1964, 1967; Hinch 1989) but not all (Hess et al., 1974; Stapleton et al., 1980). The greater increase in refusals to
allow suckling in twins was also related to a steep decline in suckling frequency, to a level well below that of singles by week 6. This is contrary to all the above studies, which found no differences between singles and twins in suckling frequency or duration at older ages. The relatively lower rate of decline in suckling frequency, and maintenance in the level of refusals of suckling, by ewes with single lambs perhaps indicates, that with sufficient milk for one lamb, a ewe finds it harder to change her lamb’s dependency on her.

These variables thus indicate, that there will be a more abrupt commencement to the weaning period in twins and possibly a more rapid weaning. Early self-weaning appears to occur in twin calves (Price et al., 1985), perhaps encouraged by their limited dependency on their mother to meet their nutritional needs. Similarly, primiparous ewes show an increased peak number of refusals to allow suckling, perhaps indicating an inability to efficiently effect the change in the relationship compared to more experienced ewes. An equally likely explanation may be lower milk production in these young ewes. Nash (1978) found an indication that older wild baboons were much later in showing rejection behaviour, though more data is needed before one could identify true parity effects.

This work has shown that in a typical domesticated hill sheep, major discontinuities in the ewe-lamb relationship occur long before classical weaning and in fact appears to involve a longer term and more gradual weaning process, than that usually portrayed. Trivers (1974, 1985) predicts that the major conflict in the mother-young relationship will be the 'weaning conflict', with an abrupt reduction in the rate of maternal care at the stage where the ewe favours halting her parental investment is countered by the lamb favouring further parental care. The end of the weaning period was not considered in this study, but dynamic changes in the ewe-lamb relationship are occurring throughout the life of the lamb, and may be considered as a complex of ewe-lamb conflicts of which the classical and final 'weaning conflict'
is but one part.
SUMMARY

Observations on spatial changes in 73 Scottish Blackface ewes and lambs over two years, showed that the ewe-lamb distance averaged 15 metres throughout most observations. The major effect on ewe-lamb distance was ewe and particularly, lamb activity. A more detailed investigation of ewe and lamb transitions showed, that the lamb became increasingly responsible for maintaining contact with the ewe from and early age. The major changes in the ewe-lamb relationship occurred at three weeks of age, and appeared to be determined by the willingness of the ewe to allow suckling and the subsequent ability of the lamb to adjust its behaviour.

Although weaning is often considered to just be the short period when the lamb no longer gets milk from the ewe, this study has shown weaning to be a much longer term and general effect. This chapter supports Martin (1984) concept of weaning, in as much that it is a long and gradual process. The commencement of weaning is when there is the most abrupt change in parental care, and both behavioural observations from this study and milk yield data from Arnold et al. (1979) show, that weaning begins at least by 3 weeks of age in sheep. The time of commencement of weaning appears relatively rigid but a number of factors, including litter size, parity and environmental conditions, will effect the degree of conflict between the ewe and lamb at this transitional time, as well as the duration of the complete weaning period. Although the end of the weaning period was not studied in detail, nutritional independence is well documented as occurring at about 150 days of age.

The classical example of parent-offspring conflict is 'weaning conflict' (Trivers, 1974, 1985) and it occurs at the end of the weaning period, when there is conflict over the continuation of parental care. Hence, although this study has shown that weaning has a major influence on the ewe-lamb relationship, the greatest changes and conflict between ewe and lamb occur at the commencement of weaning and not the final period, in sheep.
This chapter has shown, that the lamb is primarily responsible for making contact with the ewe, but it does not discuss the control of the relationship. There are major behaviour pattern changes at three weeks of age, with the establishment of a new phase in the ewe-lamb relationship. There is, however, no indication of which individual is initiating these effects, the ewe or the lamb, and it is this question, of the dynamics and control of the ewe-lamb relationship which will be discussed in Chapter 6.
CHAPTER 6

DYNAMICS OF THE EWE-LAMB RELATIONSHIP
INTRODUCTION

There are two categories, as described by Lent (1974) of mother-infant relationships in ungulates. There are 'hiders' in which mothers are separated from their infants for long periods and 'hide' their young during this separation, such as red deer (Clutton-Brock and Guinness, 1975). The second type are 'followers' in which the mother and infant maintain close spatial relationships and frequent communication, such as sheep. The maintenance of the ewe-lamb relationship requires mutual attachment and the ability for individual recognition.

The two aspects of maternal behaviour in sheep most extensively studied beyond the post-partum period relate to suckling behaviour and mutual recognition of ewes and lambs. Once suckling has begun it occurs frequently in the first week (1 suckling or more/hour) but decreases to one or two suckling periods per 6 hours by 12 weeks of age (Munro, 1956; Ewbank, 1964, 1967; Hess et al., 1974; Hinch, 1989, see Chapter 5 also). As the lamb grows older, the duration of suckling bouts also decreases from 4 minutes at 3 days to 30 seconds at 14 days (Munro, 1956; Stapleton et al., 1980). At first, the lamb suckles as long as it wants but progressively the ewe ends suckling more and more frequently by stepping over the lamb and moving off.

The behaviour of the ewe and lamb at suckling is organised into well defined patterns. The lamb invariably passes in front of the ewe before reaching the udder (Poindron and Le Neindre, 1980) and usually the ewe smells her lamb at this time, and then often again during suckling itself, when the lamb is in parallel-inverse position. The loss of olfactory perception, due to experimentation, affects both the acceptance of the ewe's own lamb to suckle and discriminatory behaviour at suckling, so allowing alien lambs to suckle (Poindron, 1976; Alexander and Stevens, 1981).
Aside from the discriminatory behaviour at suckling, olfactory clues also play a role in general maternal recognition of her lamb, when they are within 0.25m of each other (Alexander and Shillito, 1977a). Alexander (1978) found, that olfactory clues from either the tail or head region of the lamb are effective for recognition at close quarters. However, olfactory clues alone are ineffective unless other clues are also available. Alexander and Shillito (1977b) found visual clues, particularly from the lamb’s head, to be of major importance for recognition at both close quarters and at a distance. In this experiment they found that ewes avoided the approach, butted and prevented their own blackened lambs from suckling, particularly if the head area was blackened.

At a distance, both auditory and visual cues are important in mutual recognition of ewes and lambs (Alexander, 1977; Alexander and Shillito, 1977a; Shillito-Walser, 1978, 1980), but auditory cues are of secondary importance if visual cues are available. Ewes can, in most cases, recognize their own lambs using only one sense, but in all cases discrimination was maximal when all senses were available (Morgan et al., 1975; Shillito and Alexander, 1975; Alexander, 1977). Even with the help of auditory and visual clues, the environmental conditions in which ewes and lamb are kept can influence their ability to recognize each other at a distance. Animals kept indoors have very poor distance recognition compared to those kept at pasture (Poindron and Schmidt, 1985).

Other than their powers of recognition very little is known about how the ewe and lamb remain in contact under dynamic field conditions (Wood-Gush et al., 1986). Thus it is further understanding of the dynamics of the relationship to which this chapter will address itself. In chapter 5 it was found, that the lamb is primarily responsible for maintaining the ewe-lamb spatial relationship, from a very early age. This chapter will further the discussion on the development of the ewe-lamb relationship and how it is controlled.
MATERIALS AND METHODS

This chapter reports on a section of the 1987 focal animal observations. Observations were collected on individual ewes, lasting fifteen minutes, on three separate days within each of weeks 1, 3, 6 and 14 after parturition (as described in chapter 5). The data was then ordered into a singular description of every behaviour and the time that it occurred using 'Key Behaviour' (Deag, 1988). Every type of 'lamb approach' within this data set, including the time that it occurred, was subsequently selected out along with the immediately preceding and succeeding change in ewe behaviour, and their respective times. An example of a complete data set, for the ewe 734 during week 3, in the format printed from 'Key Behaviour', with the data values used in this chapter marked with an asterisk is given in Table 6.1.

It was found that the times between a change in ewe behaviour preceding a lamb approach ranged from within 2 seconds through to 900 seconds, the length of the observation period. It was necessary therefore to determine if there were different types of approaches (timewise) within the complete data set, and so log survivorship curves of these time intervals were plotted. Log survivorship curves describe the probability of an event occurring relative to the time elapsed since the last event (Lehner, 1979), and are often found to be divisible mathematically into two portions, an initial steep slope portion and a more gradual or flatter section.

The break point between these two sections can be taken to indicate the existence of two separate populations of time intervals in the data set (Martin and Bateson, 1986). The point of inflection for these data was calculated by fitting a regression line through the lower 'gradual' slope of the log survivorship plot, such that points near the 'break point' were not included. The point of inflexion was then taken to be the value which was four standard deviations above the regression line, when plotted against the original log survivorship curve. The resultant time for the
Inflexion point was 25 seconds for both full and partial approaches (see below). A similar range in the time interval between a lamb approaching to a change in succeeding ewe behaviour was found (1-840 seconds). The log survivorship analysis was repeated and the resultant inflexion points were 50 and 40 seconds for full or partial approaches respectively.

Table 6.1  Complete data set showing values selected for analysis

<table>
<thead>
<tr>
<th>Date: 15/5/87</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ewe: 734</td>
</tr>
<tr>
<td>Week: 3</td>
</tr>
<tr>
<td>Session: 3</td>
</tr>
<tr>
<td>Time: 08:43</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Key Code</th>
<th>Time (Seconds)</th>
<th>Behaviour Code</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>60</td>
<td>0.00</td>
<td>START</td>
<td></td>
</tr>
<tr>
<td>71</td>
<td>0.37</td>
<td>GRAZE *</td>
<td></td>
</tr>
<tr>
<td>201</td>
<td>89.25</td>
<td>L1PARA *</td>
<td>Lamb 1 Partial Approach</td>
</tr>
<tr>
<td>208</td>
<td>132.05</td>
<td>L1AP E *</td>
<td>Lamb 1 Approach Ewe</td>
</tr>
<tr>
<td>308</td>
<td>133.67</td>
<td>L2AP E *</td>
<td>Lamb 2 Approach Ewe</td>
</tr>
<tr>
<td>203</td>
<td>152.37</td>
<td>NSUCL1 *</td>
<td>Not allow lamb 1 to suckle</td>
</tr>
<tr>
<td>303</td>
<td>152.65</td>
<td>NSUCL2 *</td>
<td>Not allow lamb 2 to suckle</td>
</tr>
<tr>
<td>113</td>
<td>153.23</td>
<td>E LV B</td>
<td>Ewe Leave Both lambs</td>
</tr>
<tr>
<td>72</td>
<td>251.70</td>
<td>HEADUP *</td>
<td></td>
</tr>
<tr>
<td>208</td>
<td>255.67</td>
<td>L1AP E *</td>
<td></td>
</tr>
<tr>
<td>308</td>
<td>256.34</td>
<td>L2AP E *</td>
<td></td>
</tr>
<tr>
<td>305</td>
<td>257.89</td>
<td>L2LEFT *</td>
<td>Lamb 2 suckling left side</td>
</tr>
<tr>
<td>204</td>
<td>258.44</td>
<td>L1RGHT *</td>
<td>Lamb 1 suckling right side</td>
</tr>
<tr>
<td>302</td>
<td>260.94</td>
<td>NOSEL2</td>
<td>Nose lamb 2</td>
</tr>
<tr>
<td>202</td>
<td>263.01</td>
<td>NOSEL1</td>
<td>Nose lamb 1</td>
</tr>
<tr>
<td>206</td>
<td>264.79</td>
<td>L1ETER</td>
<td>Ewe terminate lamb 1 suckling</td>
</tr>
<tr>
<td>306</td>
<td>265.15</td>
<td>L2ETER</td>
<td>Ewe terminate lamb 2 suckling</td>
</tr>
<tr>
<td>87</td>
<td>267.33</td>
<td>WALK</td>
<td></td>
</tr>
<tr>
<td>113</td>
<td>267.92</td>
<td>E LV B *</td>
<td></td>
</tr>
<tr>
<td>308</td>
<td>273.87</td>
<td>L2AP E *</td>
<td></td>
</tr>
<tr>
<td>208</td>
<td>274.54</td>
<td>L1AP E *</td>
<td></td>
</tr>
<tr>
<td>411</td>
<td>275.00</td>
<td>B LV E *</td>
<td>Both lambs Leave Ewe</td>
</tr>
<tr>
<td>110</td>
<td>278.70</td>
<td>E AP B</td>
<td>Ewe Approach Both lambs</td>
</tr>
<tr>
<td>71</td>
<td>282.34</td>
<td>GRAZE</td>
<td></td>
</tr>
<tr>
<td>113</td>
<td>293.66</td>
<td>E LV B</td>
<td></td>
</tr>
<tr>
<td>87</td>
<td>296.61</td>
<td>WALK</td>
<td></td>
</tr>
<tr>
<td>71</td>
<td>301.85</td>
<td>GRAZE</td>
<td></td>
</tr>
<tr>
<td>87</td>
<td>309.58</td>
<td>WALK</td>
<td></td>
</tr>
<tr>
<td>71</td>
<td>329.39</td>
<td>GRAZE</td>
<td></td>
</tr>
<tr>
<td>63</td>
<td>904.41</td>
<td>FINISH</td>
<td></td>
</tr>
</tbody>
</table>
The results presented are comparisons between the combination of preceding and succeeding behaviours which occur with any lamb approach. Full approaches (i.e. to within 1m of the ewe) and partial approaches (i.e. a direct approach towards the ewe but not to within 1m) are considered separately throughout. The number of observations in the four time categories, formed when the preceding and succeeding times are considered in combination, along with the corresponding percentage of observations occurring in each, are shown in Table 6.2.

<table>
<thead>
<tr>
<th>Preceding Time</th>
<th>Succeeding Time (seconds)</th>
<th>Full Approaches</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>&lt; 50</td>
<td>&gt; 50</td>
</tr>
<tr>
<td>&lt; 25 Number</td>
<td>Number</td>
<td>549</td>
<td>77</td>
</tr>
<tr>
<td></td>
<td>Percentage</td>
<td>46.5</td>
<td>6.6</td>
</tr>
<tr>
<td>&gt; 25 Number</td>
<td>Number</td>
<td>403</td>
<td>150</td>
</tr>
<tr>
<td></td>
<td>LS</td>
<td>34.2</td>
<td>12.7</td>
</tr>
<tr>
<td>Total Number</td>
<td>Percentage</td>
<td>952</td>
<td>227</td>
</tr>
<tr>
<td></td>
<td></td>
<td>80.7</td>
<td>19.3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Partial Approaches</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 25 Number</td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>86</td>
</tr>
<tr>
<td>Percentage</td>
<td>20.9</td>
</tr>
<tr>
<td>&gt; 25 Number</td>
<td></td>
</tr>
<tr>
<td>Number</td>
<td>163</td>
</tr>
<tr>
<td>Percentage</td>
<td>39.5</td>
</tr>
<tr>
<td>Total Number</td>
<td>249</td>
</tr>
<tr>
<td>Percentage</td>
<td>60.4</td>
</tr>
</tbody>
</table>

Table 6.2 The number and percentage of approaches within each time category.
The resultant four categories have been labelled as: Short-Short (SS); Short-Long (SL); Long-Short (LS) and Long-Long (LL) based on the combination of times they relate to. A full description of the behaviours which occurred along with the code used for each is given in the ethogram (Appendix 2).

The data is presented as the conditional probability of a ewe behaviour succeeding a lamb approach, when the approach was preceded by a specific ewe behaviour. All preceding ewe behaviours which occurred more than 5% of the time before a lamb approach, are considered for each of the separate time categories. Due to the large variation in the proportion of lamb approaches which were preceded by each ewe behaviour, this value is shown in parentheses for each preceding behaviour. The complete data set as a first order Markov chain, was analysed through the use of transition matrices (Lehner, 1979; Martin and Bateson, 1986) and tested by Chi-square. The number of observations was inadequate to undertake a valid Chi-square (Lehner, 1979) when an individual week’s data was considered.
RESULTS

Full Approaches

Eighty percent of all observations occurred within the two categories (Table 6.2) where the succeeding time was less than 50 seconds, Short-Short (SS) and Long-Short (LS).

In SS (Figure 6.1) there were a range of preceding ewe behaviours which occurred more than 5% of the time before a lamb approach. Succeeding the lamb approach there were again a range of ewe behaviours seen but two different types of patterns tend to occur. With the preceding ewe behaviours headup/call, call or headup, the predominant succeeding ewe behaviour was suckling. The other succeeding behaviours which occurred were graze, nose lamb, and walk. When an approach was preceded by headup there were also some incidences of refusals of suckling. With the preceding behaviours graze, leave or walk, the probability of suckling occurring following the lamb approach was clearly substantially reduced. The range of succeeding behaviours seen were most likely to be graze, headup, leave or suckling refusals and also walk. There was a non-random distribution of succeeding behaviours as the frequency of occurrence of these behaviours was found to differ significantly from that expected from a random model ($X^2 = 245.60; df = 30; p < 0.001$).

For the other time categories the only preceding ewe behaviours seen of any magnitude were graze and leave (Figure 6.2). In LS, a range of successive behaviours were still seen, including headup, refusals, leave and also some suckling. Lamb approaches in both SL and LL however were succeeded predominantly by headup, leave or walk. In contrast to SS, these time categories did not differ significantly from the frequencies expected.

To obtain further understanding of the dynamics of the ewe-lamb relationship the
Figure 6.1
Ewe behaviours succeeding SS type approaches for a number of preceding ewe behaviours

Conditional Probability of succeeding Ewe Behaviour

- Headup/Call (0.08)
- Call (0.09)
- Headup (0.18)
- Graze (0.22)
- Leave (0.22)
- Walk (0.16)

S Sucke
G Graze
N Nose lamb
W Walk
H Headup
R Refusal
L Leave lamb

Succeeding Ewe Behaviour
Figure 6.2
Ewe behaviours succeeding approaches for a number of preceding ewe behaviours

Preceding Ewe Behaviour

Graze

Conditional Probability of Succeeding Ewe Behaviour

Graze

Leave

Suckling

Nose lamb

Headup

Leave lamb

Suckling

Nose lamb

Headup

Leave lamb

Graze

Walk

Refusal

(0.55)

(0.40)

(0.54)

(0.30)

(0.47)

(0.38)
pattern of these behaviours over time was considered. The two time categories, SS and LS, which had a large enough number of observations on a weekly basis were considered. The proportion of each ewe behaviour preceding a lamb approach changed over time (Figures 6.3a and 6.3b). In particular headup/call, call and leave tended to decrease over time whereas headup on its own and walk increased, and graze maintained a similar priority throughout the 14 week period. The development of the two types of approaches was even more clearly seen when the data were considered between weeks. In the first week a range of successive ewe behaviours were found with all preceding behaviours. There was already a tendency for suckling and nosing to succeed a headup/call, call or headup preceded approach (Figure 6.3a). There were very few occurrences of either refusal to allow suckling or leave.

In week 3, when the maximum number of lamb approaches occurred (see also chapter 5), there continued to be a range of succeeding ewe behaviours regardless of the preceding behaviour (Figures 6.3a and 6.3b). In addition, there was a marked increase in the number of refusals and leaves succeeding in particular, headup, graze and leave preceded approaches at 3 weeks. The majority of approaches which led to suckling occurred in the headup/call, call and headup preceded type of approaches, but not exclusively. By week 6 however, a much more ordered sequence of events had been established. All sucklings occurred following a headup/call, call or headup approach (Figure 6.3a). With headup approaches there were a greater variety of successive behaviours than with headup/call or call. Refusal to allow suckling was preceded by all behaviours with the exception of headup/call but with higher probability from headup, graze, leave or walk. Otherwise graze, leave and walk preceded approaches were followed by headup or leave, though walk was primarily succeeded by graze (Figure 6.3b). The sequences seen in week 14 were the same as those for week 6, with a notable change being, the very rare occurrence of refusal to allow suckling.
Figure 6.5
Ewe behaviours succeeding partial approaches for a number of preceding ewe behaviours

Preceding Ewe Behaviour

<table>
<thead>
<tr>
<th>SS</th>
<th>LS</th>
<th>SL</th>
<th>LL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Graze</td>
<td>Graze</td>
<td>Graze</td>
<td>Graze</td>
</tr>
<tr>
<td>Conditional Probability of Succeeding Ewe Behaviour</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Graze (0.49)</td>
<td>Graze (0.63)</td>
<td>Graze (0.70)</td>
<td>Graze (0.79)</td>
</tr>
<tr>
<td>Walk (0.16)</td>
<td>Leave (0.22)</td>
<td>Leave (0.19)</td>
<td>Leave (0.14)</td>
</tr>
</tbody>
</table>

Succeeding Ewe Behaviour

S Suckie N Nose lamb H Headup L Leave lamb
G Graze W Walk R Refusal
Figure 6.4
Ewe behaviours succeeding LS type approaches for a number of preceding ewe behaviours over time

Preceding Ewe Behaviour

<table>
<thead>
<tr>
<th>Preceding Ewe Behaviour</th>
<th>Succeeding Ewe Behaviour</th>
<th>Conditional Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Graze</td>
<td>S</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>0.62</td>
</tr>
<tr>
<td>Leave</td>
<td>S</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>G</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>0.22</td>
</tr>
</tbody>
</table>

S Suckle
G Graze
N Nose lamb
W Walk
H Headup
R Refusal
L Leave lamb
In LS, the proportion of graze preceded approaches increased throughout the observation period (Figure 6.4), while the occurrence of leave preceding a lamb approach tended to decrease. Approaches preceded by graze or leave showed similar patterns in the probability of successive behaviours occurring, to that seen in SS. Refusal to allow suckling though, was seen earlier in this category. It occurred as early as the first week, and was the predominant successive behaviour in weeks 3 and 6 with a considerably higher incidence of occurrence than in SS.

**Partial Approaches**

Unlike full approaches, there was not a clear bias to partial approaches occurring when the successive behaviour occurred within 40 seconds of the approach. Seventy percent of all partial approaches though, occurred when the preceding behaviour was greater than 25 seconds (Table 6.2) before a lamb approach.

The predominant preceding ewe behaviour throughout all categories (Figure 6.5) was graze. The only other behaviours which occurred were walk in SS and leave in the three other time categories. There were a large proportion of cases (0.29 for SS and 0.71 for LS) where no succeeding change in ewe behaviour was recorded. These were instances when a ewe continued to graze throughout the time from the lamb partial approach until the end of the observation period. The equally prominent ewe behaviour following a lamb's partial approach was headup for all time categories. Otherwise, there were only some occurrences of graze succeeding a walk preceded partial approach, in SS, or leave succeeding partial approaches, in LL.
Figure 6.3b

Ewe behaviours succeeding SS type approaches for a number of preceding ewe behaviours over time

Preceding Ewe Behaviour

<table>
<thead>
<tr>
<th>Preceding Ewe Behaviour</th>
<th>Week 1</th>
<th>Week 3</th>
<th>Week 6</th>
<th>Week 14</th>
</tr>
</thead>
<tbody>
<tr>
<td>Graze</td>
<td>(0.15)</td>
<td>(0.25)</td>
<td>(0.21)</td>
<td>(0.26)</td>
</tr>
<tr>
<td>Leave</td>
<td>(0.41)</td>
<td>(0.23)</td>
<td>(0.05)</td>
<td>(0.15)</td>
</tr>
<tr>
<td>Walk</td>
<td>(0.06)</td>
<td>(0.31)</td>
<td>(0.19)</td>
<td></td>
</tr>
</tbody>
</table>

Succeeding Ewe Behaviour

- S: Suckling
- G: Graze
- N: Nose lamb
- W: Walk
- H: Head up
- R: Refusal
- L: Leave lamb

Conditional Probability of Succeeding Ewe Behaviour

- Week 1
- Week 3
- Week 6
- Week 14
Figure 6.3a
Ewe behaviours succeeding SS type approaches for a number of preceding ewe behaviours over time

Preceding Ewe Behaviour

<table>
<thead>
<tr>
<th>Week 1</th>
<th>Headup/Call</th>
<th>Call</th>
<th>Headup</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(0.08)</td>
<td>(0.14)</td>
<td>(0.08)</td>
</tr>
<tr>
<td></td>
<td>(0.12)</td>
<td>(0.10)</td>
<td>(0.17)</td>
</tr>
<tr>
<td></td>
<td>(0.07)</td>
<td>(0.08)</td>
<td>(0.24)</td>
</tr>
<tr>
<td></td>
<td>(0.02)</td>
<td>(0.03)</td>
<td>(0.26)</td>
</tr>
</tbody>
</table>

Succeeding Ewe Behaviour

- S: Suckle
- G: Graze
- N: Nose lamb
- W: Walk
- H: Headup
- R: Refusal
- L: Leave lamb
DISCUSSION

Although there is the possibility for a wide range of ewe behaviours to be displayed, only a few occurred in any significant numbers surrounding lamb approaches. The division of the observations into separate populations of time intervals has also characterised these categories into different types of events. Short-short (SS) approaches were when the lamb approached immediately to a change in the ewe’s behaviour and was in turn succeeded by an immediate response from the ewe. This was the only group which included the preceding behaviours headup, call or the combination of headup and call. These ewe behaviours are those with, apparently, the greatest communicative potential. This category also showed a range of successive behaviours as did Long-short (LS). The LS category was when a lamb approached without any immediately preceding ewe behaviour being shown, but which again caused an immediate ewe response. The type of ewe behaviours seen in this category though, tended to be more negative, such as Refusal to allow suckling or Leaving responses, particularly in later weeks. The remaining two time categories were when there is no immediate reaction by the ewe to a lamb’s approach.

Further to the description of the development of the ewe-lamb spatial relationship over time in chapter 5, these results illustrate the development of the control of the relationship. During the first week there is flexibility in the ewe-lamb relationship with ewe tolerance of a lamb approaching her at any time. The ewe will respond to her lamb with little regard to her previous behaviour. For example, although ewes tend to nose their lambs more often after approaches preceded by headup or call, they also nosed their lambs if they had been grazing, walking or leaving before the approach. This nosing behaviour has also been reported in feral Soay (Shillito and Hoyland, 1971) and is thought to be used to maintain contact with the lamb and improve bonding and recognition. Nosing in later weeks however, only occurred
after headup or call preceded approaches.

There was also only a small tendency for suckling to be preceded by headup or vocalisation in week 1, although this excludes the large number of the sucklings that result from a ewe approach. However, over time there is a dramatic change in the sequences of behaviour associated with lamb approaches. In particular the ewe appears to be controlling the lamb's access to the udder. Suckling frequency declines with age of lamb (Munro, 1956; Ewbank, 1967; Hinch, 1989). In this data, this meant that, the percentage of observations in which suckling occurred decreased from 22.7%, 26.3% 8.9% to 5.7% for weeks 1, 3, 6 and 14 respectively (see chapter 5 also). If however, we consider the percentage of lamb approaches resulting in suckling that were preceded by headup, call or the combination of the two, then the figures are typical for that of a learning curve; 52%, 60%, 100% and 94% for weeks 1 to 14.

Previous studies in both Mountain Bighorn (Geist, 1971) and domestic Clun Forest sheep (Ewbank, 1967) have commented on the fact, that the ewe appears to "signal her readiness to suckle" by calling her lamb. Similarly work with Scottish Blackface (Lawrence, 1984) indicates that a lamb becomes conditioned to respond to a raised head by the ewe as a cue for suckling. The present study shows that the ewe increasingly allows suckling only when she has clearly communicated her willingness, through the specific behaviours, or signals, headup or calling.

Considering SS approaches which include the majority of ewe-lamb interactions, 30-40% of all lamb approaches were found to be preceded by these signal behaviours. The ewe is therefore not only directly controlling suckling, but also lamb movements 30-40% of the time. This increase in communicative control is also seen in the number of times the ewe refuses to allow suckling. These refusals predominantly occur following lamb approaches not elicited by the ewe. This is most clearly portrayed in the fact that the highest number of refusals is seen in the
Long-Short period, in which all lamb approaches can be considered as "non-ewe controlled".

The changing ewe-lamb relationship is typified by the behaviour patterns surrounding lamb approaches. In the first week of life both the ewe and lamb will approach each other and the ewe is very responsive at all times. By 3 weeks of age lamb approaches are the more prominent type of approach and although there is still quite a wide range of successive ewe behaviours following a lamb approach, the ewe begins to take some control. The lamb continues to approach at almost any time but the ewe restricts access to the udder, unless she has given the correct signals, headup or call. However, by week 6 the sequences surrounding lamb approaches has been established such that clear patterns emerge. The lamb no longer approaches as often and there is little need to refuse suckling, as the lamb has apparently learnt that the ewe will communicate her readiness to allow suckling.

An even more definite pattern is found by 14 weeks of age. Concommitant with the understanding that it will only be allowed to suckle at selected times, the lamb appears to become very aware of the ewe's movements, as shown by the continued increase in the number of partial approaches (also discussed in chapter 5). Seventy-nine percent of the time, these partial approaches were recorded as being preceded by graze, but the sequence of events is more complex than that. From my own field observations, it appears that if a ewe raises her head even momentarily from grazing, and not necessarily to a full headup position, an alert lamb will quickly attempt to approach her. But then, as the ewe resumes grazing again, the lamb will literally stop in its tracks - thus leading to the recording of a partial approach at that point.

The resulting ewe behaviour to a lamb's partial approach was either 'no response' or (when there was a change in the ewe behaviour) headup. This may be considered to indicate a ewes response to the lamb, not vice-versa, but in at least
50% of these cases the ewe’s response occurred a long time (greater than 40 seconds) after the partial approach. If the lamb was in some way influencing the ewe, then one might expect a large proportion of these partial approaches to lead to a full approach and even suckling. In practice only 28% of all partial approaches lead to a full approach and of these the majority occur with no change in the ewe’s behaviour at all. Therefore, only 7% of all lamb partial approaches result in a headup response by the ewe, which leads to a full approach by the lamb.

Signals are behaviour patterns which are used to communicate (Dawkins, 1987). The ewe therefore can be said to use both visual and auditory signals to communicate with her lamb. Vocalisation is used by many ungulates as a method of communication (Shillito-Walser, 1977) and the use of playback experiments has shown the ability of reindeer mothers and calves to identify each other by voice (Espmark, 1971). Cattle also use vocalisation to relocate each other after separation (Price et al., 1985) and although either may initiate the process, the calf traverses most of the distance between them as both continue calling.

The role of vocalisation in ewe maternal behaviour, particularly in relation to recognition, has been much studied. This work has shown, how lambs can recognize their mothers voices by individual differences (Shillito-Walser, 1980), but there are also breed differences involved in their ability to do this (Shillito-Walser, 1978, 1980). Dalesbred ewe's voices for example are more easily identified by a lamb than the voice of Jacob ewes (Shillito et al., 1982). Differences in ewe behaviour may also have influenced this result. Nonetheless, the results from the present study would indicate that Dalesbred ewes are more likely to use a greater proportion of 'call' and Jacob ewes 'headup' as signals for their lambs.

There has been no previous quantitative study of the 'headup' stance, except that it is also used as an alarm signal (Geist, 1971; Lawrence, 1984). Most sheep studies have reported on general observations and have only considered either vocalisation
or a headup stance, alone (Ewbank, 1967; Geist, 1971; Lawrence, 1984). The present results show quantitatively, that both may be involved either separately or in combination for both suckling and maintenance of contact. It may be that breed and environmental conditions influence the relative use by individuals of these two mechanisms, but this can only be answered by future investigation.

It would appear though, that despite learning the signals to approach for suckling the lamb is not fully conditioned. If the lamb was fully conditioned to headup and call one would expect this to be the only time that the lamb would approach, but this is not so. There are also a large number of lamb approaches which are not elicited by the ewe. The ewe-lamb relationship is however, a very close one and is based on mutual recognition and attachment. Hence, with the lamb responsible for approaching the ewe there will be many instances when it was the lamb which decided to maintain contact with the ewe. Ewes and lambs spend much of their time grazing together, particularly as the lamb gets older. Under dynamic field conditions this means that there will be continual spatial changes between the two, as a result of the natural grazing movements. In particular it has been described by Lawrence (1984) that ewe and lamb pairs perform 'cohesive grazing movements'. In these interactions, a lamb which had been left behind by its mother would subsequently approach her back (to within 0.25m) and then walk around her and begin grazing in front or at her head. These cohesive grazing movements also occur within ewe groups (Lawrence and Wood-Gush, 1985) and would appear to be a behaviour pattern by which individual ewes, or a lamb, avoids separation from moving sub-groups, or its mother.

In addition there are many instances where the ewe signals for the lamb to approach but then suckling does not occur. Both in this study and others (Ewbank, 1967; Lawrence, 1984) it was found that on some occasions after giving the signal to approach, the ewe would then refuse suckling and walk off with the lamb.
following. This has been suggested as a method by which the ewe attempts to keep close contact with her lambs (Ewbank, 1967; Wood-Gush et al., 1986). When a ewe raised her head in alarm the lamb would quickly approach, showing that this behaviour pattern may also have developed as an important anti-predator strategy.

It would seem therefore, that the signals which become associated with suckling are not used solely for that purpose, particularly the headup posture. Ewes raise their heads for surveillance, to walk and to ruminate as well as to communicate their willingness to suckle. There will therefore inevitably be occasions, when the ewe raises her head for some other reason than to signal suckling. The lamb may approach at this time and be refused suckling, or many of these instances may result in a partial approach (as discussed above). The reason why such an uncertain system has developed can only be speculated upon, but it may be that there has not been sufficient selection pressure to make it a completely infallible communicative system. It is probably more likely though, that it is advantageous for the ewe to be able to bring her lamb close by with the use of headup.

The use of one signal for several different purposes is not unusual in the animal kingdom. As an act of communication can be seen from two different viewpoints. The message is what the signal says about the sender, and in some way it describes the state of the individual (Slater, 1983). The meaning however, is what the recipient makes of the message, as inferred from the response. It is not unusual to have one signal which may elicit different responses in different situations. It must also be remembered that after developing into an adult the headup posture will be used as an alarm signal to cause flocking behaviour. This important anti-predator signal is therefore strongly conditioned in the lamb for future use through its connection with suckling. There may also be subtle variations within this signal, which although unknown to date, may be detected and interpreted differently by the lamb.
SUMMARY

This detailed investigation of the dynamics of the spatial relationship in Scottish Blackface ewes and lambs in a field has shown, that although the lamb is responsible for making contact, the ewe does not relinquish control of the ewe-lamb relationship. The ewe controls lamb approaches which will result in suckling by a headup posture, call or a combination of these two. This information furthers the discussion in chapter 5 such that we now know how the lamb must adapt its behaviour during the establishment of a new phase in the ewe-lamb relationship.

The lamb has to learn that it will only be allowed to suckle under the ewes control, and to learn what the appropriate signals are before approaching. The ewe will also signal for the lamb to approach under other circumstances, particularly if disturbed or to maintain contact with her lambs. The headup posture appears to have developed as an anti-predator strategy used throughout the life of the sheep. It is the ewe-lamb communication, using suckling as a reward, which establishes this system.

The following chapter will make the first attempt to investigate, whether ewe and lamb behaviours affect lamb growth, and particularly in relation to changes in the ewe-lamb relationship.
CHAPTER 7

RELATIONSHIP BETWEEN EWE BEHAVIOUR AND LAMB GROWTH
INTRODUCTION

The major advantage of sheep in agricultural systems is their ability to utilize pasture to produce saleable meat and wool. In hill and upland areas, such as used in this study, the land they use would otherwise be of little value for agricultural purposes (Speedy, 1980), and yet hill and upland sheep farming is the most common British farm enterprise (Croston and Pollot, 1985). The principal role of sheep is therefore as a grazing animal, and the aim of efficient sheep production is to maximise output from pasture. Productivity is usually measured as the kilograms of lamb weaned per ewe lambing. This value takes into account litter size, lamb survival and weaning weights for an individual ewe (O'Connor et al., 1985).

Environmental conditions, physiological factors such as temperature regulation and many other factors all influence lamb survival (see Chapter 1 for discussion). The other major variable influencing productivity is weaning weight which is primarily determined by lamb growth rate and the factors influencing it. The most common measure of growth in any farm animal is change in liveweight (McDonald et al., 1981). The typical pattern of liveweight growth is characterized by an S-shaped curve (Paratt and Young, 1983). However, liveweight measures also include unpredictable changes in gut contents, which may be as much as 20% of liveweight gain in ruminants (McDonald et al., 1981). Comparisons between animals based on a single weight are fraught with errors from this and other sources (e.g. fleece weight). An alternative is to take a series of weights over time and then mathematically describe this curve. The Gompertz equation (see Kyriazakis, 1989 for derivations) is one equation used to express these weights in a linear form and to thus obtain a unitary measure of growth.

Many factors have been shown to influence lamb growth. Most studies have been concerned with the effect of nutrition on growth (Robinson et al., 1974), the carcass composition changes as the lamb develops (Owen, 1976; Speedy, 1980; Croston
and Pollot, 1985), or have been genetic studies designed to determine predictors of breeding values (Coop and Hayman 1962; Donald, 1962; Bichard and Cooper, 1966). From such studies the factors considered to influence lamb weaning weight (the parameter used as a measure of lamb growth in these studies) are: age of ewe, sex of lamb, birthweight, litter size, date of birth (or lamb age), breed and pre-lambing and lactation nutrition as it effects ewe weight and condition (Croston and Pollot, 1985).

The only study, to date, to consider the influence of ewe behaviour on lamb growth was that of O'Connor et al. (1985). This study found, that a calibrated observation of ewe behaviour, when her lambs were handled within 24 hours of birth, was related to lamb survival, weaning weight and thus ewe productivity. Productivity (kg lamb weaned/ewe lambing) increased by 20% with an increase in this Maternal Behaviour Score (MBS) from 2 to 5. As well as considering MBS in the current study, a more detailed investigation of specific ewe behaviours will be made to determine which ewe behaviours may be important to the growing lamb.

There has been little quantitative study in any species of the influence of maternal behaviour on offspring survival and none on growth. In wild and feral animals the factors influencing infant mortality have been studied, for example in baboons (Altmann, 1980) and red deer (Albon et al., 1987; Clutton-Brock et al., 1987). This is because survival to maturity and particularly infant survival is considered the most important criteria influencing long-term reproductive potential, and not growth, which is also much more difficult to study in wild populations. Albon et al. (1987) have however, shown that in red deer early growth and development has an effect on reproductive success. There must be caution in such discussions as it may be necessary to consider infant and juvenile mortality separately as different influences may be acting on each. In baboons for example Altmann (1980) found, that infants from 'restrictive' mothers had higher chances of survival during the early months,
but as these infants develop independence more slowly, they are less likely to survive if their mothers die than offspring from 'rejecting' mothers. These studies have again shown that there is some maternal influence on infant survival, but there are no details of the specific effects of maternal behaviour.

In domestic species, growth is an important aspect of productivity and is therefore studied in greater detail. In a detailed study of cats it was found that the mothers weight and litter size played a central role in growth of kittens (Deag et al., 1987). Although it wasn’t studied they also suggest that individual differences in maternal behaviour may play a part in determining kitten growth. It may also be, that a mother’s behaviour is determined by an interaction between body condition and the demands of her kittens (Deag et al., 1987).

In earlier chapters of this thesis it has been shown that, in sheep, ewe maternal behaviour does influence lamb behaviour and this chapter will discuss the further implications of this on lamb growth.
MATERIALS AND METHODS

The growth of 111 lambs raised as either singles or twins in 1987 is analysed in this chapter. Lamb weights were recorded on a fortnightly basis from 12 May to 18 August (see Chapter 2 for all dates). Associated with the data from 111 lambs were the data from their 73 mothers. Ewe weights and body condition scores (see Chapter 2) were recorded before lambing and at three times post-lambing.

Data were analysed by using correlations and linear regression to determine those parameters which had a significant effect on lamb growth. The effects due to sex of lamb, parity, litter size and birthweight were included in the model. Male lambs were castrated on average, at one month of age, and so the sex comparison is in fact between ewe lambs and wether lambs. In addition to these variables and the physical data of the ewe, a selection of behaviour parameters were also considered in the regression model. The behaviours considered were; Maternal Behaviour Score (MBS), frequency of ewe approaches, leaves, refusals of suckling, suckling, calling and headup (all per 15 minutes), proximity index values (see Chapter 5) and the proportion of time the ewe spent with her lambs (see Appendix 2 for description of behaviours).

All these behavioural variables change over time and therefore a mean value, taken over all weeks, for each ewe was used in these analyses. Correlations between individuals' weekly observations and the overall mean showed that the strongest correlations were always to the mean values. This approach resolves the problem of repeated measures and the differing week effect between variables. The Maternal Behaviour Score (MBS) used was that described by O'Connor et. al. (1985) with an additional score (6) included to separate out those ewes at the top end of the scale. The MBS was recorded on a 6-point scale based on the flight response of the ewe to handling and tagging of her lamb(s) by the observer on the day after birth. The scores are defined as:
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 metres but maintains an interest in her lamb(s) and comes back to them as the observer leaves them.

3. Ewe retreats to 5-10 metres.

4. Ewe retreats but stays within 5 metre.

5. Ewe stays close, within 1 metre, 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.

Three dependant variables were analysed by linear regression; first lamb weight, weaning weight and B value, a growth coefficient. The B value was derived from the 9 lamb weight estimates (including birthweight) using the Gompertz equation (Kyriazakis, 1989). This equation is derived from the gompertz function which describes the change in liveweight over time, and is typically a sigmoid shaped curve. Each liveweight is then represented as a rate of growth (u), which is a proportion of the assumed mature weight (80kg in this study) such that the y-axis is now on a unitary scale. The equation is further derived to give 'G' by taking the negative natural logarithm of the negative natural logarithm of 'u'. The combination of the G values now gives a straight line relationship and hence the regression of these values on time gives the B value as the regression coefficient. The growth rate of each lamb is now therefore represented by a unitary measure, the B value.

Lamb weights were recorded on set days, not set lamb ages, and so the individual lamb age was calculated for each weight record, such that it could be fitted in the regression model for both First Weight and Weaning Weight analyses. Initially all
variables were included in a 'best-fit' regression. This uses a maximum $R^2$ improvement technique to identify the "best" single variable, the "best" two-variable model, and so forth where "best" is defined as the variables resulting in the highest $R^2$ improvement and the lowest standard deviation.

This qualitative analysis then indicated the optimal subset of the variables on which a complete stepwise regression was completed. Variables giving rise to non-significant effects (based on T-values) were progressively excluded until a final model of only significant effects was obtained. The T-values were used because they show the significance added to the model by each variable, considering all other variables in the model. This differs from the F-test, where the significance added to the model by inclusion of a variable is only tested in addition to those variables already included, and as such is very dependant on the order in which the variables are tested. Details of this regression model will be shown in the results, including F values and the general means for those factors which were significant.

Lamb mortality data is also presented from the field parturition records.
RESULTS

Correlation coefficients between ewe behaviours, weights, condition scores, general parameters and lamb growth values are shown in Table 7.1. The strongest correlations were between all ewe weight measures over time and to a lesser extent with body condition scores. Lamb growth coefficient (B value) and the lamb weight measures were significantly correlated to each other, and all these parameters were correlated to a lesser degree to some of the ewe behaviour measures and ewe weights. B value was negatively correlated with litter size, proximity index, proportion of time spent with lamb and pre-lambing ewe weight, and positively correlated to birthweight and early ewe condition score. First lamb weight was negatively correlated to litter size and also to MBS and headup frequency. It was positively correlated to birthweight and pre-lambing ewe condition score and weight. Weaning weight was also negatively correlated to litter size and headup frequency and additionally to ewe leave frequency and proportion of time spent with lamb. Weaning weight was positively correlated to birthweight, early post-lambing ewe weight and early and late ewe condition score. Litter and parity were both correlated with certain ewe weights and condition scores. There were no significant correlations with sex of lamb. The correlations between the behaviour measures in Table 7.1 are considered in more detail later.

Regression analysis found that the four variables which had a significant effect on B value were birthweight, pre-lambing and early post-lambing ewe weights and MBS (Table 7.2). All these variables, except pre-lambing ewe weight, show a positive relationship to B value. This means that an increase in their value was related to an increase in lamb growth with the exception of pre-lambing ewe weight which had a negative relationship. Table 7.3 shows that the greatest increase in B value occurred with an improvement in MBS from score 2 to 3. There were no significant effects of litter size, parity or sex of lamb on B value.
Table 7.1  Correlations between measures of lamb growth, ewe weight (Wt), ewe body condition (CS) and maternal behaviour.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Variable number</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Bvalue</td>
<td></td>
</tr>
<tr>
<td>2. First weight</td>
<td>-0.285</td>
</tr>
<tr>
<td>3. Weaning weight</td>
<td>0.395</td>
</tr>
<tr>
<td>4. Litter size</td>
<td>-0.275</td>
</tr>
<tr>
<td>5. Parity</td>
<td>-0.178</td>
</tr>
<tr>
<td>6. Sex</td>
<td>-0.051</td>
</tr>
<tr>
<td>7. Birthweight</td>
<td>0.182</td>
</tr>
<tr>
<td>8. MBS</td>
<td>0.066</td>
</tr>
<tr>
<td>9. Ewe approach</td>
<td>-0.152</td>
</tr>
<tr>
<td>10. Ewe leave</td>
<td>-0.257</td>
</tr>
<tr>
<td>11. Proximity Index</td>
<td>-0.234</td>
</tr>
<tr>
<td>12. Refusals</td>
<td>0.007</td>
</tr>
<tr>
<td>13. Ewe with lamb</td>
<td>-0.096</td>
</tr>
<tr>
<td>14. Suckling</td>
<td>-0.098</td>
</tr>
<tr>
<td>15. Ewe call</td>
<td>0.093</td>
</tr>
<tr>
<td>16. Headup</td>
<td>0.149</td>
</tr>
<tr>
<td>17. Pre-lambing CS</td>
<td>-0.105</td>
</tr>
<tr>
<td>18. Pre-lambing Wt</td>
<td>-0.301</td>
</tr>
<tr>
<td>19. Early CS</td>
<td>0.208</td>
</tr>
<tr>
<td>20. Early Wt</td>
<td>0.046</td>
</tr>
<tr>
<td>21. Mid-lactation Wt</td>
<td>0.073</td>
</tr>
<tr>
<td>22. Late CS</td>
<td>0.123</td>
</tr>
<tr>
<td>23. Late Wt</td>
<td>-0.012</td>
</tr>
</tbody>
</table>

Variable number:
- 1. Bvalue
- 2. First weight
- 3. Weaning weight
- 4. Litter size
- 5. Parity
- 6. Sex
- 7. Birthweight
- 8. MBS
- 9. Ewe approach
- 10. Ewe leave
- 11. Proximity Index
- 12. Refusals
- 13. Ewe with lamb
- 14. Suckling
- 15. Ewe call
- 16. Headup
- 17. Pre-lambing CS
- 18. Pre-lambing Wt
- 19. Early CS
- 20. Early Wt
- 21. Mid-lactation Wt
- 22. Late CS
- 23. Late Wt

Note: P < 0.05 is r > ± 0.195, P < 0.01 is r > ± 0.254, P < 0.001 is r > ± 0.321.
Table 7.2  Results of regression analysis on B value

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Coefficient</th>
<th>F value</th>
<th>P (df= 1,95)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MBS</td>
<td>0.00018</td>
<td>5.11</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Birthweight</td>
<td>0.00019</td>
<td>6.00</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Pre-lambing ewe weight</td>
<td>-0.00012</td>
<td>13.93</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Early post-lambing ewe weight</td>
<td>0.00012</td>
<td>26.08</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

Table 7.3  Mean lamb growth values for MBS

<table>
<thead>
<tr>
<th>MBS</th>
<th>n</th>
<th>B value</th>
<th>First Weight</th>
<th>Weaning Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>10</td>
<td>0.0070±0.0003</td>
<td>10.08±0.64</td>
<td>26.80±1.15</td>
</tr>
<tr>
<td>3</td>
<td>23</td>
<td>0.0078±0.0002</td>
<td>8.98±0.54</td>
<td>28.16±0.97</td>
</tr>
<tr>
<td>4</td>
<td>52</td>
<td>0.0080±0.0001</td>
<td>8.01±0.33</td>
<td>26.67±0.43</td>
</tr>
<tr>
<td>5</td>
<td>14</td>
<td>0.0080±0.0002</td>
<td>7.11±0.42</td>
<td>25.89±0.57</td>
</tr>
<tr>
<td>6</td>
<td>9</td>
<td>0.0078±0.0003</td>
<td>8.11±0.57</td>
<td>26.22±1.22</td>
</tr>
</tbody>
</table>

This model explained 32.2% of the variance, where as the qualitative regression analysis obtained a maximum $R^2$ of 37.3%. The primary four parameters in this analysis were the same as those in the completed final model. The other best seven variables out of the eleven found by the 'best-fit' technique to contribute to B value although not at a significant level, included further behavioural measures. These seven variables were litter size, sex of lamb, ewe approach frequency, ewe leave frequency, proportion of time spent with lamb, headup frequency, and mid-lactation ewe weight.

In comparison, the final regression model for weaning weight included six
significant variables but no behavioural measures (Table 7.4).

**Table 7.4. Results of regression analysis on weaning weight**

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Coefficient</th>
<th>F value</th>
<th>P (df = 1, 95)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter Size</td>
<td>-1.840</td>
<td>69.38</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Birthweight</td>
<td>2.407</td>
<td>26.05</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Lamb Age</td>
<td>0.1616</td>
<td>22.13</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Parity</td>
<td>-1.348</td>
<td>5.03</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Early post-lambing</td>
<td>1.365</td>
<td>6.59</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>condition score</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid-lactation ewe weight</td>
<td>0.1047</td>
<td>6.60</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

Similarly, the three main effects, litter size, birthweight and lamb age were included in the final model for first weight (Table 7.5). Three other variables, pre-lambing ewe weight, proportion of time ewe spent with lamb and suckling frequency were included in the final model.

**Table 7.5 Results of regression analysis on first weight**

<table>
<thead>
<tr>
<th>Independent Variables</th>
<th>Coefficient</th>
<th>T value</th>
<th>F value</th>
<th>P (df=1, 95)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter Size</td>
<td>-0.716</td>
<td>-2.86</td>
<td>81.03</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Birthweight</td>
<td>1.456</td>
<td>8.91</td>
<td>58.46</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Lamb Age</td>
<td>0.332</td>
<td>17.35</td>
<td>346.14</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Pre-lambing ewe weight</td>
<td>0.034</td>
<td>2.07</td>
<td>5.86</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Ewe with Lamb</td>
<td>-3.72</td>
<td>-2.52</td>
<td>4.30</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Suckling frequency</td>
<td>0.591</td>
<td>1.98</td>
<td>1.43</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

Suckling frequency was left in the model initially, because it was significant in the T-
test. The inclusion of suckling frequency improved the final model by both increasing the $R^2$ and by allowing both time spent with the lamb and pre-lambing ewe weight to reach significance, which was an effect no other variable attained.

The means for litter size and parity on the two weight variables are shown in Table 7.6. Singles were significantly heavier than twins early in life and this difference was maintained or even increased at weaning 3 months later. There was no effect of parity on first lamb weight but by weaning, lambs from primiparous ewes were slightly heavier than those from multiparous ewes. Although two-factor interactions were considered in all of the regression models, none proved significant and as a consequence were removed from the analyses.

Table 7.6  Effects of litter size and parity on lamb weights

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Mean ± s.e. First Weight (kg)</th>
<th>Weaning Weight (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Singles</td>
<td>34</td>
<td>9.72 ± 0.47</td>
<td>29.74 ± 0.54</td>
</tr>
<tr>
<td>Twins</td>
<td>73</td>
<td>7.72 ± 0.22</td>
<td>25.52 ± 0.31</td>
</tr>
<tr>
<td>Primiparous</td>
<td>78</td>
<td>8.21 ± 0.27</td>
<td>27.05 ± 0.39</td>
</tr>
<tr>
<td>Multiparous</td>
<td>29</td>
<td>8.46 ± 0.41</td>
<td>26.33 ± 0.64</td>
</tr>
</tbody>
</table>

As with B value, the qualitative analysis for both weight measures included all those significant variables in the quantitative regression analyses. Additionally it was found that the same variables which contributed, non-significantly, to B value were also contributing to both lamb weight measures. Those variables being litter size, birthweight, frequency of ewe approach, leave and headup, proportion of time spent with lambs and pre-lambing ewe weight. In addition MBS was included in first weight and sex and mid-lactation ewe weight included in the weaning weight model. The age of lamb and frequency of ewe call were included in both weight models.
Table 7.7 shows the number and cause of lamb deaths. The deaths at birth include both those from dystocia and from starvation/exposure. The lamb which died by misadventure was smothered when its mother sat on it a few hours after birth. The overall lamb survival was 90.8% but it was found that all lamb deaths were from primiparous ewes. Lambs from primiparous ewes had only a 88.6% survival rate compared to 100% in lamb from multiparous ewes. Singles and twins were equally likely to die.

### Table 7.7 Causes of lamb deaths in 1987

<table>
<thead>
<tr>
<th>Cause</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>In Utero</td>
<td>1</td>
</tr>
<tr>
<td>Premature</td>
<td>1</td>
</tr>
<tr>
<td>At Birth</td>
<td>6</td>
</tr>
<tr>
<td>Predation</td>
<td>2</td>
</tr>
<tr>
<td>Misadventure</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>11</strong></td>
</tr>
</tbody>
</table>
DISCUSSION

Lamb survival rates were very high in this study and hence the major variable influencing production was lamb growth rate. It was found that many variables, including ewe behaviour parameters, influenced lamb growth.

With all three dependant variables, B value, first weight and weaning weight, lamb birthweight showed a significant effect on lamb growth. This indicates that not only does lamb birthweight have an important influence on lamb survival (Hight and Jury, 1970; Dalton et al., 1980) but also affects the growth of the lamb in the longer term.

Litter size also had a marked effect on lamb growth, although it was not significant in the regression model on B value. Litter size is well documented as having an influence on lamb weights (Donald, 1962; Bichard and Cooper, 1966; Croston and Pollot, 1985). Bichard and Cooper (1966) consider it the major influence on lamb weight, especially to six weeks of age and still of importance at 16 weeks. Litter size was highly correlated with birthweight and to a lesser extent pre-lambing ewe weight, which were both significant variables in the B value regression.

Although sex of lamb is normally considered an important influence on lamb growth (Donald, 1962; Owen, 1976; Black, 1983; Croston and Pollot, 1985), it was not a significant effect in this study. It did however explain an increased percentage of the variation and was therefore included in the qualitative analysis for both B value and weaning weight. It is likely that the lack of a strong effect was because the male lambs were castrated and this led to a reduced growth rate (Owen, 1976; Speedy, 1980; Black, 1983). Castrated males (wethers) are still likely to grow faster than females (Speedy, 1980), but the check in 'male' growth with castration means that this difference may only be observed at older ages. This was indicated by the lack of any influence of sex of lamb on first weight, but that it contributed to weaning
weight differences.

An influence of parity was only seen with weaning weight. Age of ewe is known to influence lamb weight (Bichard and Cooper, 1966; Croston and Pollot, 1985). Parity was also strongly correlated to ewe weight and condition score, which were significant variables in all of the lamb growth final regression models.

Initial lamb growth, particularly the first six weeks after lambing, depends largely on the amount of milk available (MLC, 1981). Both litter size and ewe condition affect milk production, but the most important factor is the number of lambs reared (Owen, 1976; Hammond et al., 1978; MLC, 1981; Geenty and Sykes, 1983; Treacher, 1983). This effect on milk yield may be an additional influence of litter size on lamb growth.

The effect of ewe condition on milk yield is usually discussed in terms of body-weight loss during lactation (Robinson et al., 1974; McDonald et al., 1981; Geenty and Sykes, 1983). In the present study any effect of milk yield can only be assessed through the varying ewe weights and condition score parameters, as it was not measured directly. The effect of pre-lambing weight is perhaps the most complicated, having a negative relationship to B value and a positive one to first lamb weight. Pre-lambing ewe weight is a reflection not only of ewe weight at this time but also of litter size and birthweight effects, due to the number and size of the foetus(es). In the B value analysis the pre-lambing ewe weight also appears to be explaining some of the litter size effect. In the first weight analysis though, with both litter size and birthweight taken out as individually important variables, this variable returns to explaining primarily ewe weight alone. Pre-lambing ewe weight was also the only ewe weight measure available to express any influence on first lamb weight, because it was the only ewe weight measure at that time.

It may well be, that direct effects on milk production only occur in extreme situations
of underfeeding in late pregnancy (Treacher, 1983) and as such, the body condition of the ewe at the start of lactation may also be important. This concept would be supported by both early lambing condition score and weight being significant effects in the weaning weight and B value regression models. Similarly, the mid-lactation weight which has a significant effect in the weaning weight model and also included in the qualitative 'best-fit' model for B value, is a good indicator of the level of ewe weight loss and therefore indirectly the maintenance of ewe milk production. There may well be an additional direct effect of ewe weight on lamb growth as suggested by Donald (1962), but this has still not been assessed.

A further indicator of the importance of milk consumption to lamb growth is shown by the inclusion of suckling frequency in the first lamb weight regression. It is the increase in suckling frequency of twins versus singles, which is believed to enhance the milk production in twin-bearing ewes (McDonald et al., 1981). During the first month of life, 75% of the variation in lamb growth can be associated with the level of milk consumption (Owen, 1976; Treacher, 1983). It is not surprising therefore, that suckling frequency only contributed to the first weight analysis. After this time, the lamb becomes progressively less dependant on ewe's milk and its consumption of grass increases, although continuation of some milk consumption in late lactation is still beneficial to the lamb (Owen, 1976).

The major behaviour parameter to have a direct effect on lamb growth was Maternal Behaviour Score (MBS). MBS had a significant effect on B value and was also part of the 'best-fit' first weight analysis. It was previously shown (O'Connor et al., 1985) that weaning weight was influenced by MBS, although the effect was not large and the analyses did not include as many variables as in this study. The present result confirms these previous findings and strengthens them in that, in this more accurate measure of lamb growth, there is still a relationship between MBS and lamb growth, particularly early lamb growth. This indicates, that a simple measurement taken
near birth can help predict long term production performance.

O'Connor et al., (1985) found that both parity and litter size influenced MBS. In the present study, MBS was also found to be strongly correlated to parity but not litter size. In this study however there were only comparisons between twins and singles compared to much higher litter sizes in the New Zealand study. It is not apparent why this 'score' should be the one behavioural measure to show a relationship to lamb growth. MBS is however also strongly correlated to the frequency of ewe headup and call. It may be that this score of ewe attentiveness towards her lamb(s), taken early in the lambs life, is a good indicator of long term ewe attentiveness. This would indicate an association between ewe attentiveness or awareness of her lambs and lamb growth.

One of the other major behaviour variables to show a relationship with lamb growth was the proportion of time the ewe spends with the lamb. 'Ewe with lamb' had a negative correlation to all the lamb growth measures. This may indicate, that in a weaker ewe-lamb relationship or where there is inadequate milk production, the lamb will stay closer to the ewe. Although this behaviour strategy ought to enable the lamb to take every advantage of any suckling opportunity, the ewe ultimately controls access to the udder (see Chapter 6). It appears therefore, that in practice there is likely to be little or no benefit to the lamb of staying close to the ewe, in terms of increased suckling or increased growth rate. This indicates that it is not a 'quantity' estimate of the ewe-lamb relationship, such as time spent together, but the 'quality' of the relationship which is important to lamb survival, growth and development.

Three other behaviour parameters which were included in the qualitative analysis but did not make a significant contribution to the relationship, were the frequency of ewe approach, leave and headup. Ewe approach and leave, if considered together, are correlated to all other behaviour parameters. In particular, they are both
significantly correlated to Proximity Index, proportion of time spent with lamb and the frequency of ewe call. Proximity Index, a combination of ewe and lamb approaches and leaves, was highly correlated to B value. When considered without ewe condition scores, it was the single variable explaining the most variance for all three lamb growth measures, but was lost as a main effect when ewe condition was included. There is no clear indication as to why this should be so.

It is not surprising that the two measures which will determine the time spent with the lamb, namely the frequency of approaches and leaves are all correlated. The correlation of approaches and leaves to the frequency of ewe call is again a reflection of the communication involved in the ewe-lamb spatial relationship, as discussed in Chapter 6.

Frequency of headup was also correlated to ewe call frequency and both these parameters may be considered as indices of ewe attention. They have already been shown in Chapter 6 to be critical in the ewe's control of her lamb(s) movements and particularly in allowing access of the lamb to the udder. These two variables may well be good indicators of the 'quality' of the ewe-lamb relationship and their inclusion in the qualitative 'best-fit' models suggests that they may have some role in influencing lamb growth.

It is also interesting to note that the frequency of ewe refusing to allow suckling did not affect lamb growth. This variable, as discussed in Chapter 6, simply reflects the changes occurring in the ewe-lamb relationship at this time and hence although it involves rather dramatic ewe-lamb interactions it is not a limiting factor to growth.
SUMMARY

The use of a single growth coefficient, B value, has previously been shown to be a more precise indicator of lamb growth than liveweight. This term gives a unitary measure for the whole growth period and as such is not confounded by individual 'day' anomalies. The present study considered this as the main growth parameter, but used comparisons to both an early and late lamb weight to highlight some of the time effects. This comparison emphasised the need for the B value, particularly as the major effect on the weight variables was age of lamb at weighing.

Other variables such as birthweight and some description of ewe weight and condition, and litter size were common effects on all the growth descriptors. Maternal Behaviour Score was the only single behaviour parameter to show a significant effect on B value. Other behaviour measures (considered elsewhere in this thesis) did appear to have some influence on lamb growth, although their effect failed to reach significance. It would appear that some aspects of ewe behaviour are influencing the growth of the lamb in addition to the other basic lamb and ewe physical effects.

The inclusion of a number of behaviour patterns in the analysis may have effectively cancelled any individual variable effects and it may be, that some global description for each individual ewe would be a more appropriate measure. With the large individual differences observed in these behaviours, combining them through a unique descriptor of ewe 'character' or 'temperament' may be a more effective means of examining effects of behaviour on lamb growth.
CHAPTER 8

GENERAL DISCUSSION
Maternal behaviour is a unique complex of activities which appear at particular times and is well adapted to ensure that young animals are fed, cleaned and protected until they have developed enough to look after themselves (Shillitowalser, 1977). Changes in maternal behaviour between birth and weaning of the young are synchronised with the behavioural and physical development of the young, and their growing ability to function independently (Rosenblatt, 1987). Considering that this concept, of maternal behaviour adapting to the development of the young, is so widely reported it is surprisingly difficult to find long term studies of maternal behaviour to support these arguments. The majority of studies, particularly with sheep, concentrate on parturition and the early post-partum period. Rheingold (1963) comments on, the struggle of all those working in the field of maternal behaviour with, the necessity of studying the behaviour of two different organisms at once, the mother and the offspring. This is even further complicated by the fact that each stimulates the behaviour of the other and as the young develops it contributes new stimuli to which the mother must respond (Rheingold, 1963).

The reciprocal stimulation of the ewe-lamb pair is clearly shown by the factors influencing ewe grooming behaviour (Chapter 3). Ewe grooming behaviour appears to directly influence lamb behaviour at parturition, particularly lamb activity and sucking behaviour. The lack of a large parity effect and the little variability between individuals suggests that there is a genetic component in the control of grooming. However the lamb does also have an impact on ewe grooming behaviour with a marked enhancement of grooming by ewes with twins versus singles. Other evidence for environmental influences on grooming is the inability of primiparous ewes to switch their grooming activity to the second-born twin as rapidly as multiparous ewes. It would appear therefore, that the initiation of grooming is genetically controlled and that environmental factors influence the further development of grooming.
The lamb has further influences on the ewes behaviour at this time, as it stands and begins to seek the udder. The resulting effects are dependant though, on the ewe's previous experience. Many multiparous ewes assist their newborn lamb to move along her side and may even arch their back and tilt their teats forward to assist the lamb in finding them (Kilgour and Dalton, 1984). The first standing movements of the lamb, and particularly any attempts to seek the udder, to a large degree appear to confuse and distress a primiparous ewe (Chapter 3). This study has shown that primiparous ewes are perfectly adequate at grooming their newborn lambs and appear to concentrate on this behaviour to such a degree that any movement by the lamb to a position no longer directly in front of her results in the ewe moving, usually in a circling motion, until the lamb is back in front of her again. Experience of only a few hours and the persistence of the lamb to try and suckle does eventually mean the primiparous ewe will adapt her behaviour to allow suckling.

To determine the extent to which lamb behaviour influences the ewe during this early post-partum period an experiment was designed to investigate the interactions between ewe grooming behaviour and lamb activity. The Mule lambs, which were intended to be inactive relative to pure Blackface lambs, were not in the event inactive but rather failed to show appropriate behaviours (Chapter 4). It still remains untested therefore the degree to which the lamb influences the ewes responses at this time, although there are indications that lamb activity has the greatest influence. These results suggest again the importance of considering both partners in the relationship, as it would seem that it is not 'poor' maternal behaviour but 'poor' lamb behaviour that is a limiting factor in lamb survival in the Mule breed.

Descriptions of lamb behaviour, such as those described in this thesis, must be encouraged in similar studies rather than the use of subjective assessments such as 'vigour' used too often in previous work (Alexander et al., 1959; Alexander and Peterson, 1961; Shelley, 1970; Arnold and Morgan, 1975; Atroshi and Osterberg,
1979; Stevens et al., 1982). Much more work needs to be done considering both the ewe and lamb in a variety of breeds under separate lambing conditions to be able to truly understand the dynamics of this relationship. Merino ewes already have a poor reputation (Alexander et al., 1983a, 1983b) for their ability to care for lambs, particularly twins, but why they behave as they do is not understood. It maybe that again part of the problem lies with the inappropriate behaviour of the lamb and not 'poor' maternal behaviour.

Further effects of both ewe and lamb behaviour on each other were found in the changing long-term ewe-lamb relationship (Chapter 5). During the first few days of life the ewe is very attentive and remains close to the lamb, which sleeps for long periods. Within the first week though, the lamb has already developed into a very mobile animal and although it doesn't wander far from the ewe it has become far more responsible for maintaining contact with the ewe (Chapter 5). Previous work describing social behaviour and especially the ewe-lamb relationship relied largely, on social distance changes with age (Arnold and Morgan, 1974; Arnold and Pahl, 1974; Arnold and Grassia, 1975; Hinch et al., 1987). Chapter 5 illustrates how much these data are influenced by a variety of environmental effects.

Domestic animal studies have rarely considered long term, extensive studies of maternal behaviour and as such too little of the methodology and theories put forward by other researchers has been utilised. In particular, mother-young relationships in primates has been much studied and widely considered as a model for all dyadic relationships (Hinde and Spencer-Booth, 1967a; Hinde and Atkinson, 1970; Altmann, 1980; Simpson et al., 1986). Some of the concepts and particularly methodology from these studies were used in this work and proved fruitful. In particular, the Proximity Index and related ewe and lamb movement data showed far more about the changing ewe-lamb relationship than distance data has, or ever can, show. The ewe-lamb relationship, previously considered as a strong 'bond'
established at birth and only broken at weaning was found to be a far more complex and continually changing relationship. The major changes in the relationship occurred not at the typical nutritional weaning age of 4-5 months but at 3-4 weeks.

Those workers studying lamb growth already consider that after this age (1 month) the lamb is progressively less dependent on the ewe for milk, as grass consumption increases (Owen, 1976; Treacher, 1983). At this time it was found that major changes in the ewe-lamb relationship were occurring. Not only did the lamb become primarily responsible for maintaining contact but it also had to adapt to the ewe refusing to allow it to suckle at any time. The lamb had to learn that it would only be allowed to suckle when the ewe gave particular cues, a headup posture or call (Chapter 6).

It would appear therefore that in the longer term it is the ewe again, that can be seen as controlling the ewe-lamb relationship. It is the ewe which directly influences lamb behaviour, at this time, through restricted access to the udder. There was very little effect of the lamb on ewe behaviour beyond the immediate post-partum period. Litter size did however effect the pattern of suckling behaviours, in particular refusals to allow suckling. There is a distinctive peak in the frequency of refusals to allow suckling at 3 weeks in ewes with twins, which results in a marked decline in suckling frequency. In contrast singles did not have as many refusals at 3 weeks but the frequency was maintained through to 6 weeks. The resulting decline in suckling frequency from 6 to 14 weeks is also less dramatic than with twins.

The development of the new relationship, at 3 weeks, may be a response to nutritional needs of the lamb, or the change in behaviour by the ewe may cause the changes in nutritional options. We do not know as yet the cause and effect of the situation but it would appear that two different patterns of change in the ewe-lamb relationship occur, depending on litter size. In ewes with singles there is ample milk
supply (Owen, 1976), and so although the ewe begins to refuse suckling at 3 weeks it is not truly effective until 6 weeks when, with a single lamb’s growth rate, there is no longer enough milk supply to meet its needs and so it must increase its grazing time. In twins however, the lack of milk supply occurs earlier and with an increased number of refusals the twin lamb is forced to graze earlier. Ewes with twin lambs will not allow one lamb to suckle on its own, even when she has communicated her willingness to allow suckling and so at 3 weeks of age there is likely to be even more refusals to allow suckling, merely because both lambs are not present. There is therefore an additional learning burden on twin lambs at this time, in that they not only must learn the cues for suckling but also, that they must only approach the ewe together.

It is generally accepted, through parental investment theory (Trivers, 1974, 1985), that there is a stage where the ewe will decrease her investment in the current offspring. The events occurring at 3-4 weeks appear to relate to this stage. In order to decrease her investment the ewe would have to decrease milk production and use the energy obtained from feeding to build up her own body condition to ensure a successful reproductive season in the following year (Trivers, 1985). Physiological changes have never been considered but may also play a part in the changes occurring at this time. Hence, the growth and development of the lamb is primarily determined at 3-4 weeks of age when the ewe begins to control suckling bouts, the lamb begins to eat more grass, behave more independently and a new stage in the ewe-lamb relationship is established. The ewe therefore initiates the changes in the relationship but the onus is on the lamb to adapt to these changes. More experienced ewes are better able to effect these changes than primiparous ewes.

The frequency of both headup and call were behaviour parameters which had significant effects on many aspects of the ewe-lamb relationship. These two behaviours are the main communication signals used by the ewe (Chapter 6). The
headup posture maybe established as an anti-predator strategy in the flock in later life by using suckling as a reward in the lamb. It was also suggested that ewe behavioural measures, in particular the frequency of headup and call, influenced lamb growth (Chapter 7).

Maternal Behaviour Score (MBS) was found to significantly affect lamb growth. We can only speculate at the present time as to why MBS has such a consistently significant effect on lamb growth. This score taken within 24 hours of birth is based on the flight distance of the ewe from a human observer and might be viewed as only a measure of timidity. The relationship to long term lamb growth however, indicates that it is, as initially intended, measuring some aspect of ewe attentiveness towards her lamb(s). This is further indicated by the correlation of MBS to headup and call, which are both prominent indicators of ewe awareness through her communication with her lambs. Future investigation to determine the important aspects of the ewe's behaviour that this score is measuring and in particular detailing other accurate measures of ewe attentiveness will aid in our understanding of the ewe-lamb relationship.

It would seem that measurements of the quality of the ewe-lamb relationship, using parameters such as headup, call and MBS are most likely to be important influences on lamb survival, growth and development. Two measures, MBS and Proximity Index, were derived from behaviour measures in this study and both had an influence on the ewe-lamb relationship and lamb growth. In future studies the use of a unique descriptor of ewe 'character' utilising actual behaviour measurements, such as these, would be an interesting approach to studying maternal behaviour in domestic animals.

Throughout this study there were considerable individual differences between ewes and lambs with preliminary analysis indicating consistency between individuals in ewe-lamb distance. The use of an individual ewe 'character' measurement may be
the most effective means of describing individual differences and their consistency over time, and also of improving our understanding of the development of the ewe-lamb relationship.


GENSTAT 4.01 MANUAL (1977). The statistics department. Rothamsted Experimental Station.


# APPENDIX 1

Parturition Record Sheet

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Time First Lamb</th>
<th>Time Second Lamb</th>
</tr>
</thead>
<tbody>
<tr>
<td>First appearance of lamb at vulva</td>
<td>13:48</td>
<td>17:46</td>
</tr>
<tr>
<td>Final expulsion (Time 0)</td>
<td>13:58</td>
<td>17:51</td>
</tr>
<tr>
<td>Length of labour</td>
<td>10 min</td>
<td>5 sec</td>
</tr>
<tr>
<td>Time from birth (Time 0 above)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ewe first stands</td>
<td>0.07</td>
<td>17.51*</td>
</tr>
<tr>
<td>Ewe commences grooming</td>
<td>0.09</td>
<td>18.02</td>
</tr>
<tr>
<td>Lamb first attempts to stand</td>
<td>7.42</td>
<td>26.34</td>
</tr>
<tr>
<td>Lamb first stands successfully</td>
<td>16.30</td>
<td>31.47</td>
</tr>
<tr>
<td>Lamb first attempts to find udder</td>
<td>16.35</td>
<td>33.36</td>
</tr>
<tr>
<td>Lamb first suckles successfully</td>
<td>?</td>
<td>67.23</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Lamb number</th>
<th>062 (R47)</th>
<th>063 (R48)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td>M</td>
<td>F</td>
</tr>
<tr>
<td>Birthweight</td>
<td>4.25</td>
<td>3.5</td>
</tr>
<tr>
<td>Additional Notes</td>
<td>White face patch</td>
<td>Very black head</td>
</tr>
</tbody>
</table>

* (Ewe standing for 2nd lamb's birth)
APPENDIX 2  
Ethogram for study

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Approach</td>
<td>Ewe or lamb approaches to within 1m of the other</td>
</tr>
<tr>
<td>Call</td>
<td>Ewe or lamb vocalises</td>
</tr>
<tr>
<td>Drink</td>
<td>Ewe or lamb drinks water</td>
</tr>
<tr>
<td>Graze</td>
<td>Ewe or lamb holds head down, searching for, biting and chewing grass</td>
</tr>
<tr>
<td>Headup</td>
<td>Ewe holds head up above shoulder height</td>
</tr>
<tr>
<td>Headup/Call</td>
<td>Ewe stands with her head up and vocalises</td>
</tr>
<tr>
<td>Leave</td>
<td>Ewe or lamb moves to more than 1m from the other</td>
</tr>
<tr>
<td>Lie/Ruminate</td>
<td>Ewe or lamb lies with head up chewing cud</td>
</tr>
<tr>
<td>Nose</td>
<td>Ewe sniffs at lamb's body</td>
</tr>
<tr>
<td>Partial Approach</td>
<td>Ewe or lamb moves directly towards the other but not to within 1m</td>
</tr>
<tr>
<td>Play</td>
<td>Lamb runs, jumps, gambols, butts etc., alone or with a group of lambs</td>
</tr>
<tr>
<td>Refuse suckling</td>
<td>Ewe does not allow suckling following an attempt by the lamb</td>
</tr>
<tr>
<td>Ruminate</td>
<td>Ewe or lamb stands with head up, chewing cud</td>
</tr>
<tr>
<td>Suckle</td>
<td>Ewe stands still and allows lamb to suck</td>
</tr>
<tr>
<td>Terminate Suckling</td>
<td>Ewe moves forward terminating a suckling bout or lamb stops suckling</td>
</tr>
<tr>
<td>Walk</td>
<td>Ewe or lamb walks with head up</td>
</tr>
</tbody>
</table>