A STUDY OF SOME ASPECTS OF SEXUAL BEHAVIOUR IN THE SHEEP (OVIS ARIES).

A thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Zoology at MASSEY UNIVERSITY

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1973

"The importance of the initial descriptive phase in the study of behaviour has often been neglected".

R.A. Hinde.

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CHAPTER I

INTRODUCTION

Studies of sheep mating behaviour have, in the past tended to concentrate on the statistical parameters associated with mating behaviour and the copulatory act (Bermant et al., 1969,a,b,c; Haughey,1959; Hulet et al., 1962a,b,c; Inkster,1957; Lambourne,1956; Lindsay and Ellsmore,1972; Lindsay and Robinson,1961; Pepelko and Clegg,1965) and have all but ignored a close analysis of the motor acts of the ram and the ewe and their relationship to one another. The result is a body of knowledge having immediate application, especially in efficiency studies, but lacking a firm foundation so that studies could still be found as recently as 1967 on sheep mating behaviour, that gave brief descriptions of some motor acts that were, and remained, unnamed (Mattner et al.,1967).

Banks (1964) drew attention to this situation and although his study did much to rectify this, it was by no means complete. The account of Hafez et al. (1969) can be viewed in much the same light - though providing more descriptive information than many other investigations (Bourke,1967; Lindsay,1966; Lindsay and Fletcher,1972) including several of his own (Hafez,1951; Hafez,1952), certain basic inadequacies were still apparent. The inadequacies of previous descriptive studies became especially evident during the preliminary stages of the present study, when it became obvious that the sexual behaviour of sheep was much more complex than the earlier studies had indicated.

Preliminary observations were conducted in 1972 to provide information for a more detailed study in 1973 and enable recording and management techniques to be refined. The preliminary observations consisted of:

a) observations of the sexual behaviour of a Southdown flock consisting of one ram and fifty-six entire ewes during March and April of the 1972 breeding season,

and b) observations of the sexual behaviour of two vasectomized Romney rams and twelve ovariectomised Romney ewes in which oestrous behaviour was induced using Oestradiol Benzoate (O.B.) during August, September and November 1972 and January,1973.

Because of the above mentioned inadequacies in previous investigations, this study aimed to record and investigate the sexual behaviour of domestic sheep, and secondarily to propose a standardization of the

nomenclature of the sexual behaviour patterns of sheep as a basis for future studies. During the 1973 breeding season, studies of the sexual behaviour of sheep were conducted on a mixed flock of entire and ovariectomized ewes running with a Southdown ram. As a result of these observations the thesis presents a detailed description of sexual behaviour patterns in sheep with a discussion of some possible functions (Chapters Two, Three and Six) and also discusses an investigation of a behavioural management problem and the statistical findings regarding physiological and behavioural responses to the hormone treatment given to the ovariectomized ewes during this investigation (Chapters Four and Five).

CHAPTER II

THE SEXUAL BEHAVIOUR PATTERNS OF THE RAM AND EWE

Description of Sexual Behaviour Patterns

The sexual [1] behaviour patterns [2] described are composite descriptions compiled from recordings of the sexual behaviour of entire (Southdown) and ovariectomized (Romney) ewes and entire (Southdown) and vasectomised (Romney) rams observed over a period encompassing two natural breeding seasons as well as observations of artifically induced sexual behaviour occurring outside the natural breeding season.

One of the most noticable features of the sexual behaviour of sheep is the great variation in the performance of the sexual motor acts between individual animals. Similar findings were made by Banks (1964), Lambourne (1956) and Hulet et al. (1962a).

Because of the composite nature of the descriptions and the individual variation in performance of sexual behaviour patterns, the following descriptions are generalised accounts only.

Names used for the motor acts described in this study are generally the ones with the most common usage or those that aid description. Many of the names given are ones that were used by Geist (1971) though several were 'coined' during this study.

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1 The term 'sexual behaviour' was used instead of 'reproductive behaviour' (which pertains not only to sexual behaviour, but also behaviour associated with parturition and care of young) or 'mating behaviour' (which is behaviour associated with the mating act only) because some of the behaviour patterns described are used in encounters between the ram and anoestrous ewes in which sexual acts, but not copulation occur.

2 The terms 'behaviour pattern' and 'motor act' were used rather than 'fixed action pattern' (F.A.P.) not because any assumption was made of the development of the behaviour pattern but because the term fixed would be an incongruous label for patterns that are not overtly fixed, but show wide variation between individual animals.

The procedure of separating the 'male' and 'female' behaviour patterns as adopted by Banks (1964), Lambourne (1956) and Hafez et al. (1969), has not been followed here because very few of the behaviour patterns listed are strictly male or female prerogatives, but may be performed by both rams and ewes.

Approach

An approach is a movement towards an animal of the opposite sex, so that the animals come 'into contact'.[3] Either sex can approach the other. An approach may be preceeded by staring at the animal about to be approached. This staring appears to be an intention movement and has been reported by Geist (1971) as occurring in the wild sheep he studied.

A common form of approach occurs when a ram ends a bout of feeding by walking to a group of ewes and sniffing each in turn. The ram is then said to have 'approached' the ewes, that is, he has initiated a sexual interaction with each ewe he sniffed.

Most approaches are made from the side or rear of a stationary animal and most approaches culminate in some type of investigatory or (other) courtship behaviour. Some approaches are terminated short of the approached animal. There is evidence to suggest that sheep recognise each other by sight (Geist,1971) and this is proably the reason for interrupted approaches.

An approach was scored as a directional arrow on the recording sheet (see Appendix One), indicating which animal displayed the initiative in originating the contact. A y behaviour patterns, such as a 'low stretch', that accompanied an approach were recorded separately.

Sniffing (see Plates 1,2,3,4,5 and 6)

The three areas that attracted olfactory investigation were distinguished between during recording. These areas were :

a) the face and neck

b) the flanks

c) the perianal region and genitalia.

Sniffing was performed by both rams and ewes and mutual sniffing was common. Most sniffing occurred at the commencement of an interaction but it could also continue to occur throughout the interaction, especially sniffing of the genitalia.

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[3] Mattner et al. (1967) used the term 'approach' to describe a number of investigatory and courtship behaviours of the ram.

Whether the face and neck or flank is sniffed depends on the orientation of the animals to one another. Neither of these two regions seemed to be more important than the other, but the perianal and genital region was favoured by both sexes and they would often sniff this region after sniffing the face or flank.

Sniffing the flank, face or perineum affords olfactory recognition of individual sheep (Ewer,1968). Such recognition of individual animals allows a ram to act adaptively when meeting known flockmates, and the animals can then carry out necessary functions with a minimum waste of energy. While the basic function of sniffing is investigation and recognition, there is no doubt what so ever that it is also used as a general courtship pattern after the need for investigation has been satisfied.

Nosing (nuzzling) of the perineum and genitalia, and occasionally face and flank, is a common behaviour in rams and ewes. It was included in the 'Sniffing' category of behaviour during recording because of the difficulty in distinguishing between an actual sniff, and a sniff involving nosing (contact). Licking is included in this category for the same reason. It occurs most often in rams investigating the vulva of the ewe. Banks (1964) observed that some rams may actually nibble the vulva of the ewe, and Geist (1971) reports that gustatory contact often takes place when rams sniff the rear of ewes or subordinate rams.

The perianal-genital region appears to be quite important in precoital behaviour, probably because it supplies important olfactory, and possibly gustatory, cues to the identity and oestrous state of the ewe (and ram), (Eisenberg and Kleiman,1972; Fletcher and Lindsay,1968; Lindsay 1965). The nuzzling of the vulva by the ram, and conversely the scrotum and penis by the ewe, involves more pressure than is actually required for investigation and may be used to prompt or induce oestrus in ewes, and therefore could be one of the factors involved in the 'Whitten effect' [4] (Fraser,1968).

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[4] The 'Whitten effect' is a phenomenon in which synchronization and induction of oestrus in mice can be achieved by the introduction of a male mouse into a colony of female mice. There is evidence that such an effect is manifest in a variety of ungulate species. It has already been recognised as occurring in sheep, (Clegg and Gangong,1969; Hulet,1966; Lishman and Hunter,1966; Riches and Watson,1954; Schinckel, 1954 a,b).

PLATE 1

Ram and Ewe in a Face-to-Face Encounter
Involving Sniffing and Licking, following a Twist.

PLATE 2

Ewe Nuzzling the Chest of the Ram.

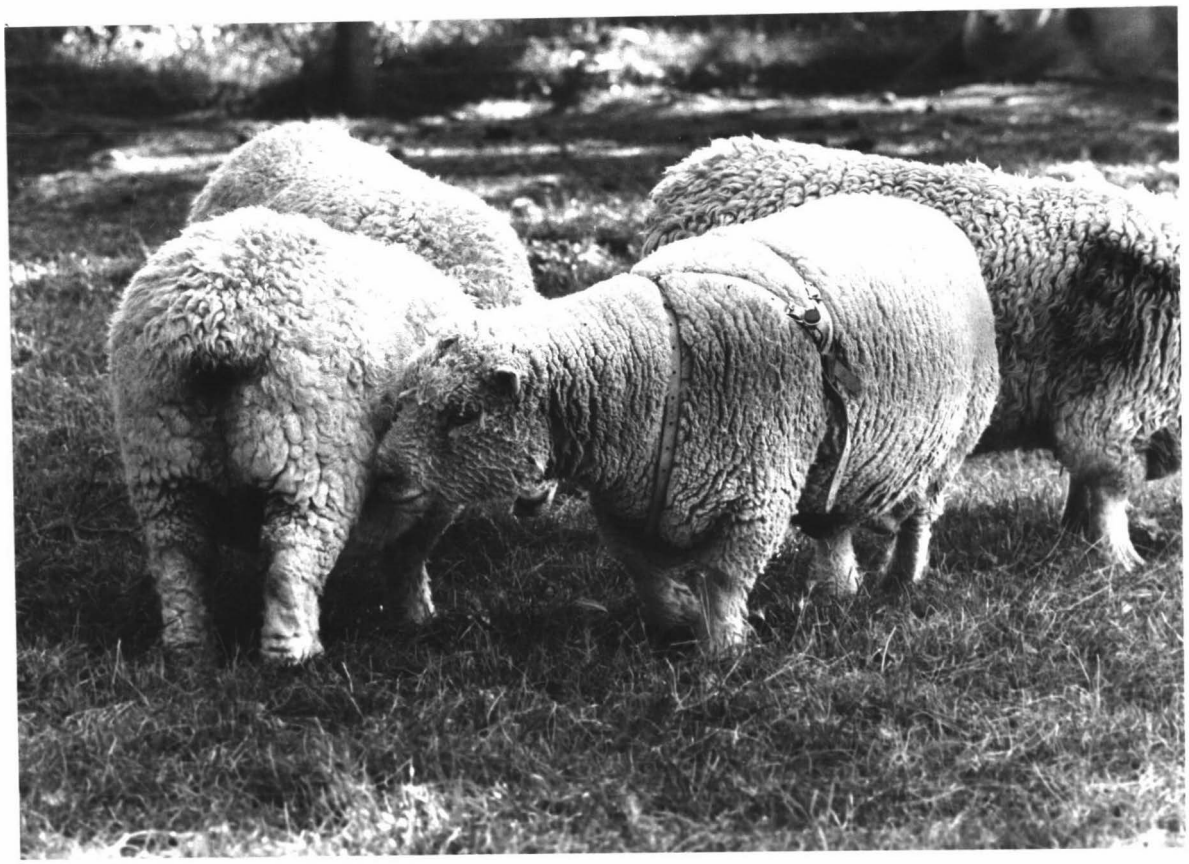

PLATE 3

Ram Sniffs the Flank of a Ewe.

PLATE 4

Ewe Sniffing Perineum of Ram.

PLATE 5

Ewe Sniffing Genitalia of Ram.

PLATE 6

Ram Sniffing Genitalia of Ewe.

Facial sniffing and other face-to-face encounters are conducted with much mutual pinnae movement. Generally the pinnae are moved back and forth in a horizontal plane. Pinnae movements in the ram, especially depression or flicking back and forth also accompany copulation and the Flehmen. None of these movements were quantified but they appeared at their most 'expressive' (involving the most frequent, and greatest degree of movement) in the face-to-face sniffing encounters. Because of the aggressive implications of face-to-face encounters (This study and Geist,1971) the pinnae movements are probably of importance. Pinnae posture in elephants (Kühme,1963 cited by Hinde,1971) and cats (Leyhausen,1956 cited by Hinde,1971) is partially indicative of aggressive and fear tendencies, so it is probable that pinnae movements in sheep express similar tendencies and are therefore, communicative — perhaps fulfilling an appeasement function during courtship.

Urination Response (see Plate 7)

In the courtship context, the ritualised urination response is performed by a ewe for the ram, but it may also be performed by a subordinate ram when a dominant ram is 'courting' it. Only urination responses that occurred during ram-ewe interactions were considered. (Urination as a ritualised response occurs in other contexts as well, see Chapter Three, Section B).

Ewes urinate from a squatting position though the degree to which a ewe crouches to eliminate urine varies from ewe to ewe. A ewe urinates in response to the approach, sniffing or courtship of the ram. Some ewes urinate quite readily for the ram, others only after persistent courting, sometimes followed by aggressive butting. Geist (1971) found "the more often a ewe was courted, the less often she urinates," and concluded this was "probably because she ran out of urine". This facet of the urination response wasn't examined in this study.

Sniff urine (see Plate 8)

In the sexual context, the urine sniffing behaviour is performed by a ram over the urine of a ewe. Usually, the ram is behind the ewe as she begins to urinate, but if not he will attempt to thus orient himself when a ewe starts to urinate. If he is successful he may nose and lick the urine as it is voided as well as lick at the vulva. If the ram does not reach the ewe until she has finished micturating he usually

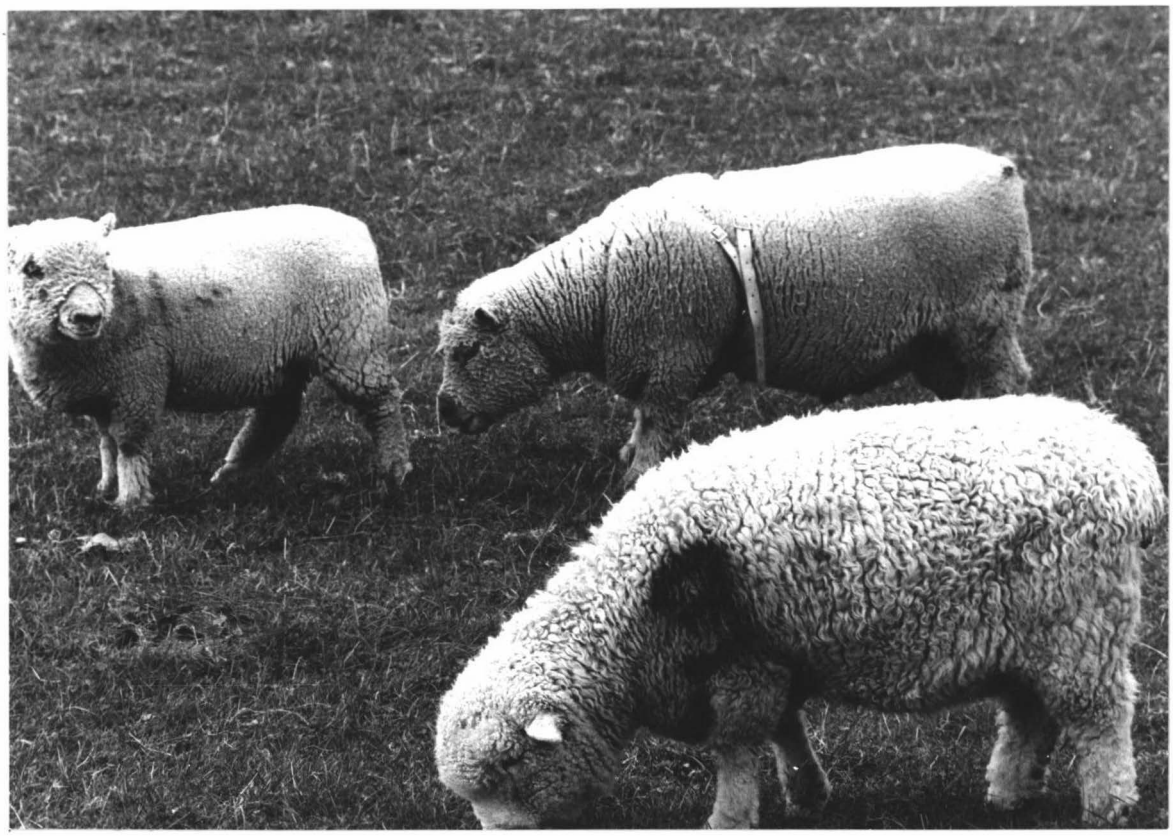

PLATE 7

Ewe Urinating for the Ram.

PLATE 8

Ram Sniffing the Urine of a Ewe.

sniffs and noses the wet urine patch on the ground and sometimes sniffs, licks or nuzzles the vulva of the ewe. It is not usual for a ram to ignore the urination response of a ewe in his proximity. On occasions it was noticed the ram failed to respond to a ewe urinating, but the observer could not be sure that the ram was aware of the ewe doing so. Rams have been seen to pay attention to urine spots they encounter on the ground several minutes after a ewe had left it, and also respond (with Flehmen - see below) after sniffing the vulva of a ewe who urinated several minutes prior to his approach.

In other contexts, such as ram-ram encounters, rams may sniff each other's urine, or in aggressive encounters involving females a ewe may sniff the urine of another ewe. Only once was a ewe seen to sniff the urine of another ewe in a sexual context. She was part of the ram's harem and sniffed the urine just after the ram had done so.

The Flehmen (lip curl or 'olfactory reflex') (see Plates 9 and 10)

The Flehmen was first named and described by Schneider (1930; cited by Banks, 1964) as a behaviour common to most ungulates. The Flehmen in sheep has been described by a number of authors, including Banks (1964), Geist (1971), Hafez et al. (1969) and Hattner et al. (1967). The behaviour is sometimes called a lip curl or olfactory reflex but Flehmen has the most wide usage.

In sheep its most common occurrence is in the ram, just after the ram has sniffed or tasted the urine or vulva of a micturating ewe. It may also occur in male interactions when a ram flehms after sniffing or tasting the urine of a second ram, or its own urine (or ejaculate- Geist,1971). Ewes are also capable of performing this behaviour though it occurs only rarely. Two ewes were seen to flehm during the course of observation for this study. Both Flehmens were over the urine of another ewe.

After smelling or tasting the urine of a ewe the ram raises his head swiftly and holds it approximately 30 degrees above the horizontal. The mouth is opened slightly and the upper lip is retracted (curled) to expose the palate while the bottom lip is lowered to expose the incisors. With the nostrils flared he then pants with short breaths, apparently through both the nose and mouth, and may also move the tongue back and forth within the mouth. These activities permit an unimpeded passage of air onto the palate and into the nostrils.

PLATE 9

The Flehmen Response.

PLATE 10

The Flehmen Response.

The pinnae are usually flicked forward briefly at this time, then moved back until the finish of the Flehmen. The ram sometimes swings the head slowly to each side in a horizontal arc and often finishes the behaviour by licking his lips and nose. The duration of the behaviour varies (10-100 seconds) between rams and also with time for each individual ram, as does the degree of head raising and/or lip curling. The Flehmen is sometimes repeated, usually at a lower intensity than the first and sometimes without sniffing the urine for a second time.

The usual orientation of the ram when performing the Flehmen is behind the ewe with the nose close to the ewes' vulva and the body in line with, or at an angle to that of, the ewe. The Flehmen does not appear to be directed at the ewe, who usually moves away or begins to feed after urinating without watching the ram, nor at any other sheep in the vicinity of the ram. The function of the Flehmen is still in doubt, though a number of theories have been put forward as to its possible function. Knappe's (1964) theory that the Flehmen posture enables the vomeronasal organ to indulge in sensory activities, and some evidence in support of it, is discussed in Chapter Three, Section 'B'.

Low Stretch, Twist and Front Kick (see Plates 11,12,13 and 14)

The next three behaviour patterns to be detailed have been described by Banks (1964) who considered them as sub-acts of the one display (he) called the 'nudge'. During this study the behaviour patterns were treated as separate displays because each pattern could be, and often was, performed in isolation without the other two. When the three patterns were performed together, any one of the three patterns could be performed at any frequency in the encounter, or be omitted from it, and the patterns were performed in no particular order. For this reason they appeared to be somewhat independent of each other and so were treated as separate displays during recording. Geist (1971) also described the behaviours as separate displays and named them. The names that were given to the three displays in this study have been changed to those used by Geist (1971).

As with the other behaviour patterns so far described, there is a great deal of variation in the performance of these behaviour patterns between individual rams, and at different times by the same ram. Some rams fail to perform one or more of the patterns or may perform modified forms of them.

The displays are used outside the true courtship context by dominant rams on subordinate rams. Ewes were not seen displaying any of these behaviour patterns but Geist (1971) saw Bighorn (C.canadensis) ewes display in the low stretch on several occasions.

i) Low Stretch. To perform this display the ram crouches and lowers and twists its head to point at a particular animal. The behaviour is directed at a courted female (or male), usually in close proximity to the ram, though on one occasion a ram was seen to direct the display at a ewe at least 40 metres from him. The display is often accompanied by a slight wrinkling of the nose and rapid tongue flicking, as well as harsh, 'burbling' vocalisations.

Some rams fail to perform this display while in others it varies from a momentary twisting of the head directed at a ewe, to a very noticable crouch with the body and legs tense, the head lowered and twisted and accompanied by tongue flicking and vocalisation. The duration of the display is variable (2-20 seconds) and the display may be repeated. Its most frequent occurrence is when a ewe avoids a courting ram. The ram follows the ewe, stops several metres from her and displays in a low stretch. The ewe usually watches the ram as he performs this behaviour pattern and often responds by standing for further courtship.

Geist (1971) concluded that the low stretch was a horn display, and described the behaviour as one of the most common social patterns used by the sheep he studied. The lack of horns in many domestic breeds could account for the greater variation in, and apparent low intensity of performance of the low stretch in domestic breeds compared with its execution in the wild sheep(C.canadensis, C.dalli, C.dalli stonei, C. nelsoni) Geist (1971) observed, if the low stretch is a horn threat.

ii) The Twist. In this displays' most typical form the ram orients himself behind, and faces the same direction as, the ewe. The ram then brings his shoulder into contact with the flank of the ewe, lowers and twists his head and makes a short jab with his mussle at the ewe's flank. At the same time the ram usually makes the 'burbling' vocalisations (courtship call- Banks,1964) and flicks his tongue in and out of the mouth (tongue flicking), and he may lick the flank of the ewe. The ewe often turns her head to watch the ram during this display.

The difference between the twist and low stretch is;

PLATE 11

Ram Displaying in Low Stretch.

PLATE 12

Ram Performing Twist Display.

a) The twist involves shoulder, and sometimes muzzle, contact with the ewe's flank whereas the low stretch does not,

b) There is a specific orientation for the twist display while the low stretch is directed toward the ewe from any ram position, and,

c) the twist is often accompanied by the front kick.

Banks (1964) failed to distinguish between the low stretch and twist and so recorded that the twist (nudge sub-act) did not require contact. Geist (1971) makes the distinction and observes "the twist is similar to an intensified low stretch". It is possible that the low stretch is an intention movement for the twist (see Chapter Six).

iii) Front Kick. The front kick is performed with an extended foreleg which is lifted straight in a swift, chopping motion directed at the flank, udder or hind legs of the ewe. Occasionally the ram may strike the ewe on the chest or front legs while executing a front kick. The front kick is also performed by dominant rams in encounters with subordinate males.

The kick is often repeated and may be accompanied by a shoving of the recipient animal with the chest of the ram performing the kick. In the sexual context when the ram is interacting with ewes the behaviour often accompanies a twist, being delivered simultaneously with the jabbing motion of the ram's muzzle at the flank of the ewe. The front kick is only rarely performed by ewes, and then only by dominant ones. (Geist,1971).

One of the study rams often executed a 'front kick' with a hind leg although he was capable of performing it with a front leg also (see Plate 14). It is not known how wide spread this variation is or whether it was just an isolated aberrant case.

Many other ruminants display the front kick (Ewer,1968) though there is some variation between groups. Because of its association with other display threats Geist (1971) believed the front kick function[ed] as "a contact display threat". Observations in this study indicated that in the courtship context, the front kick could serve as an intention movement for the mount (see Chapter Six).

Mount and Tupp[5] (see Plates 15,16,17,18 and 19 and 20)

Male behaviour patterns association with service include; mounting, erection, pelvic oscillations, intromission, ejaculation. As

PLATE 13

Ram Lifting Fore Leg to Perform Front Kick.
Ewe 41 is Attempting to Interfere with
the Ram and Ewe 3.

PLATE 14

Ram Performing Modified Front Kick
with Hind Leg.

well as these major events there are other patterns such as chinning, false mounts, ejaculatory leap, orgasm reaction and aggressive butting.

For the mount the ram orients himself behind the ewe, raises his fore end off the ground and lunges forward to straddle the rear quarters of the ewe, clasping her flank with his fore legs. Partial penile erection usually occurs as the ram mounts the female.

It is common for the mount to be preceeded by a behaviour called 'chinning' in which the ram rests his head and throat on the rump of the ewe (Walther,1958, cited by Ewer,1968, describes a similar behaviour in the Kudu, Tragelaphus strepsiceros. It is also common in many other bovids.), and by attempted mounts in which the ram only partially raises his fore end off the ground then slumps back to a standing position. Both of these behaviour patterns may be repeated before a mount occurs or the mounting attempts may be broken off by the ram or ewe at this stage.

Once mounted, the ram may slide off the back of the ewe without showing any clasping, thrusting or intromission, in which case a 'false mount' is said to have occurred (Fraser,1968). If the ram stays mounted, clasping takes place, pelvic oscillations begin and full erection occurs as the ram thrusts for the vulva of the ewe. This behaviour constitutes a true mount. The ram may dismount at this stage and remount again, repeating this activity several times, and may then break off the encounter or continue to mount[6] and thrust until the tip of the penis meets a lack of resistance at the vagina. Pepelko and Clegg (1965) report that at this stage the ram pauses briefly, "sometimes almost too brief a time to recognise". A pause at this stage was not detected in the rams observed for this study.

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[5] The words tupp, service and copulation, as used in this study, are synonymous with intromission. This is not always the case in husbandry terminology, for a raddle marked ewe may be referred to as having been tupped or served when often there is only evidence of mounting.

[6] Up to eleven mounts have been recorded before the ram was successful in achieving intromission on the twelfth mount.

With the start of intromission the ram makes a very deep thrust that is often of sufficient strength to move the ewe forward and to lift the ram's hind legs off the ground. Ejaculation almost always[7] follows this deep thrust. Banks (1964) noted that pelvic oscillations continued after intromission had been accomplished, a finding which contrasts with the single ejaculatory thrust (on intromission) noted in this study and by Hafez (1962), Hafez et al. (1969), Mattner et al.(1967) and Pepelko and Clegg (1965).

Upon ejaculation the ram's respiratory rate increases (Banks, 1964), the pinnae are pulled back, the nose wrinkles, the eyes open wide and the muscles of the hind legs contract (see Plate 18). These events are called the 'orgasm reaction' (Hafez,1962) and it is the ejaculatory thrust, orgasm reaction and following quiescent period that are the behavioural evidence of a service (or tupp).

After ejaculation the ram dismounts and the penis retracts back into the prepuce. The behaviour of the ram immediately after service is variable, but most often the ram stands quietly, his head drooped, paying little attention to the ewes in his vicinity. It is common for the ram to lie down or begin feeding after several minutes of standing quietly following a service. Sometimes the ram may begin to court the ewe he has just served, or a fresh ewe. On several occasions, when a ewe persisted in soliciting the ram after he had served her, the ram put his head against her head or neck, uttered a harsh growl and then butted and chased the ewe away.

Mounting, like many other courtship patterns, is used in the expression and maintenance of dominance in sheep - particularly males, and the mounting of rams by a more dominant ram is a common occurence. Erection and thrusting occurs in dominance mounting but anal intromission and ejaculation were not observed, nor reported by Geist (1971) who also observed dominance mounting. Mounting by females, of males or females, is rare (Geist,1971) and was not observed during this study.

A further ram sexual behaviour is 'spontaneous ejaculation' or masturbation. It was observed only twice and Geist (1971) reports it as being relatively uncommon also. In spontaneous ejaculation the penis is

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7 Pepelko and Clegg (1965) found that out of fifty observed intromissions, only three were unaccompanied by ejaculation and in these three the thrusts had been weak and penetration probably shallow.

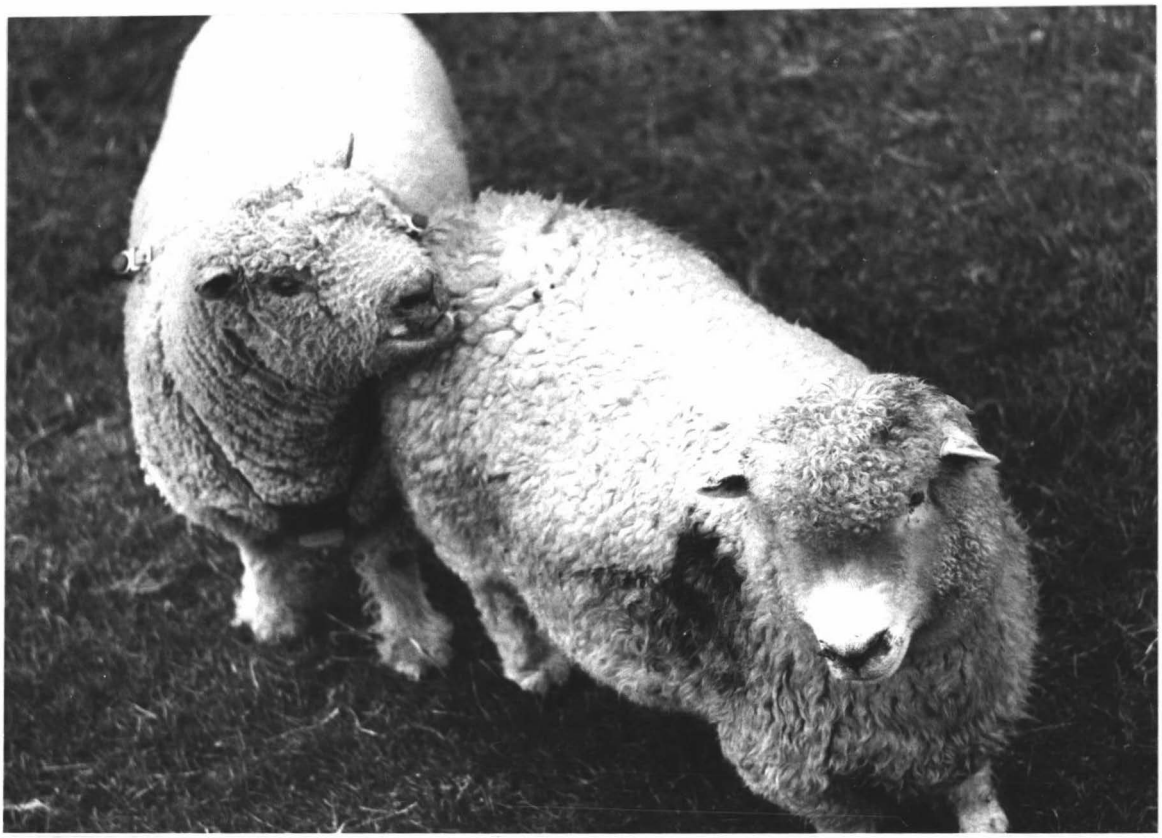

PLATE 15

Ram Orienting for Mount.

PLATE 16

Ram Chinning Prior to Mount.

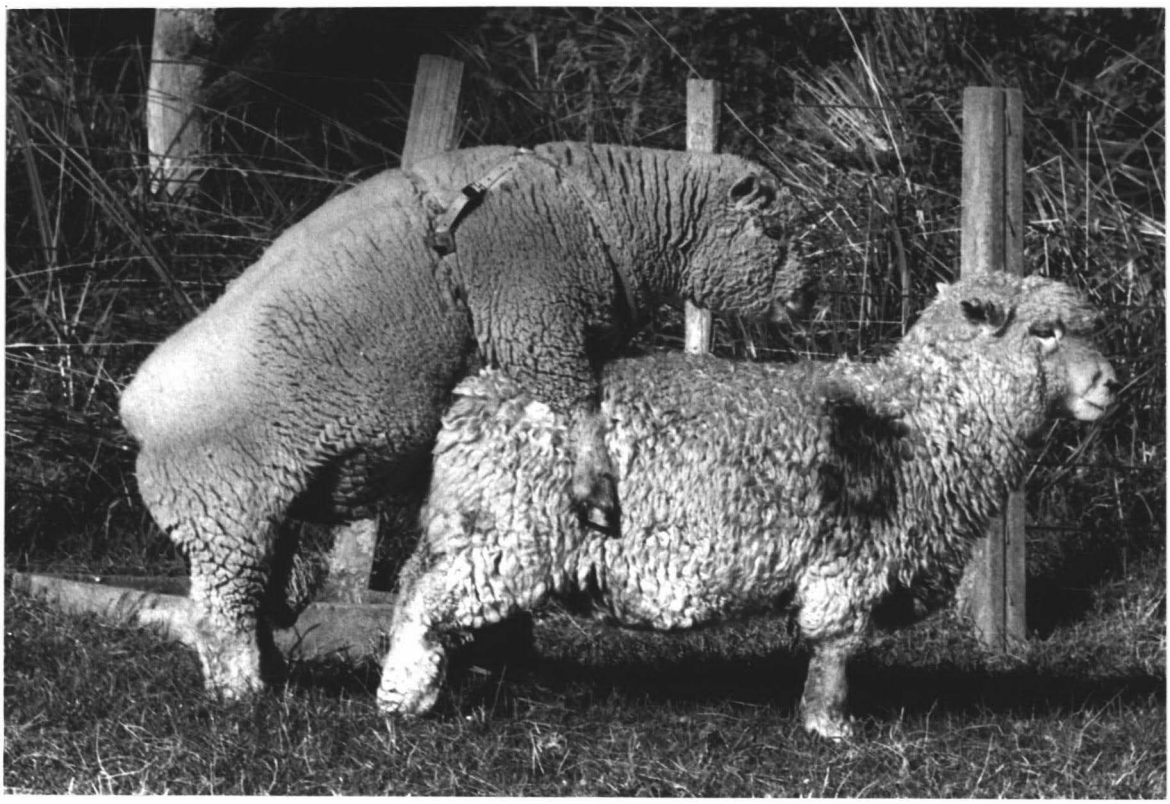

PLATE 17

The Mount.

PLATE 18

Service, showing Ejaculatory Response.
Note the Position of the Pinnae and
the 'Startled' Expression of the Ram.

PLATE 19

Post - Copulatory Standing Response.

PLATE 20

Ram Butts Ewe after she has

Persisted in Courting him, following Service.

extruded fully and the back is hunched to bring the penis to the side of, and beyond, the forelegs. The ram then executes several stumbling steps and ejaculates, apparently by stimulating the penis with the forelegs. A ram may also nuzzle the penis while masturbating in this manner. Spontaneous ejaculation is widespread in the caprids and rupicaprids also and is usually associated with some social activity, either with males or females, or may occur after arising in the morning (Geist,1971).

The behaviour patterns associated with service that were recorded as separate patterns were; attempted mounts, mounts, tupps and chinning. Other responses that occurred in conjunction with these patterns, such as feeding, resting and other courtship activity, were recorded also.

Looking Back (see Plate 21)

The behaviour pattern called 'looking back' is peculiar to ewes (and subordinate rams) when courted by a ram, or when approached by a courting ram from the rear. To 'look back' the ewe swings her head to the side and stares back past her shoulder at the ram. This staring at the ram can last for up to 30 seconds and may be repeated often during the encounter with the ram. It is most commonly exhibited by oestrous ewes standing for the ram's courtship. As head rotation is not necessary for a ewe to see a ram standing behind or to her side, the degree of head rotation involved in 'looking back' indicates that this behaviour is more that just functional (to sight the ram) and is a communicative courtship display.

Looking back is one of the most passive of the ewe displays and is often the first behavioural indication (for the observer) that the ewe is approaching heat. Banks (1964) defined the activity (and ram following which is often associated with it) as a low intensity response that appears in the first 3-5 hours of the ewe's oestrus.

Following

Following was not recorded as a separate ewe display - the status that Banks (1964) gives the activity - in this study. Following is exhibited by oestrous ewes that are part of the ram's harem and attempt to stay in the harem by moving with the ram when he moves. The equivalent of following was corded by; a) noting the identity of the animal that initiated the interactions between the ram and ewe, and b) noting at various times throughout the observation period, the identity of the ewes in the ram's harem.

Rams will follow ewes at times, usually if a ewe moves away from the ram while he is courting it, or if a ram wishes to investigate a ewe who is on the move. This type of following was not considered an actual display, but part of active investigative behaviour.

Tail Fanning

The tail fan is a courtship behaviour exhibited by oestrous ewes. When tail fanning the ewe waggles the tail rapidly from side to side. A similar behaviour occurs in does (Hafez et al.,1969), but unlike ewes, the doe raises the tail and waves it like a small flag. Tail fanning is exhibited about the middle of the ewe's oestrous period when her courtship may become very active, and is usually in response to courting by the ram or during rubbing and nuzzling of the ram by the ewe.

Tail fanning was not seen in anoestrous ewes nor in males being 'courted' by a dominant ram. Geist (1971) does not mention the behaviour but Banks (1964), Hafez (1962) and Hafez et al. (1969) record it. Hafez et al. (1969) report that tail fanning can occur in males though it is rare. It is quite common in the ewe, probably occurring more frequently than recordings indicate because it is difficult to detect if the ewe is facing away, or is any great distance from (50 metres or more), the observer.

The function of tail fanning is not known, but it is interesting to note that it also occurs in nursing lambs, another type of encounter requiring close contact.

Rubbing

In the rubbing display, the ewe (or subordinate male) rubs the head, neck and body against the ram, quite often rubbing itself along the full length of the ram's flank. Rubbing is one of the more intense female sexual behaviour patterns in sheep and it is often used by an oestrous ewe to distract or interrupt a ram when he is courting another ewe (interference - see below). In the ewes observed, rubbing was not as frequent nor as intense as that described by Geist (1971) in Stone's sheep (O.dalli stonei). Neither did the rams stand in the 'present'[8] when being rubbed by females.

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8 A horn threat behaviour described by Geist (1971) that was not seen during the observations for this study.

Rubbing (and nuzzling) is at its highest intensity when used as an approach to solicit the attention of the ram. The ram's response to this behaviour on the part of the ewe is vigorous courtship. However if a ewe that has just been served solicits in this manner the ram usually butts her.

Interference (see Plate 22)

This is not a particular display pattern in itself but the utilization of one or more of the ewe's displays in such a manner that it disrupts the courtship of the ram and another ewe, and draws attention to the interfering (soliciting) ewe. When behaviour patterns occurred as interference they were noted in a separate category because of the important part that interference played in courtship.

Patterns used for interferring with the courtship of the ram and other ewes were; nuzzling, rubbing, tail fanning and pushing (see below), also the interfering ewe might insinuate herself between the ram and courted ewe, or might butt and chase other courted or courting ewes, or butt the ram when he mounted other ewes.

Both Banks (1964) and Hafez et al. (1969) record interference as occurring when a number of ewes compete for the attention of the ram. Banks (1964) conducted his study in small breeding pens and noted under these conditions, competition for the ram among oestrous ewes was intense and therefore the frequency of interference was high. He found in these circumstances it was the dominant ewes that interferred more than the subordinate ones. Under the paddock mating conditions observed in this study, the detection and analysis of any hierarchial structure among the ewes would have been exceedingly difficult because of the low frequency of interactions between the ewes that would establish (for the observer) the existence of a dominance hierarchy and the large number of ewes involved. Therefore a similar observation relating frequency of interference and dominance status can not be made.

Interference is more common in sexually experienced ewes than in maiden ewes (this study). This may be a result of the dominance effect discovered by Banks (1964).

Interference appears at the peak of the ewe's oestrous period, though not necessarily in all ewes. By its very nature it is an intense sexual act and indicates a high sexual 'motivation' (tendency to act sexually - Hinde, 1970) in the ewe performing the interference. Some acts

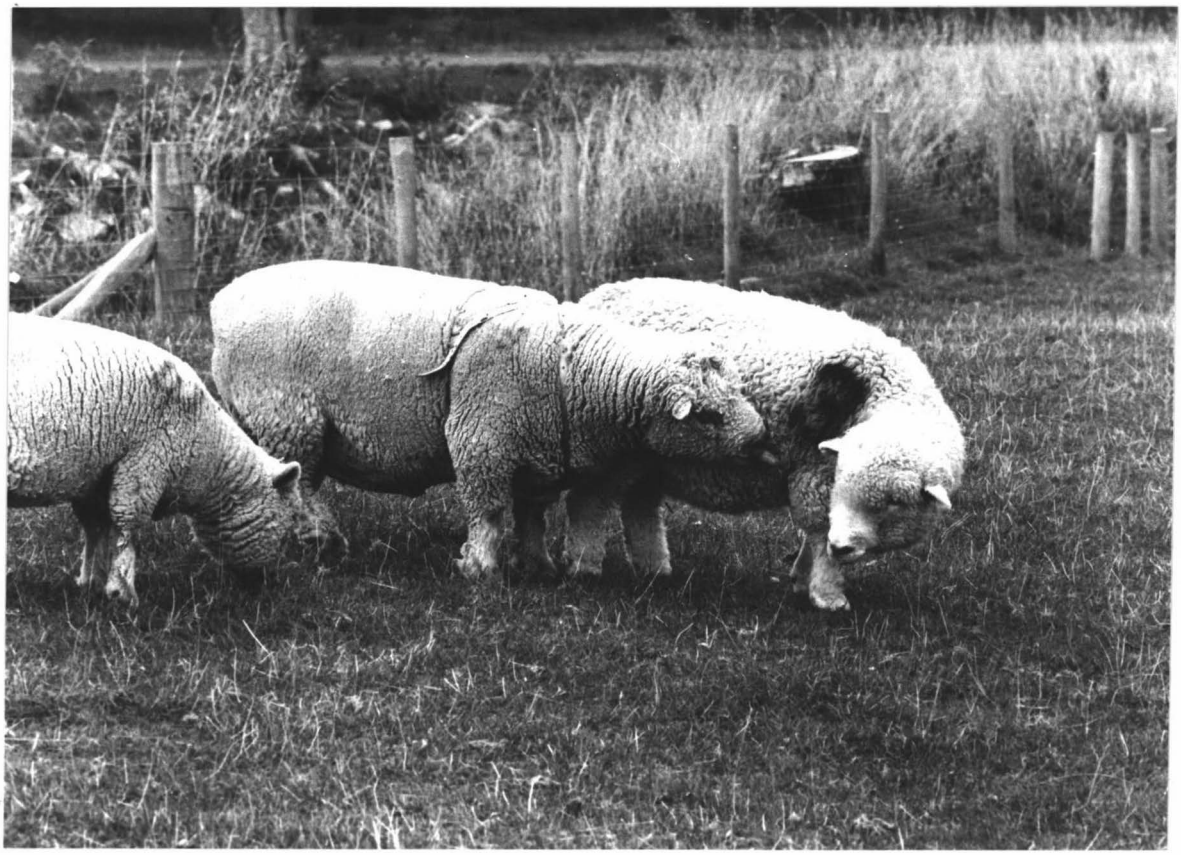

PLATE 21

Ewe Looks Back at Ram Displaying in Twist.

PLATE 22

Ewe Interferes by Insinuating herself between the Ram and Ewe 15.

used for interference are more overtly intense than others. For example, butting a mounted ram is more intense than tail fanning at a ram courting another ewe. An interfering ewe usually employs at least several of the sexual behaviour patterns in her repertoire in an interaction involving interference. Possibly the only other female behaviour pattern that would be more sexually active than the acts used to interfere is the mounting of the ram, which, as mentioned above, is fairly rare.

Interference was not seen in anoestrous ewes, nor in subordinate males. Banks (1964) found that it occurred only when ewes were in oestrus, and that if ewes were exhibiting only low intensity sexual behaviour patterns (i.e. sniffing, looking back) they rarely attempted to interfere in the courtship of the ram and another ewe.

Standing, Lordosis and Pushing (see Plate 23)

The three behaviour patterns termed 'standing, lordosis and pushing' are separate sexual display acts, each appearing to require different levels of sexual motivation.

Both females and subordinate males will stand for a ram. A female need not be in an oestrous state to stand, but generally an anoestrous ewe stands only for a short time before moving away to avoid any further advances from the ram. Most ewes assume the standing stance when a ram sniffs or begins to court them. The ewe may respond further by; moving away, urinating, by looking back or as is normal in the case of oestrous ewes, by standing for further courtship and mounting.

Standing for investigation by the ram is widespread, irrespective of oestrous condition, but standing for courtship is a characteristic of oestrus, appearing in the first few hours of oestrus and remaining for almost the duration of oestrus. A ewe will only stand for vigorous courtship and mounting about the middle (for a period of 6-10 hours, 5-6 hours after the onset of oestrus) of her oestrous period. At this stage a second phase of the standing display appears, called the 'mating stance' (Hafez, 1962) or the 'lordosis response' as it is more commonly known.

For lordosis the ewe spreads her hind legs slightly and lowers her pelvis by arching the back. Lordosis both signals the ewe's receptivity to mounting to the ram and also aids the ram in intromission. Not all ewes display lordosis. The response may be an acquired one (though it isn't in rats) for it seemed to be lacking in a large proportion of the maiden two-tooth (sexually inexperienced) ewes observed. Subordinate males have

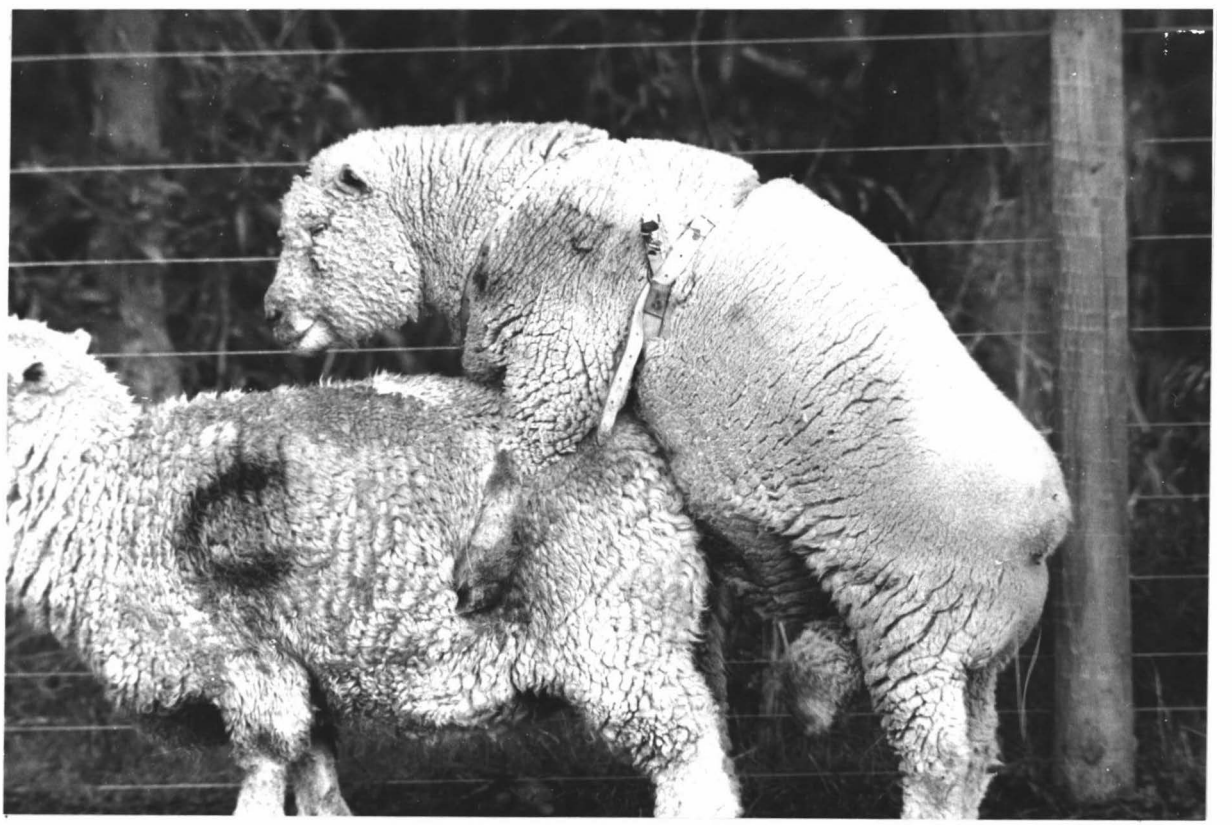

PLATE 23

Ram Mounted on Ewe Exhibiting Lordosis Response. Note Arching of Ewe's Back.

been seen to assume this posture when mounted by other rams, and Geist (1971) mentions it as being common in subordinate males in the species he observed.

The behaviour pattern called 'pushing' was not common to all ewes in the study group. Geist (1971) mentions having observed an interaction between a male and female Stone's sheep (O. dalli stonei) in which it occurred but does not indicate how common it was. Banks (1964), Hafez (1962) and Hafez et al. (1969) do not mention the behaviour.

Pushing appeared only in ewes that were in mid-oestrus and were being courted by the ram, and usually only when the ram was slow to mount after the ewe had assumed the mating stance. A ewe might then step backwards and press her rump against the chest of the ram, making pushing and wriggling movements with her rump before assuming the mating stance again. The usual response of the ram to this behaviour was to mount the ewe, but if he failed to do so the ewe usually repeated the pushing display.

Lordosis and pushing appear to be variations of the standing display but seemed to require higher sexual motivational states than standing does.

All three behaviours are accompanied by pinnae movements, usually they are depressed and flattened against the head. During mounting and tupping the ram also makes a number of pinnae movements. Although pinnae movements weren't quantified, they seemed to follow a consistent pattern. The movements probably have a communicatory function.

Hafez (1962) mentions that some female farm mammals may experience an 'orgasm-like' response to mating. An 'orgasm-like' response was not detected in the ewes in this study, but post-coital behaviour similar to that exhibited by rams (standing with lowered head, or lying down) was often observed.

Wheeling

The wheeling display was often exhibited by oestrous ewes in response to investigation or courtship by a ram. It is performed when a ram orients itself behind a ewe to sniff, court or mount the ewe. The ewe responds (sometimes) by turning herself about and orienting behind the ram so that she can sniff or nuzzle his scrotal area. The behaviour is often repeated several times as the ram attempts to re-orient itself for courtship or mating. The result is a circling movement of the two animals and it appears to excite the ram and "to bring about an enhancement of the ram's attempts to mount", Banks (1964).

Geist (1971) does not state if 'wheeling' occurred in the species

he examined, but he does describe a similar type of activity. In this behaviour pattern the ewe runs or bounds away from the courting ram only to turn and rush back towards it. The behaviour is repeated. It is possible that wheeling is derived from this pattern, or that they have a common origin, for both behaviours are reciprocating and both appear to have the same result — that of heightened excitement in the ram.

For some time it was not clear if wheeling was indeed a sexual display because it was also employed by anoestrous ewes and subordinate males wishing to escape the attentions of the ram. In such cases the ewe or subordinate male usually terminated the interaction by running away, so in encounters where the wheeling behaviour was combined with elements of escape behaviour, it was not recorded as a sexual display.

Supplementary Behaviour Patterns

Five other sheep behaviour patterns (other than courtship displays) were recorded so that the analysis of displays could be examined as a behavioural continuum and not as courtship display in vacuo. These behaviour patterns were mainly those associated with movement or maintenance and were the patterns most frequently interspersed with the courtship behaviour.

Feeding. 'Normal' feeding behaviour was the most frequently indulged in behaviour pattern once an interaction involving courtship had been terminated. The qualification 'normal' was made because a second type of feeding was observed during courtship. It was very brief and was usually performed by the ram. It involved ingestion of grass on some occasions but appeared out of context and therefore was probably a type of displacement activity. Geist (1971) also mentions an instance of out-of-context feeding, again in a situation that could have involved conflict (see Plate 24).

Resting. Quite often a ewe or ram would lie down at the end of a bout of sexual activity, or would move to a 'camping' area to lie down. Often when a ram lies down the ewes in the harem follow suit, actually lying against each other in a small group.

Butt. Most butting is performed by the ram but occasionally a ewe will turn and butt the ram if he is persisting in courting her. The ram may butt ewes when they solicit attention when he is feeding, courting another ewe or after he has just served the soliciting ewe. In some wild sheep, butting is part of the courtship display (Geist,1971), but in the sheep observed butting tended to disrupt the 'coupling' process between the ram and ewe and so was considered an aggressive act.

The butt is usually delivered with the head but may be modified to a shove with the chest. A ram may display in a low stretch before butting a ewe.

Paws. (see Plate 25)

The motor act called 'pawing' is performed by both ewes and rams. The ram often uses the behaviour to induce a resting (lying down) ewe to stand up so that he can investigate and/or court her.

To paw, the sheep lifts a fore leg and sweeps it down and back in a scooping motion. It is usually used to scratch a bedding place but may also be used by ewes and rams to distrub other sheep lying down so that they might usurp the other's sleeping place. The pawing motion is repeated in bouts of three to ten movements at a time.

Moves Away.

Most courtship interactions finish with one or both of the animals moving to another vicinity. Moving away is a fairly passive activity and denotes lack, or end of, interest. It was distinguished from more active departures termed 'avoidance' that involved a quick change in locality, usually by an anoestrous ewe wishing to escape the attentions of the ram. Coupled with these behaviours were following and chasing behaviours, both self-explanatory, with following being more passive than actual chasing.

Moving away and avoidance, and following and chasing were only arbitary distinctions, with the discrimination based on the pace at which the activity occurred.

The motor acts described in the sections above were recorded on prepared sheets during the observations conducted on a breeding flock in 1973 (plus preliminary work in 1972). The remainder of the thesis considers the relationships between these patterns, their possible functions and their importance in the sexual behaviour of sheep.

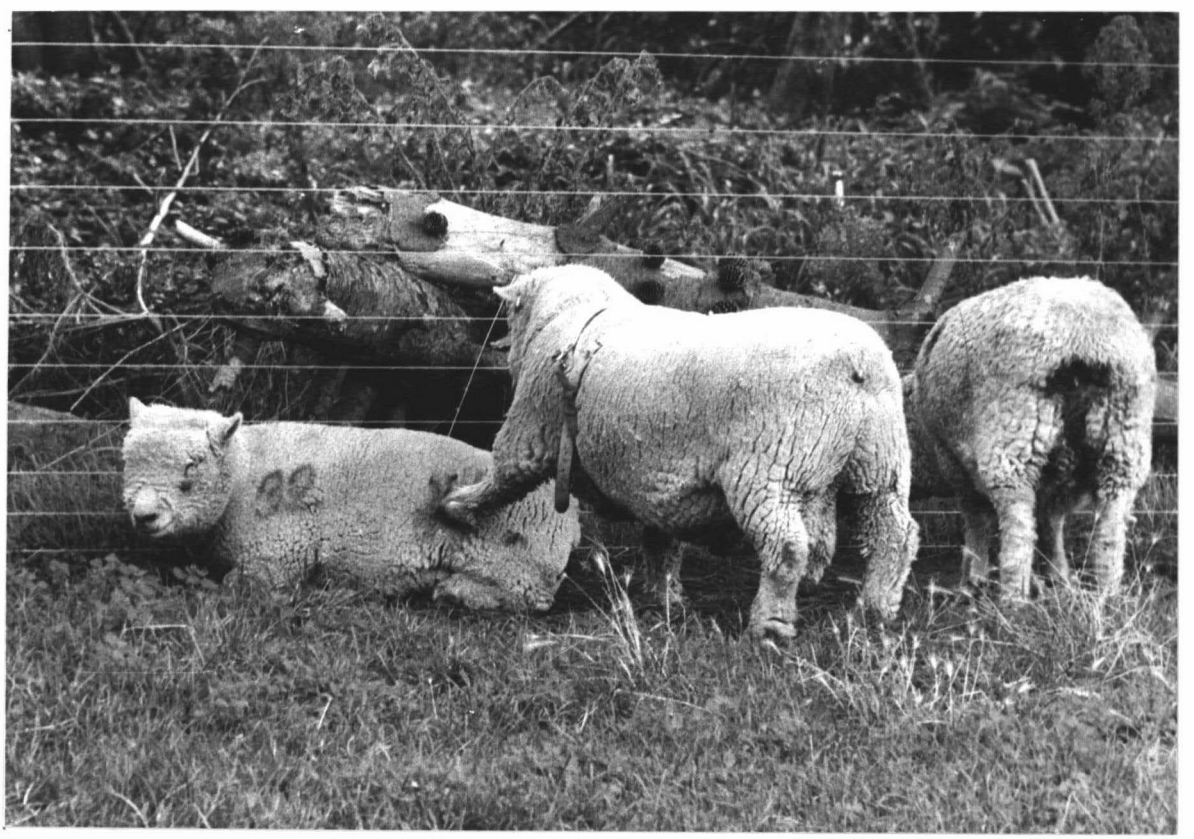

PLATE 24

'Displacement' Feeding in the Ram.

PLATE 25

Ram Pawing at Ewe Lying Down.

CHAPTER III

NOTES ON SEXUAL BEHAVIOUR

A. Courtship Behaviour Sequences

To understand the courtship behaviour of sheep it is necessary to consider the requirements imposed on sheep behaviour by the reproductive cycle of the ewe (a seasonally polyoestrous species), the social structure of sheep in the wild state and the modifications to this structure caused by domestication and husbandry methods.

In New Zealand the non-pregnant domestic ewe undergoes cyclical ovarian activity with ovulation occurring at intervals of 15-19 days, during a breeding season that typically begins in February-March and ends in July-August. The duration of sexual receptivity (oestrus or heat), during which the ewe displays oestrous behaviour patterns, is variable. Ranges of 3-84 hours have been reported both between and within breeds (Robinson,1959), though generally speaking ewes can be expected to exhibit oestrus for 16-36 hours. The ewe's reaction pattern to a ram varies within this time. The early stages of oestrus are characterised by an interest in the ram, with the display of low intensity courtship (looking back, following and sniffing) but a refusal to stand for the ram's courtship. A middle period follows of up to 20 hours duration in which the ewe is in a very receptive condition and exhibits high intensity courtship behaviour patterns (tail fanning, lordosis, pushing, interference). This is followed by a third period in which her sexual responsiveness declines. During the anoestrous phase of the cycle the ewe displays little interest in the ram and will actively avoid the advances of a courting male.

In the wild state[9] sheep form two social groupings. One group contains mature males, and the other group, females and juveniles of both sex. Dominance hierarchies are established within these groups and outside the group so that mature males dominate females and juveniles. Male dominance is established on the basis of age, size of horns and fighting prowess (Geist,1971), whereas, within the female-juvenile group it is usually based on age.

In the wild state a ewe entering oestrus is courted by the most dominant male available, who at the same time has to keep other males at

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9 Data is for North American species, but similar habits are common to European species also.

bay. The courting male must endeavour to hold the ewe's interest without frightening her away. A ram that courts vigorously and scares an oestrous ewe away is selecting against himself because the chances are that other rams waiting in the vicinity will join in the chase and one of them might serve her. Also a ram courting quietly may not attract other competing males or predators. A second selection pressure is present, selecting for a brief service, for two reasons. The first reason is that mounted animals are particularly vunerable to predators (Ewer,1968) and the second is that with competition from other rams, quick service by a ram is called for and any hesitation or protracted copulation is strongly selected against (Geist,1971).

In the domestic situation several of these factors have been reversed. The ratio of oestrous ewes to rams is inverted so that the oestrous ewes now have to compete for the attention of the ram and also the ram may no longer be faced with competition from other rams. Also, to some degree, the natural selection pressure (predators and ram competition) for brevity in copulation is replaced by an artificial selection pressure for a ram to hasten courtship and copulation because he now has large numbers of ewes to attend to. There will no longer be such a strong selection pressure for quiet, gentle courtships, and, it might be added, probably no longer a strong selection pressure for precise, accurately executed courtship as exists in the wold state.[10] An artifical selection pressure for successful courtship behaviour exists only indirectly as a selection for fertility in domesticated rams and ewes.

Within the framework imposed by the social structure of the flock and the husbandry practices of a domestic situation the ram and ewe react in a fairly predictable pattern. For example, the following behaviour patterns can be expected of sheep in a typical domestic breeding situation involving a ram and a number of anoestrous and oestrous ewes.

To contend with this situation the ram must first select from the group of ewes, those ewes requiring service (the oestrous ewes) and ignore those not (the anoestrous ewes). Therefore the ram's first behaviour patterns are likely to be investigatory behaviour patterns involving sniffing

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[10] During the observations for this study it was noticed that the behaviour patterns described and photographed by Geist (1971) as occuring in wild sheep, also exist in the domestic breeds observed but often in a modified or "toned down" form.

and nussling behaviour,[11] as he attempts to sort oestrous from anoestrous ewes. Having found the oestrous ewes the ram must then determine their exact state, whether they are receptive, becoming receptive or in the closing stages of oestrus and no longer receptive to the ram. To do so he can judge their state on the basis of their behaviour, by their reaction to his behaviour or by olfactory cues.[12]

Having established the state of the ewes in his flock the ram must serve the most receptive ewes, then attend to those that are becoming receptive. Because other ewes will be coming into heat, the ram must be in a condition to serve them and so it is adaptive if a ram does not expend itself on only a few oestrous ewes with repeated matings. Hence rams display a greater interest in ewes freshly in oestrus than those that are still in the receptive stages of oestrus but whom he has already tupped.

The general pattern of the ram's behaviour then, will be, investigation of ewes, courtship of ewes freshly in oestrus until they are served, and then seeking of further 'fresh' oestrous ewes. Oestrous ewes that have been served tend to follow a ram for some time and a ram may return to service these followers, usually when fresh oestrous ewes can not be found. However, as mentioned above, it is adaptive if a ram does not waste too much time and energy in repeated matings with these ewes. It is also highly adaptive that a ram be able to 'remember' the identity and state of the ewes in his flock so that he does not need to keep rechecking the condition of each ewe. Observations indicate that the ram can recognise ewes in the flock by sight and smell so there is probably an association of the recognised ewe with a 'remembered' oestrous state.

This then is a simplified, hypothetical pattern of the ram's activity in a breeding flock. These generalised patterns can be shown to exist by an examination of interactions (contacts between the ram and ewe involving sexual and social behaviour patterns) that occurred between the

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[11] It is recognised that olfaction plays a major part in the determination of a ewe's oestrous state. (Bruce,1967; Lindsay,1965).

[12] It is believed that the olfactory powers of rams are able to discriminate to this extent. There would most certainly be a selection pressure for such a mechanism so it would be highly adaptive for a ram to possess such powers. There is evidence to suggest that this might be the role of the Flehmen (see Chapter Three, Section B).

ram and ewes in one of three different oestrous states. The states chosen were; fresh oestrus, late oestrus after a ewe had been tupped at least once, and anoestrus, and 100 interactions chosen at random were considered in each case.

Because the large number of behaviour patterns recorded would have become unwieldy during analysis, calculation was simplified by grouping all recorded sexual behaviour patterns into one of five types of behaviours. These five designated types of 'behaviours' were:

1) Sniffing (Sn.) into which all sniffing, licking and nuzzling behaviour was grouped,
2) Flehmen (Fl.) into which behaviour associated with the urination response and Flehmen was grouped,
3) General Courtship (GC.) All other behaviours that reduce individual distance in the sexual context and induce the ewe to stand and receive service,
4) Mounting (Mt.) which held attempted mounts, chinning, false mounts and true mounts that didn't result in service,
5) Tupping (Tp.) which included the service as well as the orgasm response and quiescent postcoital period.

Interactions were then classified on the basis of what 'behaviour' occurred within them. There were twenty-three possible combinations of the five 'behaviours' (Tupping and Mounting being linked), so there were twenty-three categories in which an interaction could be scored. A further distinction made on the basis of the sex that initiated the interaction between the ram and ewe resulted in there being forty-six categories into which an interaction could be classified.

Table I shows the scores of 300 interactions that occurred between the rams and ewes in one of three oestrous conditions, fresh oestrus, late oestrus and anoestrus.

There are a number of patterns in the data in Table I that conform with the generalised outline of a ram's behaviour toward oestrous and anoestrous ewes as given above. For instance, as a ewe's oestrous condition progresses she becomes less attractive to the ram. This is evidenced by the decline in Tuppings and Mountings between fresh oestrous ewes (column A) and the ram (19 and 10 respectively) and ewes late in oestrus but still receptive (column B) and the ram (12 and 2 respectively). However, a greater proportion of the mountings are successful in the second group, showing the ewes' increased receptivity and experience with the ram.

A second indication of the ram's loss of interest with oestrous ewes he has already tupped is the increase in ewe initiation of interactions with the ram. The recently tupped ewes (column B) show a greater rate of initiation of interactions (72%) than do the ewes fresh in oestrus (column A), (48%), establishing that they remain receptive to the ram, enthusiastic in fact, but that they now have to compete with other more attractive ewes - the ones becoming receptive. This increase in competition among the tupped ewes of column B is shown by the category in their column (B-females) having the highest number of interactions - the courtship category composed mainly of behaviour patterns such as rubbing and butting used as interference.

Investigation, in the form of sniffing behaviours appears to increase between the fresh oestrous ewes (column A-7 instances) and the tupped, late oestrous ewes (column B-14 increases), thereby refuting the suggestion that the ram remembers individual ewes and their oestrous state. However a great deal of investigatory activity that occurred between the ram and fresh oestrous ewes led on to higher categories of interaction, involving General Courtship, Mounting and Tupping whereas in the ewes that were still receptive but had been tupped, the likelihood of any investigation going further was less because of the ewes' declining attraction for the ram. Therefore if all interaction categories involving investigation (Sniffing behaviours) are compared for the two groups of oestrous ewes it is found that 70% of all interactions involved or included Sniffing behaviours in fresh oestrous ewes and only 44% involved or included Sniffing behaviours in the late oestrous, tupped ewes, the drop in investigative behaviour being due to the ram's use of remembered information about the ewes he had already served.

Interactions between the ram and anoestrous ewes are mainly confined to investigatory behaviour and a small amount of General Courtship, with no Mounting and therefore no Tupping. Two notable features of these interactions is the proportion of interactions initiated by the ram - 98%, indicating very low ewe interest in the ram - and the large number of interactions in which the urination response and Flehmen occurred (42% in anoestrous ewes as opposed to 11% in fresh oestrous ewes and 9% in tupped late oestrous ewes interactions with the ram), reinforcing the thought that the Flehmen is a type of investigatory activity.

Figures 1,2 and 3 express diagrammatically the general sequence of behaviour patterns between a ram and oestrous and anoestrous ewes. Forty

TABLE I. Composition of Interactions between the Ram and Ewes in one of three Oestrous States; 'Fresh' Oestrous, 'Late' Oestrous and Anoestrous, and the Sex Initiating the Interactions.

BEHAVIOURS IN THE INTERACTION					COLUMN A		COLUMN B		COLUMN C	
					Ram and 'Fresh' Oestrous Ewes		Ram and 'Late' Oestrous Ewes		Ram and An– Oestrous Ewes	
					INITIATED BY		INITIATED BY		INITIATED BY	
SN	FL	GC	MT	TP	Ram	Ewe	Ram	Ewe	Ram	Ewe
SN					4	13	4	10	44	1
	FL								1	
		GC			6	5	4	47		1
			MT							
			MT	TP						
SN	FL							1	24	
SN		GC			19	18	9	8	12	
SN			MT							
SN			MT	TP						
	FL	GC			2	3	1		1	
	FL		MT							
	FL		MT	TP						
		GC	MT		1					
		GC	MT	TP	3		1	1		
SN	FL	GC			1		1	1	16	
SN	FL		MT							
SN	FL		MT	TP						
SN		GC	MT		2	4	1	1		
SN		GC	MT	TP	9	5	3	2		
	FL	GC	MT							
	FL	GC	MT	TP			2			
SN	FL	GC	MT		3					
SN	FL	GC	MT	TP	2		2	1		
					52	48	28	72	98	2

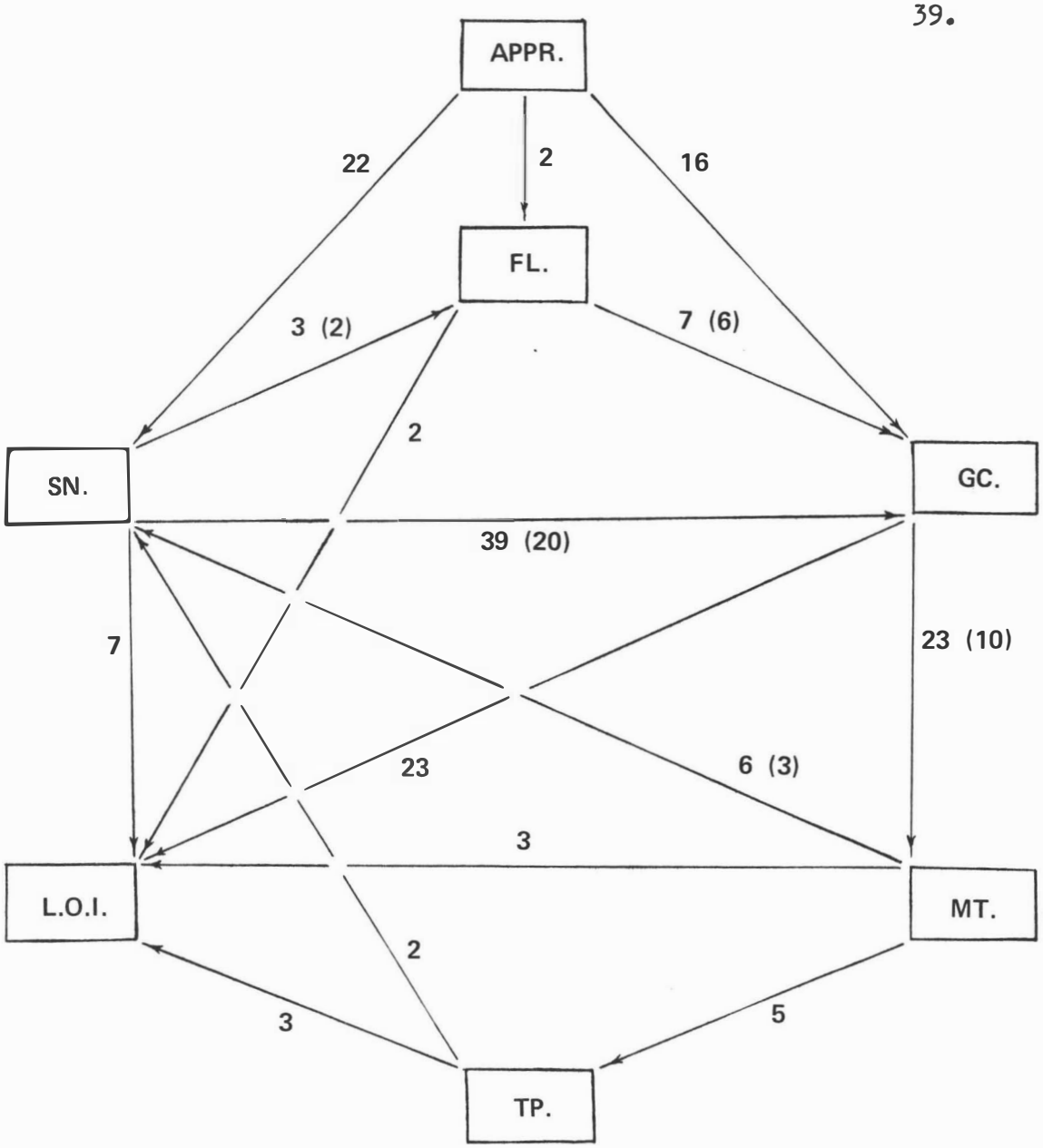

FIG. 1 COURTSHIP BEHAVIOUR SEQUENCES IN INTERACTIONS BETWEEN THE RAM AND 'FRESH' OESTROUS EWES.

APPR.	—	approach.
SN.	—	sniffing behaviours.
FL.	—	Flehmen behaviours.
GC.	—	general courtship behaviours.
MT.	—	mounting behaviours.
TP.	—	tupping behaviours.
L.O.I.	—	loss of interest.
10	—	frequencies in the direction of the arrow.
(4)	—	frequencies in the opposite direction.

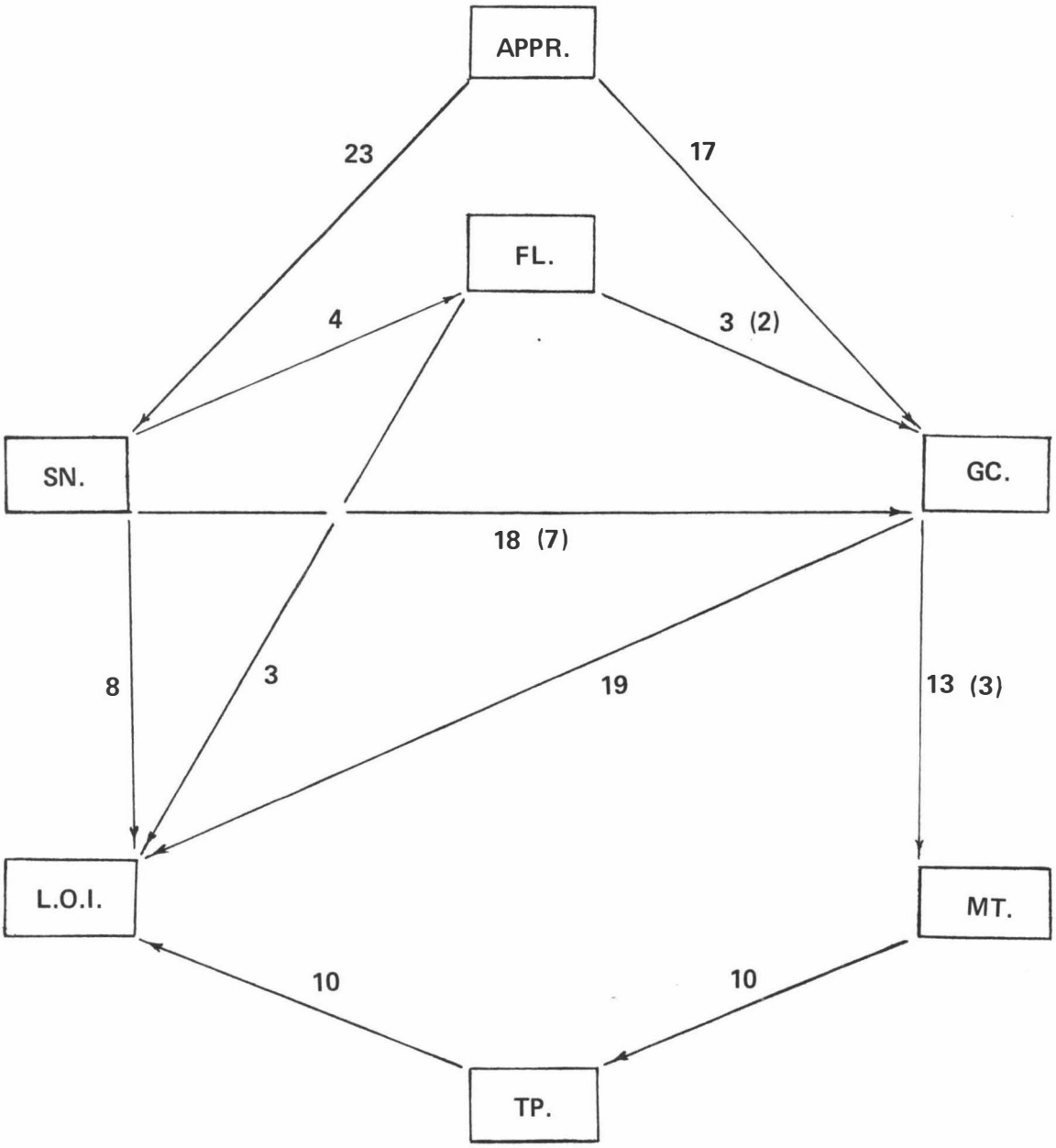

FIG. 2 COURTSHIP BEHAVIOUR SEQUENCES IN INTERACTIONS BETWEEN THE RAM AND 'LATE' OESTROUS EWES.

APPR.	—	approach.
SN.	—	sniffing behaviours.
FL.	—	Flehmen behaviours.
GC.	—	general courtship behaviours.
MT.	—	mounting behaviours.
TP.	—	tupping behaviours.
L.O.I.	—	loss of interest.
10	—	frequencies in the direction of the arrow.
(4)	—	frequencies in the opposite direction.

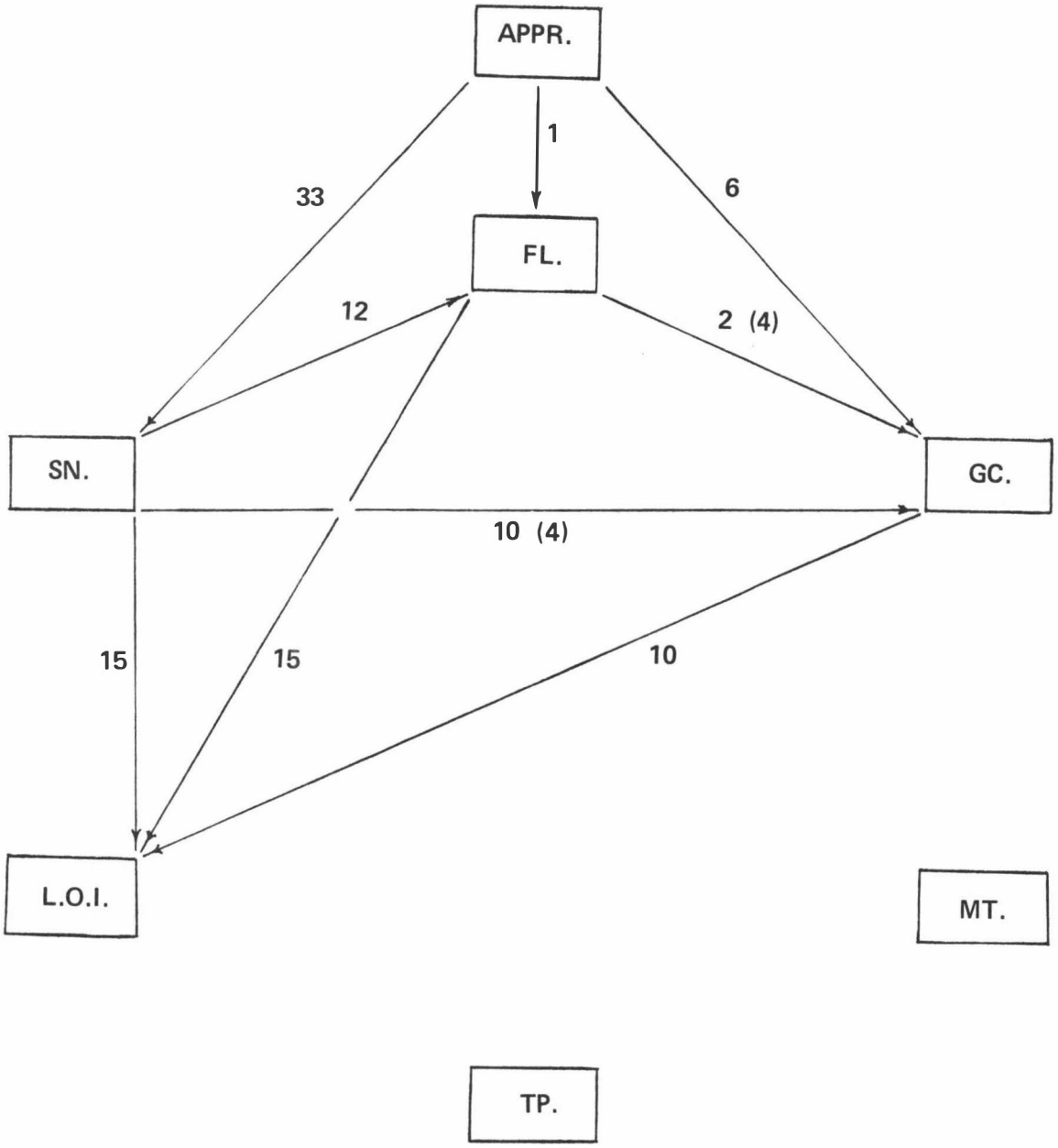

FIG. 3 COURTSHIP BEHAVIOUR SEQUENCES IN INTERACTIONS BETWEEN THE RAM AND ANOESTROUS EWES.

APPR.	—	approach.
SN.	—	sniffing behaviours.
FL.	—	Flehmen behaviours.
GC.	—	general courtship behaviours.
MT.	—	mounting behaviours.
TP.	—	tupping behaviours.
L.O.I.	—	loss of interest.
10	—	frequencies in the direction of the arrow.
(4)	—	frequencies in the opposite direction.

interactions each, between the ram and fresh and late oestrous ewes and anoestrous ewes were analysed. The numbers indicate the frequency of sequences of behaviours proceeding in the direction of the arrow while the numbers in parentheses indicate frequencies in the reverse direction to the arrow. The coding is the same as that used for 'behaviours' (see above).

The above account is a simplistic approach to a complex situation. There are many variations to the general pattern described because sheep, and rams in particular, tend to be very individual in their performance of behaviour patterns. However, the account is useful for it describes the usual course of events and in so doing, indicates the functional utility of some of the behaviour patterns.

B. The Flehmen and Urination Response

The urination response is being examined in conjunction with the Flehmen because an obvious relationship exists between the two behaviours in the courtship situation.

One of the most common behaviour patterns that occurs in interactions between a ram and an anoestrous ewe involves a brief bout of investigational and courtship behaviour followed by a performance of the urination response by the ewe and the sniffing of the urine and Flehmen by the ram. The usual outcome of an interaction in which a Flehmen occurs is that the ram then moves away from the anoestrous ewe, leaving her alone. Geist (1971) mentions this sequence of behaviour and notes that it may also occur when a dominant ram interacts with a subordinate ram. He concluded from his observations of this behaviour,"it appears that sheep urinate to the dominant, who upon lip curling (Flehmen), for some reason, leaves them in peace". It was apparent, from observations made during 1972, and from Geist's (1971) observation, that there may be an element of appeasement behaviour in the urination response - Flehmen behaviour sequence.

During this study, the possibility of an appeasement function for the urination response and Flehmen was investigated. As the urination response occurred in another context as well (an aggressive one), it was examined there also. The aggressive context urination response commonly

occurs after a clash involving females. A clash[13] (see Plate 26) is an instance of head-to-head butting between two sheep. Butting may also occur between sheep when one or more sheep butt the flank of another. The outcome of head-to-head clashes only were recorded, for only in these instances of aggression was it possible to determine which ewe withdrew from the clash. The withdrawing ewe was assumed to be the subordinate ewe. It was found that of the clashes observed (N=37), it was possible to determine which ewe had withdrawn (subordinate) from the clash interaction in 95% of the cases (n=35). It was also found that 77% (n=27) of the withdrawing ewes urinated to the other ewe (the dominant) before moving away or resuming their preclash behaviour. (In one instance the ewe that didn't withdraw urinated as well as the one that withdrew).

It was felt then, that the urination response was an appeasement behaviour, or at least appeared to be so when it occurred in aggressive situations. Whether it has a similar function in the courtship context though is debatable. The aggressive interaction urination responses were not followed by a Flehmen (except in one instance) though they invariably are in the courtship interactions, so although urination confers some benefit upon an anoestrous ewe when courted by the ram, and although the urination response does appear to be an appeasement behaviour in aggressive interactions, the appeasement behaviour explanation is not satisfactory in describing the function of the urination response and associated Flehmen in courtship interactions.

One theory that does give a satisfactory explanation for the urination response - Flehmen sequence, and for which there is a good deal of evidence - albeit circumstantial - is put forward by Knappe (1964).

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[13] Clashes between ewes are not common. They usually occur during feeding, during competition for the ram or in altercations over sleeping positions. The number of clashes were artificially increased to give further data for this aspect of the study by placing small mounds of table salt about the paddock. The salt attracted the ewes and brought them into close contact with one another and this resulted in an increase in the frequency of clashes between the ewes.

PLATE 26

Ewes Clashing

Knappe (1964) suggested that the Flehmen[14] was associated with stimulation or activation of the Jacobson's organ.[15] He envisaged that substances exist in the urine of some female mammals that are capable of indicating to the males of the species, the oestrous state of the female. These substances with a pheromonal function Knappe (1964) saw as being either hormone metabolites or vaginal secretions. It was thought that the male detects these substances with the vomeronasal organ and that the Flehmen was involved in the conveyance of these pheromonal substances to the vomeronasal organ.

There is a reasonable amount of circumstantial evidence in favour of Knappe's (1964) suggested function of the vomeronasal organ and the Flehmen. Some of this evidence is inclusive of all species exhibiting Flehmen while other evidence is restricted to a few species only or sheep in particular.

Before discussing evidence it could be stated that there is a definite need for male animals to 'know' the oestrous state of the females of their species. There are many ways in which a male can come to achieve this 'knowledge', such as by observing the overt behaviour of the female or her reaction to the behaviour of the male, but a mechanism that is capable of acute detection of very subtle changes of sexual state would be of great value, so there is both a potential need and use for such a mechanism.

The following findings are presented in support of Knappe's (1964) suggested function for the vomeronasal organ and the Flehmen.

Tucker (1963) established, by simultaneous recording from olfactory and vomeronasal nerve twigs, that some substances were consistently more

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[14] His theory is not restricted to sheep but is inclusive of all animals exhibiting Flehmen. Verberne (1970) found that all mammal species capable of performing Flehmen still have a functional Jacobson's organ.

[15] The Jacobson's (vomeronasal) organ is a small paired structure usually situated on the median septum of the nose. It is a blind sac with one end open to the nasal cavity, usually via the nasopalatine duct that joins the buccal and nasal cavity in most mammals. Moncrief (1967) suggests the function of the vomeronasal organ is as a subsidiary olfactory organ, while Tucker (1971) concedes, "The vomeronasal system is of unknown function but morphologically it is parallel or accessory to the olfactory system". There are a number of theories for the possible function of the vomeronasal organ, but that of Knappe (1964) appears to have gained most acceptance.

effective for olfactory receptors and others were more effective for vomeronasal receptors. He found that the vomeronasal receptors (in the gopher tortoise Gopherus polyphemus) respond better to the lower molecular weight fatty acids while the olfactory receptors respond better to the longer chain acids. Similar results hold for the aliphatic alcohols. Here then is evidence that the vomeronasal organ is capable of responding to odiferous substances, and that there are discriminatory responses between the olfactory sense and the vomeronasal sensing apparatus.

Ewer (1968) takes Tucker's (1963) finding a step further. He found that a pet male meer cat (Suricata suricatta Erxleben) would regularly flehm in response to the smell of sherry. This draws the connection between the detection of lower aliphatic alcohols (ethanol in sherry) by the vomeronasal organ and the Flehmen response to this vomeronasal detected substance.

Further evidence is supplied by Poduschka and Firbas (1968; cited by Eisenberg and Kleiman,1972) who deomonstrated in the hedgehog (Erinaceus europaeus)"that licking a substance, lifting the nose, opening the mouth and salivating (i.e.Flehmen) stimulated the vomeronasal organ" since the tongue tip was actually pushed up to the dorsal opening of the nasopalatine canal in the buccal cavity, thus transferring potentially odiferous substances in solution to the vomeronasal organ via the nasopalatine canal (duct).

Bruce (1967) acknowledged that sexual recognition is a function of the olfactory system in mammals, and Lindsay (1965) established that the sense of smell of rams played a significant role in the selection of oestrous from anoestrous animals. However neither authors distinguished between olfactory sensing and vomeronasal sensing. Micheal and Keverne (1968) did manage to conduct studies that separated the two sensory modalities and found that the olfactory and not the vomeronasal apparatus was responsible for the detection of a hormone dependent, olfactorily acting pheromone, possibly of vaginal origin, in Rhesus (Macaca mulatta) monkeys. However, this can not be used as contrary evidence to the suggestion of Knappe (1964) because Micheal and Keverne (1968) did not establish whether or not Rhesus monkeys performed the Flehmen, or if

their vomeronasal organ is still functional.[16] It is no longer functional in man and this may well be the case for other primates also.

An examination of a sheep's head (Plate 27) was made for this study to see if any further association could be drawn between the Flehmen and vomeronasal organ stimulation. It was found that light pressure on the upper palate and curling the upper lip caused the incisive papillae in the buccal cavity to open, thus enlarging the entry to the nasopalatine duct from which the vomeronasal organ extends (see Plates 28 and 29). Such movement was highly artifical but the dental pad and palate is relatively pliable and it only requires a small movement and little pressure, as would probably occur during Flehmen, to open the ductus incisivus.

A second finding was that where the nasopalatine duct opened into the nasal cavity, it was in a forward sloping (toward the nostril) trough that contained a small projection forward of the opening of the nasopalatine duct in the nasal cavity (see Plates 30 and 31). One effect of this projection would be to impede the flow of mucus from the nostril causing some to pool over the nasopalatine duct. To clear this mucus so that air could enter and flow through the nasopalatine duct, a ram would have to lift his head and/or sniff back through the nose. Both actions occur during Flehmen in the ram, as well as tongue movements and a forced type of panting through the mouth. (All these activities that occur during Flehmen would aid the passage of air and odiferous substances through the nasopalatine duct and thereby into the vomeronasal organ).

The evidence presented in support of Knappe's (1964) suggestion

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[16] Van Hooff (1967) described a 'Flehmen like' behaviour termed 'protuded-lips face' he observed in Macaca nemestrina, M.silenus and once in M.mulatta.

He first called the display 'the flehmen face' but because this presupposed a homology of which he was not certain, he changed the name to the purely descriptive one of 'protuded-lips face'. He also conceded a similar puckering of the face occurs in humans when sniffing intently. As humans do not have a functional vomeronasal organ the protuded-lips face described by Van Hooff (1967) may have no relationship to true Flehmen though quite conceivably could have been derived from it. It can not then be used as counter evidence to Knappe's (1964) suggested function for the vomeronasal organ and Flehmen.

PLATE 27

Sheep's Head Showing Portion of Nose Removed for Examination of Nasopalatine Duct.

PLATE 28

Incisive Papillae (arrow) on Upper Palate

PLATE 29

Incisive Papillae Opened by Bending
the Upper Palate

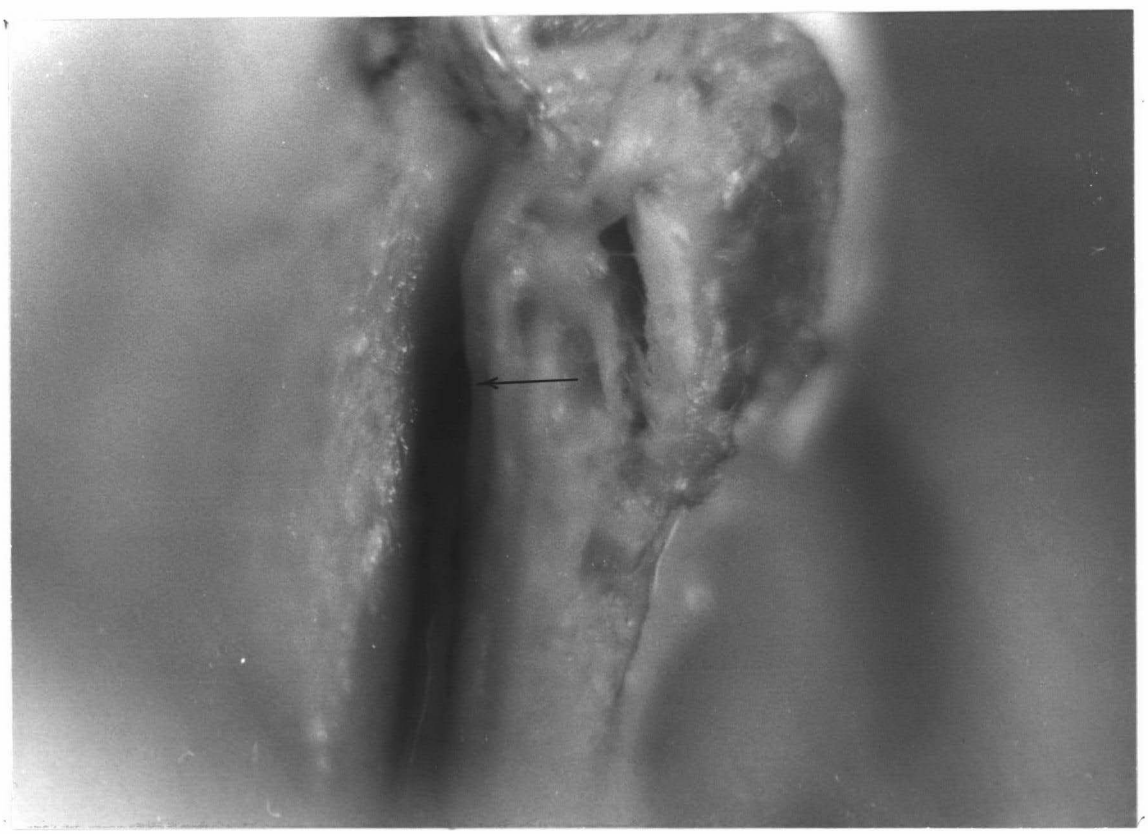

PLATE 30

View from above of Trough in Nasal Cavity.

PLATE 31

View of Trough in Nasal Cavity Showing Opening to Nasopalatine Duct (arrow) and Projection.

is circumstantial or inferrential. However, in association it presents a fairly strong case for vomeronasal organ sensory activity aided by physical actions evoked by the Flehmen posture.

Further evidence in support of Knappe's (1964) suggestion comes from the application of the implied function to the behaviour observed in the field. In the observations for this study it was found that little notice was taken of a ram performing the Flehmen by ewes or other rams. From this observation it was inferred that the Flehmen had little, if any, signal function to sheep other than the one performing the Flehmen. The Flehmen is however, performed quite frequently by some rams and rams often go to a great deal of trouble to induce a ewe to urinate for them. The time and energy spent by rams in the pursuit of the urination response and Flehmen behaviour sequence indicated that it was important.

One aspect of courtship that is important at the stage of interaction that the Flehmen seems to occur most frequently in, is the detection of oestrous ewes, so it is not unreasonable to link this behaviour with the investigation and discrimination of oestrous and anoestrous ewes.

If behavioural interactions are examined it is found that there is a close correlation between suggested function and observed activity. For example, most Flehmens occur in interactions between the ram and anoestrous ewes - the ones the ram is trying to determine the oestrous state of. If vomeronasal sensing is his most acute and reliable means of sensing the oestrous state, it is not unexpected that the ram use this on the anoestrous ewes for a final determination of what his other senses may have indicated, or failed to indicate. There is little need to flehm with oestrous ewes for the ram is already aware of their state (usually), so it should not be unexpected to find that the urination response and Flehmen is not all that common in oestrous ewe - ram interactions. A similar finding was made by Geist (1971).

Geist's (1971) observation that there appears to be some benefit in an anoestrous ewe urinating for the ram is now understandable. If a ram is unsure of the sexual state of an anoestrous ewe, there is a great deal of benefit for the ewe if she responds to the ram's courtship and unwanted attention by urinating, for by urinating she establishes the fact (assuming the ram has an acute sensory device that he can test the urine with), that she is definitely not in heat. The ram is able to establish that she is indeed anoestrous and leaves her "in peace" (Geist,1971). There in lies the benefit in the urination response for the ewe, and in the Flehmen for the ram.

This does not preclude an appeasement function for the urination response as exists in aggressive interactions, but it does add a further possibility as to how this appeasement function may have evolved.

To look at the urination response in isolation as it occurs in aggressive interactions, it is a simple matter to postulate that the urination response evolved from a fear reaction. Urination by a frightened animal in an aggressive situation would evolve a signal function stating ... "I am scared". From here the signal could progress to ..."you have scared me, so you are dominant to me". Acknowledgement of the other animal's dominance becomes appeasement and so a normal physiological response to fear becomes an appeasement behaviour.

However, there are complications to this possible development of the response, caused by its inclusion in the possible sensory function of the urination response and Flehmen, because the urination response could have evolved its appeasement function as a consequence of the urination response - Flehmen sensory mechanism. The urination response in the courtship situation is performed to a dominant (the ram) and providing the ewe is ancestrous it confers some benefit upon her. It could have evolved the secondary function of appeasement in aggressive situations from its potential (pseudo) appeasement connotations in the courtship situation.

Whether the urination response has the same meanings in the two contexts (aggression and courtship) can not be determined by the findings of this study. Nor can its evolution be determined.

Other facets of the urination response and Flehmen have been overlooked in this discussion. They are the reasons for the repetition of Flehmen, the changes in the intensity of its performance (see Plates 32 and 33), the reasons why a ram will sometimes urinate when sniffing the urine of a ewe and the reasons why a ram will Flehmen over the urine of another ram. No reasons for these factors were discovered during observation for this study. With regard to the frequency and intensity changes in Flehmen, Verberne (1970) states "Although this behaviour (Flehmen) functions merely as a support for a mode of sensory perception, specific regularities became apparent in the performance of sniffing and Flehmen (especially in the case of frequent repititions) which can not be explained solely by changes in sensitivity occurring in the receptors of the Jacobson's organ".

A possible explanation for ram Flehmen over the urine of another ram is that the Flehmen has become a fixed action pattern that is

'released' by the urination of another animal.. This possibility is reinforced by the fact that rams will flehm over their own urine, a behaviour which can convey no sexual information or be involved in appeasement. Then again, the urination response may retain its appeasement value in ram - ram interactions and the sniffing of the urine and Flehmen may have developed a secondary function of acknowledgement of appeasement.

There are some unexplained events surrounding the urination response - Flehmen behaviour sequence that Knappe's (1964) suggested function for Flehmen does not yet answer. However, Knappe's (1964) suggestion is the most suitable offered to date and it has not only a good deal of evidence backing it but its suggested function for the Flehmen and vomeronasal organ fits the behaviour of mammals as it is observed in the field. In time it may be extended so that it does explain phenomena that have no apparent function at the moment.

Only selective ablation or nerve twig recording studies for olfactorily and vomeronasal detected substances coupled with studies showing the ability of such detected substances to induce Flehmen, and the isolation of these substances from the urine of female mammals will settle the controversy surrounding the Flehmen and vomeronasal organ. A similar conclusion was made by Knappe (1964) when he stated "A final decision about the relationship between the functioning of the Jacobson organ and the Flehmen is only possible by physiological methods".

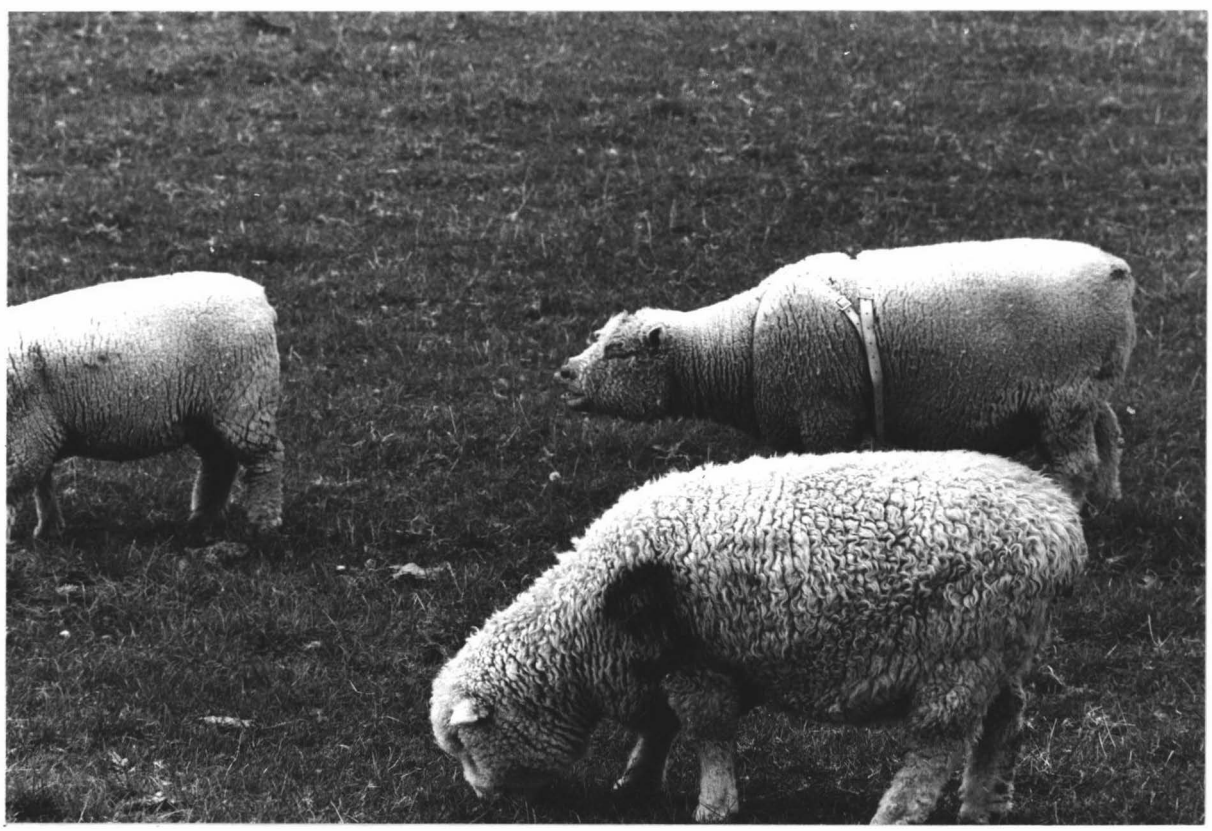

PLATE 32

Ram Performing High Intensity Flehmen.

PLATE 33

Ram Performing Low Intensity (repeat) Flehmen.

CHAPTER IV

A STUDY OF RAM FATIGUE (Experiment ONE)

A. Aims

Many rams suffer a rapid loss in physical condition over the breeding season (Hafez et al., 1969) yet very little work has been done on ram fatigue caused by continual mating and the consequence of fatigue on the behavioural interaction between the ram and ewe, although a number of investigations have examined the short term effects of sexual satiation and libido reduction (Anderson,1969; Bermant et al., 1969a; Hafez,1962; Hafez et al., 1969; Lambourne,1956; Pepelko and Clegg,1965).

Reasons as to what actually causes the loss of physical condition are in doubt. It could be a direct result of mating activity, though a consideration of the estimated amount of energy expended by a ram at each mating[17] (Tomme and Odinec,1940) would tend to contradict this. That the loss of condition could be a result of reduced food consumption (Hafez et al., 1969) is contrary to the findings of Hulet et al. (1962a), who concluded that the time spent eating by rams (in small breeding pens) did not have a significant negative correlation with the number of ewes in oestrus, nor the number of ewes mated.

The aim of this experiment was to record the behaviour involved in interactions between the ram and ewes at successsvice stages throughout the breeding season, so that any changes that occurred in the type of behaviour during ram - ewe interactions at different heats, might be detected.

It was envisaged that certain changes would occur in the type of interaction at successive heats and that these changes might be shown to be a result of fatigue in the ram. Had changes in behaviour been revealed it may have then been possible to show that these fatigue - induced changes reduced breeding efficiency by modifying courtship patterns - or that these changes in behaviour had no affect on breeding efficiency because of other compensatory behavioural mechanisms.

B. Materials and Methods

A flock of seventy sheep consisting of one ram and sixty-nine

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[17] 126.8 Cals./mating. "mating" was not defined so it is not known if this includes the preliminary courtship as well.

ewes of mixed ages were observed during the 1973 breeding season. Eleven of the ewes were ovariectomised (spayed) and underwent hormone treatment to induce oestrus. These spayed ewes were therefore able to 'return' to a second heat, thereby providing behaviour recordings at two stages of the breeding season. The sexual "motivation" of these ewes should have been identical at both recording stages because the major controlling factor, the amount of Oestradiol Benzoate (O.B.) administered, was the same.

The remaining fifty-eight ewes were entire and cycled normally and so provided a natural setting for the experiment and as well, furnished information that could be compared with the experimental animals, and also be used in Chapters Two and Three. The ram was run with the ewes throughout the period encompassed by the experiment. The sheep were contained in a small paddock (0.7 hectare) during observations and their behaviour observed from an elevated hide in the paddock's centre (see Plates 34 and 35). Notes on male and female sexual behaviour patterns were made and a record kept of the sequences in which they occurred.

i) Animals and their Management

The Ram. The ram used for this experiment was a four-tooth Southdown ram from the Massey University Sheep Farm stud flock. The same ram had been used for an experiment in the 1972 breeding season (see Introduction, Chapter One) and had one seasons' breeding experience.

The ram was fitted with a 'Sire Sine' harness and raddle,[18] the colour of which was changed on the nineteenth day of the experiment. The harness was fitted with reflector tape and 'Cat's Eye' reflectors so the ram's position could be seen at night quite easily. Normal feed was supplemented with lucerne nuts. A watch was kept on general condition and the feet of the ram inspected every second day.

Southdown Ewes. The fifty-eight Southdown ewes, comprising; thirty two-tooths (no mating experience), thirteen four-tooths, seven six-tooths and eight full mouth ewes (variable mating experience) were part of the stud flock and except for the two-tooth ewes had led normal reproductive lives.

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[18] The 'sire sine' harness is a device fitted with a crayon (raddle) that is strapped to the brisket of the ram. When the ram mounts a ewe the crayon rubs the rump, marking the ewe and indicating she has been mounted, and possibly tupped.

PLATE 34

The Observation Paddock showing the Pen and Hide.

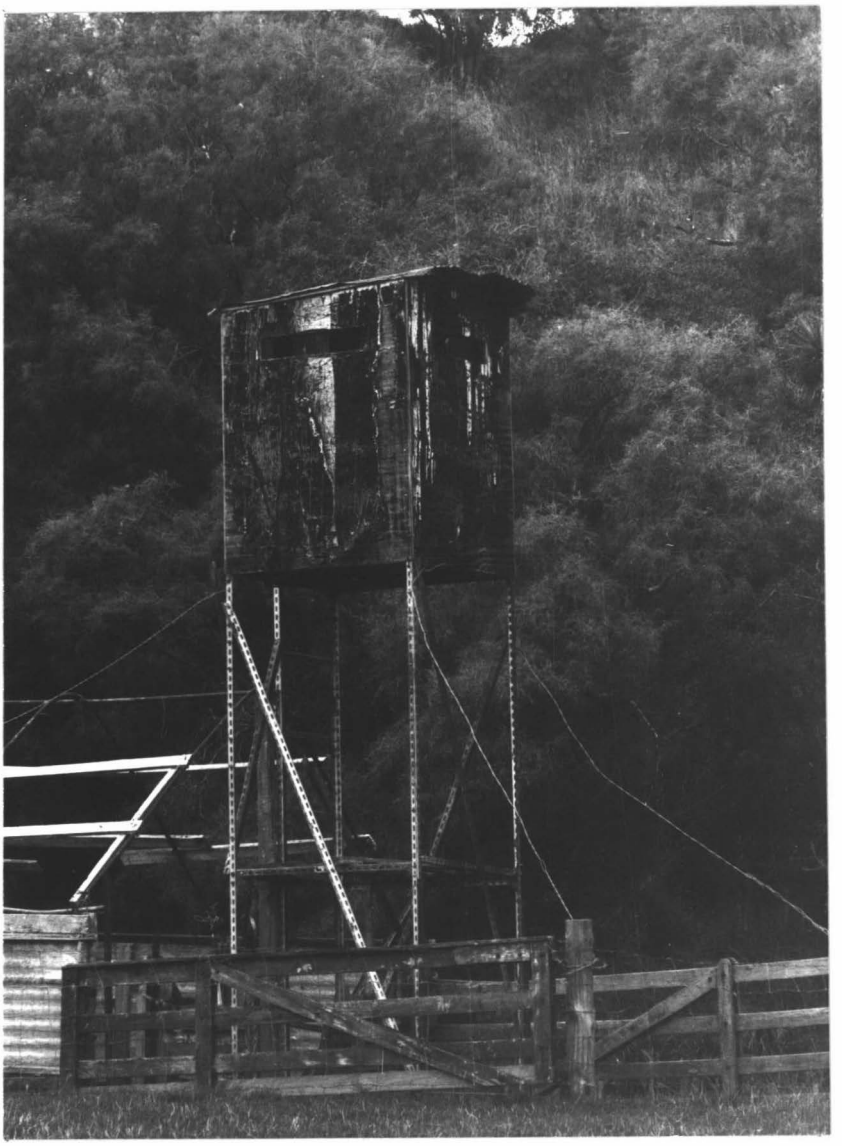

PLATE 35

The Observation Hide.

Each ewe was individually marked with a number sprayed on to the shoulder on both sides of the animal with an aerosol marking brand. The ewes received no supplementary feed though their general condition was watched closely. Any lameness was attended to immediately.

Romney Ewes. The eleven Romney ewes were a group of culled-for-age ewes, all were full mouths and had normal reproductive histories. They were ovariectomized (July 1972) and used at intervals through (the remainder of) 1972 and early 1973 for behaviour experiments (see Introduction, Chapter One). They were individually branded but in a different colour to the Southdown ewes. The Romney ewes were allotted to three treatment groups so that each group contained ewes of a similar range of (body) sizes.[19] As with the Southdowns the Romneys received no supplementary feed but the general health of these ewes was watched carefully.

ii) The Hormone Treatment

Medroxyprogesterone acetate (M.P.A.) (Upjohn Pty.Ltd.) and Oestradiol Benzoate (O.B.) (Organon Laboratories Ltd.) were used to induce oestrous behaviour in the ovariectomized ewes. The treatment method was a modification of that used by Lindsay and Robinson (1961). The first modification was to substitute M.P.A. impregnated tampons for progesterone injections for progesterone priming, because a) it had proved more reliable in previous experiments and b) it reduced the amount of disturbance to the flock. A second modification was an increase in the amount of O.B. injected into the ewes, from the near endogenous levels[20] (approx. 25 µg) used by Lindsay and Robinson (1961), Lindsay (1965),(1966a), (1966b), and Lindsay and Ellsmore (1968), to 100 µg OB/ewe.

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[19] Treatment Group — Ewes

A	0,2,3,4
B	8,9,10
C	1,5,6,7

The body size of a ewe in any one group was matched by placing a ewe of a similar size in each of the other two groups, so that overall the groups contained a range of sizes that was the same for each group. This was done to eliminate, as much as possible, any variation in the affect of O.B. and M.P.A. due to differences in the body weight of the ewes.

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[20] Robinson (1959) estimated the production of endogenous oestrogen at the time of oestrus in entire ewes, equivalent to a dose of 25 µg O.B. injected into spayed ewes.

The final modification involved shortening the forty-eight hour interval between the last progesterone (M.P.A. in this case) treatment and the O.B. injection, to twenty-four hours. This period was shortened for convenience of ewe handling and had shown to be satisfactory in previous trials.

The sponge rubber tampons used were approximately 6 cm. in length and 2 cm. in diameter. They were threaded with a double nylon thread, approximately 40 cm. in length. When the tampon was inserted in the ewe the thread projected from the vulva and so aided the removal of the tampon.

The tampons were impregnated with 40 mg of M.P.A. dissolved in absolute alcohol, and stored in a plastic bag at room temperatures until required. For insertion into the ewe, the tampons were smeared with an antiseptic cream and placed inside a speculum also smeared with the cream. The tampon was held in place with a short rod while the speculum was inserted into the vagina, the speculum withdrawn from around the tampon while the rod held the tampon in place, then the rod was withdrawn. Tampons were removed at the desired times by gentle traction on the nylon thread.

The oestrogen (O.B.) treatment consisted of an intramuscular injection of 1 ml of peanut oil containing 100 µg O.B., given approximately twenty-four hours after the tampon removal.

iii) The Study Area

A paddock (No.7) on the Massey University No.1 Sheep farm was used for the study. The paddock was divided into two parts by a sheep netting fence. One part, 0.7 hectares in area, was used as the observation area while the second part, 1.9 hectares in area, was a feeding and holding area used when observations were not in progress.

In the centre of the observation paddock there was a lambing pen (approx. 8m x 3m). For the insertion or removal of tampons, O.B. injections, cleaning of the ram's raddle or feet inspections, the flock was driven into the pen where the sheep could be captured and handled without difficulty. The observation hide was erected at one end of this pen. From small shutter windows in each side of the hide, every part of the observation paddock could be seen. A fence around the base of the hide prevented sheep from entering the area directly beneath the hide where they would have been difficult to observe.

In general, there was very little traffic on the adjacent farm road and only occasional movement of people and stock in the neighbouring paddocks so that disturbance to the flock was minimal.

iv) The Observations

Both daylight and night observations were made of the sheeps' sexual behaviour. Approximately half-an-hour before each period of daylight observation began the sheep were moved from the large holding paddock into the observation paddock. When night observations were made, the sheep were placed in the observation paddock during the afternoon before the observations were to take place. At the end of each observation period the sheep were released into the larger paddock.

Daylight observations began at dawn as soon as it was possible to read the indentification numbers on the ewes through binoculars[21] and concluded at dusk on the same day when the numbers again became indiscernible because of darkness. At the start of the season the starting and finishing times of the observations were (approximately) 06.00 hr and 19.00 hr respectively, but by the end of the season these times had changed to 06.45 hr and 18.15 hr because of the shortening day length.

The behaviour patterns (see Chapter Two) were recorded on prepared sheets (see Appendix One) as the behaviour occurred in the field. Provision was made on these sheets for the recording of both ram and ewe behaviour patterns and the relationship in which they occurred so that reciprocating patterns were able to be recorded for analysis. Each behaviour pattern was denoted by a particular code letter, or letters. Also the time at which the interaction occurred was noted, the identity of the ewe(s) involved and a note was made of the animal that initiated the interaction. On each sheet a short note was made of the weather conditions at the time. During daylight, binoculars (8x40 wide angle) were used to read ewe identification numbers and observe details of behaviour. As well as the recording of sexual behaviour, some notes were made on other activities such as fighting, feeding and resting patterns.

Night observations were made either between the hours of; half-an-hour before dusk until 00.30 hr or between 23.30 hr and half-an-hour after dawn, and were aided by the use of a 12 volt spotlight powered by a motor cycle battery. The spotlight was switched on every 7.5 minutes for several seconds to allow a sighting of the ram to be made.

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[21] This was usually 10-15 minutes before the identification numbers became visible to the unaided eye.

Every second sighting, on the quarter-hour, the "class"[22] of behaviour the ram was engaged in at the time was noted.

If the spotlight was left on too long the sheep became agitated, so the noting of ewe identity and full recording of behaviour patterns - as made during the daylight observations - could not be attempted at night. However, by recording the "class" of behaviour the ram was indulging in, a reasonably accurate impression of the ram's activity could be obtained. The purpose of the night observations was to determine what proportion of the ram's sexual activities occurred at night, and therefore was missed by the dalight observations.

The fifteen minute interval between the behaviour ("class") recordings appeared to be an adequate (checked by split-interval observations every 7.5 minutes) record of behaviour. The "classes" of behaviour seldom changed so quickly that shorter recording intervals were warranted. On the few occasions when the ram did change "classes" of behaviour more than once within a fifteen minute recording period, a note was made of the fact.

v) The Observations Calendar

An example calendar appears in the appendices (see Appendix Two). It shows the time relationship between observation periods and treatments as well as the organisation of the flock and study area.

The spayed ewes (three groups) were treated with M.P.A. and C.B. so that a group of ewes came into heat for approximately three days and returned to a second three (approx.) day heat period, eighteen days after the start of the first one. The experiment was structured so that each group of ewes completed a cycle of two heat periods with a fifteen day anoestrous period between each oestrous period, during which time the other groups would each have an oestrous period.

Daylight observations were made over a three day period that coincided with the three days of heat in the ewes of either one of the three treatment groups. There was then an interval of three days followed by a further three days of observations. In all there were planned six

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[22] The behaviour of the ram was classified into three categories. These were

1) Resting
2) Feeding and locomotory
3) Sexual

heat periods and therefore six observation periods. During the intervals between the daylight observation periods, night observations and day-time filming of behaviour took place. Hormonal treatment of ewes occurred between the three day oestrous periods a) because it was necessary to remove tampons and inject C.B. during this time, and b) because it was convenient to insert tampons at this time while other sheep were being handled.

Tampon insertion took place thirteen days before the day on which heat started. Tampons were removed on the eleventh day after insertion and the intramuscular injection (i.m.i.) of C.B. took place on the twelfth day, approximately twenty-six hours after tampon removal. The ewes came into heat sometime on the day following the C.B. injection.

Mixing of the Romney (ovariectomized) and Southdown (entire) ewe flocks was scheduled for 5/3/73, ten days before ram introduction to allow the ewes sufficient time to settle down before observations started. Unfortunately a shortage of feed delayed the mixing of the flocks until the 12/3/73 but this delay did not appear to affect the experiment in any way. On the first day of the ewe flocks being mixed, the two flocks remained apart and there was some fighting between a number of the Romney and Southdown ewes. However, by the third day following their mixing the two breeds interspersed themselves about the paddock and fighting showed a marked reduction.

The Romney ewes were marked on the 5/3/73 and treatment began on that date for the A group ewes, with the insertion of tampons. The Southdown ewes weren't marked until the morning of 12/3/73, several hours before being mixed with the Romney ewes.

The ewes and ram were joined on 15/3/73. Observations were to start on 18/3/73, but had to be delayed until 20/3/73 because the observer took ill. Tampons had been removed from the group A ewes (0,2,3,4) on 16/3/73. These had to be replaced until the 18/3/73. C.B. injections for the group A ewes were given on the 19/3/73 and these ewes (0,2,3,4) came into heat on 20/3/73. Because the group B ewes had their tampons inserted on 11/3/73, the two day delay in starting observations meant an extra two days of M.P.A. treatment for the ewes of that group. Group C ewes were unaffected by the delay, the insertion of their tampons being held over until 19/3/73, from 17/3/73 as was originally planned.

C. Results and Discussion[23]

This experiment was not able to run its full term. The ram took ill on 3/4/73 and was removed for veterinary examination. On 4/4/73 he was returned, apparently in good health. His removal on this occasion interferred with observations being made on the group C ewes (1,5,6,7). On 8/4/73 the ram's behaviour was most erratic and he was again removed and the experiment terminated. At the time of his second removal observations were being made on the second (return) heat of the group A ewes.

The behaviour of the ram had appeared normal (normal in the sense that his behaviour compared favourably with his performance the previous season and also with that of other rams that had been observed) on all days except those on which he was removed. X-Rays showed he was suffering from brain lesions, probably incurred during rutting fights with other rams before commencement of the experiment. The ram later died as a result of these injuries.

A certain amount of data was salvaged from the results obtained from the first two observation periods (20-22/3 and 26-28/3) that occurred before the ones involving the ram's removal. The results of the two night watches that were made are discussed in Chapter Six and some of the more general results and notes on sexual behaviour are discussed in Chapters Two and Three. The response of the ewes to the hormone treatment provided some useful information and this is presented in the following section. Some conclusions can also be drawn from the behaviour observed before the ram was removed.

i) Time to oestrus following C.B. injection and duration of oestrus in ovariectomized ewes.

Table II shows that for four treatment groups the average time interval taken to come into oestrus (to start exhibiting oestrous behaviour) after C.B. injection was <16.5 hours. The average duration of oestrus for two of these groups of ewes was >54.5 hours.

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[23] The termination of this experiment and therefore a change in the results from what was expected, necessitated a short explanation of the termination and the reasons for it, before presentation of the findings of the experiment.

As this meant a discussion of the results before they were presented, and therefore a departure from the norm, it was considered that the best means of overcoming the difficulty was to combine the Results and Discussion sections.

TABLE II. Interval to Oestrus following O.B. and Duration of Oestrus (to nearest 0.5 hours) in Ovarectomized Ewes.

Ewe Number	Hours to Oestrus following O.B	Hours to Cessation of Oestrus following O.B	Duration of Oestrus
0	16.0	65.0	49.0
2	< 14.5	75.0	> 60.5
3	15.0	75.0	60.0
4	15.0	72.5	57.5
average	< 15.0	72.0	> 57.0
8	15.5	63.5	48.0
9	< 15.0	74.0	> 59.0
10	20.0	67.0	47.0
average	< 17.0	68.0	> 51.0
1	< 16.0		
5	< 16.0		
6	22.0		
7	42.5 **		
average	< 18.0		
0	17.0		
2	< 15.5		
3	< 15.5		
4	< 15.5		
average	< 16.0		
average all ewes	< 16.5	70.0	> 53.5

** Ewe 7 avoided the ram but showed other signs of being in heat.
Her first contact with the ram was 42.5 hours after O.B.
The average for the group was calculated by using the times of ewes 1, 5, and 6 only.

All ewes had received 100 µg C.B. but the length of time the M.P.A. "primer" tampons were in place varied for each group.[24] This variation was considered to have little affect on the time taken to come into heat (oestrus) following the administration of C.B., and probably also on the duration of oestrus. Fletcher et al.(1971) found no significant difference in the mean duration of oestrous behaviour, induced by a single injection of 24 µg C.B., when the dose of primer progesterone injected was varied between 5, 10 and 20 mg .

A comparison of the results of this experiment with the findings of Fletcher et al. (1971), Lindsay (1966), Lindsay and Fletcher (1972), and Scaramuzzi et al. (1971), (Table III) necessitates the consideration of two important factors relating to experimental procedure.

The first factor is the difficulty in determining the exact onset and termination of oestrus. If a ewe was found to be in oestrus at the commencement of observations on the day following the C.B. injection, the time to oestrus was recorded as 'less than' (<) the time at which she was first seen in oestrus, back to the C.B. injection. Furthermore, if a ewe was in oestrus at nightfall, but not in oestrus the following morning, the time of leaving oestrus was recorded as 'greater than' (>) the time last seen in oestrus, back to the time of the C.B. injection. It will be realised that while these time differences were probably only of the order of a few hours, they were indeterminable and so when they were involved in the calculation of intervals or durations, the qualification of 'less than' or 'greater than' was retained.

The second factor that should be considered is the criteria on which "behavioural oestrus" was based. For this experiment, a ewe was considered to be in an oestrous state if she behaved in a sexual manner with or towards the ram (A 'sexual manner' was considered as any of the following; insistent approaches made to the ram by the ewe; interference with the ram when interacting with other ewes; tail fanning in the presence of the ram; repeated sniffing and nuzzling of the ram; allowing the ram to mount and serve).

This contrasts with the criterion used by Lindsay (1966), who measured the time to onset of oestrus as "the time in hours from the injection of C.B. until ewe first mounted by the ram". The criterion

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[24] Group A ewes, 12 days — Group C ewes, 11 days
Group B ewes, 13 days — Group A ewes, 11 days (2nd.heat)

TABLE III. Comparison of Experimental Results for Interval to Oestrus following O.B. and Duration of Oestrus (in hours) for Different Hormone Treatments.

Source	Progesterone Treatment	Dose of O.B. (μg)	Hours to onset of Oestrus following O.B.	Duration of Oestrus (hours)
Lindsay (1966)	6, 20 mg imi in 12 days	24.4 15.6 10.0	)) 28.05 $\pm$ 6.81)	10.49 3.21 3.21
Scaramuzzi, Lindsay and Shelton (1971)	5, 20 mg imi in 9 days and 1, 10 mg imi on day eleven	10.0 24.3 59.2 144.1 350.5	23.6 $\pm$ 0.88 22.3 $\pm$ 2.65 18.9 $\pm$ 1.50 16.6 $\pm$ 1.26 13.8 $\pm$ 0.42	10.4 $\pm$ 5.88 26.7 $\pm$ 5.30 34.7 $\pm$ 5.18 53.4 $\pm$ 6.35 67.7 $\pm$ 3.82
Lindsay and Fletcher (1972)	5, 20 mg imi in 9 days 1, 10 mg imi on day 11	200	15	60
Ross (1973)	40 mg M.P.A. tampons	100	$<$ 16.5	$>$ 53.5
Fletcher, Allison and Lindsay (1971)	12 days @ 5 mg/day 12 days @ 10 mg/day 12 days @ 20 mg/day	24.3 24.3 24.3	– – –	32.2 33.4 33.2

Lindsay (1966) used for determining when oestrus had ended was not mentioned though it was probably the last observed mount.

Scaramuzzi et al. (1971) and Lindsay and Fletcher (1972) also gave figures for the time to oestrus following O.B. and duration of oestrus but did not mention the criteria used to determine the oestrous condition of their ewes. It was assumed, since D.R.Lindsay took part in both experiments, that it was the same criterion used by Lindsay (1966).

The results of the present experiment compare favourably with those of Scaramuzzi et al. (1971) who had used comparable levels of O.B. One could have expected the results of this experiment to show a somewhat larger value for the duration of oestrus and a shorter interval from O.B. to oestrus than other workers found, considering the different criteria used to determine heat.[25]

One conclusion that can be made, in view of the results obtained was that the 11 - 13 day treatment with a tampon impregnated with 40 mg of M.P.A. (as employed in this experiment) was equivalent in affect to intramuscular injections of progesterone when used at the same levels and timing as employed by Scaramuzzi et al. (1971). Furthermore, if at certain levels, the tampon and progesterone injections are equivalent, in instances where repeated handling of stock creates experimental difficulties the tampon method of priming may prove superior to the intramuscular injections of progesterone.

ii) Composition of ram-oestrous ewe interactions and the sex initiating them.

The method of determining the oestrous condition of the ovariectomised ewes was mentioned above. The same criteria were applied when determining the condition of the entire (Southdown) ewes. However the stage of oestrus in the entire ewes was more difficult to gauge than in the ovariectomized ewes because the entire ewes could have entered heat during the night, whereas the ovariectomized ewes were in a controlled oestrus and the time to onset following O.B. and the duration of oestrus could more or less be adjusted to fall within observation periods. Also the observations were designed to follow the ovariectomized ewes through three days of oestrous behaviour. Unfortunately a number of the

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[25] Hulet et al. (1962a) found a time interval from first 'tease' (ram courtship) to first mount of 2.6 - 3.6 hours and a time interval between last mount and last 'tease' of 4.5 - 8.4 hours in entire ewes.

entire ewes observed did not conform to the same pattern and use had to be made of other entire ewes for which there was no first, second or third day(s) of heat observation results. The ewes used for this comparison, and the days of heat that were analysed are shown in Table IV.

For the purpose of analysis, the behaviour patterns recorded were arranged into five basic 'behaviours' according to the proceedure outlined in Chapter Three, Section A. (The five 'behaviours' were sniffing, Sn; Flehmen, Fl.; General Courtship, GC.; Mounting, Mt.; and Tupping Tp.).

Table V shows the composition of 228 interactions that occurred between seven different ovariectomized ewes and the ram over a six day period. Table VI shows the composition of 166 interactions that occurred between the ram and sixteen entire ewes over the same period. Table VII presents the results of the sex initiating the interactions for each day of heat as a percentage of the total interactions.

For both ovariectomized ewe - ram and entire ewe - ram interactions there is a gradual decline in the number of interactions as the oestrous period progresses .....

For ovariectomized ewes 71.3% interactions on day 1, 19.9% day 2, 8.8% day 3
For entire ewes 73.0% " " " 1, 21.0% " 2, 6.0% " 3

an almost identical decline in activity over the three days of heat for both ovariectomized and entire ewes.

A decline in attention given to ewes once they have been tupped has been reported by Hulet et al. (1962a) and Pepelko and Clegg (1964). A feature of these results for both ovariectomized and entire ewes is the drop in ram (and ewe) initiated activity over the three days of heat. Such behaviour is commensurate with the economies expected of an efficient ram.

A second feature of the results is that 86% of all interactions between ovariectomized ewes and the ram (N=228) involved general courtship and/or investigation (both 'behaviours' i.e. Sn. and Fl.) or combinations of these behaviours without progressing to mounting or mounting and serving. The figure for entire ewes was 82% of all interactions (N=166). Only 1% of the interactions between the ram and ovariectomized ewes resulted in a ewe being served, while the figure for entire ewes was 12%. Therefore, although a ram spends a great deal of time, and expends much energy in sexual activity during its waking hours, much of this activity is of an investigatory nature only and very few interactions result in the (immediate) servicing of a ewe.

TABLE IV. Oestrous Ovarectomized and Entire Ewes used for the analysis of Behavioural Interactions and their Initiation.

Observation Period	Date of Observations	Ewes in Oestrus and day of Oestrus			No. of ewes in Oestrus	
		First Day	Second Day	Third Day	Entires	Spayed
I	20 / 3	0,2,3,4,44,30,19	28,43	–	5	4
	21 / 3	31,23	0,2,3,4,44,30,19	–	5	4
	22 / 3	16,42	31,23	0,2,3,4,19	5	4
II	26 / 3	8,9,10,63,40	26	–	3	3
	27 / 3	22,61,68,48	8,9,10,63	31	6	3
	28 / 3	–	22,61,48,68	8,9,10,63	5	3

TABLE V. Categories of Behaviours in Interactions Initiated by the Ram or Ovarectomized Ewes of Groups A and B for the Three Days of their First Oestrus.

BEHAVIOURS					DAY 1 OF OESTRUS		DAY 2 OF OESTRUS		DAY 3 OF OESTRUS		
SN	FL	GC	MT	TP	Ram init.	Ewe init.	Ram init.	Ewe init.	Ram init.	Ewe init.	TOTALS
SN					26	30	12	7	5	1	81
	FL				1						1
		GC			7	30		8		2	47
			MT								
			MT	TP							
SN	FL				4			1			5
SN		GC			19	18	5	4	4	1	51
SN			MT								
SN			MT	TP							
	FL	GC			2	2					4
	FL		MT								
	FL		MT	TP							
		GC	MT								
		GC	MT	TP	2						2
SN	FL	GC			3	2			2		7
SN	FL		MT								
SN	FL		MT	TP							
SN		GC	MT			1					1
SN		GC	MT	TP	5	4	2	1	3		15
	FL	GC	MT								
	FL	GC	MT	TP	1		1				2
SN	FL	GC	MT		1				1		2
SN	FL	GC	MT	TP	5		2	2	1		10
					76	87	22	23	16	4	228

TABLE VI. Categories of Behaviours in Interactions Initiated by the Ram or Entire Ewes for the Days of their First Observed Oestrus.

BEHAVIOURS					DAY 1 OF OESTRUS		DAY 2 OF OESTRUS		DAY 3 OF OESTRUS		
SN	FL	GC	MT	TP	Ram init.	Ewe init.	Ram init.	Ewe init.	Ram init.	Ewe init.	TOTALS
SN					22	11	10	2	5		50
	FL				1						1
		GC			7	18	1	5		1	32
			MT								
			MT	TP							
SN	FL				4	1	1		1	1	8
SN		GC			16	9	6	2	1		34
SN			MT								
SN			MT	TP							
	FL	GC									
	FL		MT								
	FL		MT	TP							
		GC	MT		1						1
		GC	MT	TP		1	1	1			3
SN	FL	GC			6		2		1		9
SN	FL		MT								
SN	FL		MT	TP							
SN		GC	MT		5	2	1	1			9
SN		GC	MT	TP	10	1	1				12
	FL	GC	MT								
	FL	GC	MT	TP	1						1
SN	FL	GC	MT		2						2
SN	FL	GC	MT	TP	2	1	1				4
					77	44	24	11	8	2	166

TABLE VII. The Sex Initiating and Interaction on Each Day of Oestrus Expressed as a Percentage of the Total Interactions.

Day of Oestrus	Day One		Day Two		Day Three	
Sex initiating interaction	Ram	Ewe	Ram	Ewe	Ram	Ewe
Ovarectomized ewe results	76	87	22	23	16	4
expressed as a % of total	33.3%	38.0%	9.7%	10.2%	7.0%	1.8%
Entire ewe results	77	44	24	11	8	2
expressed as a % of total	46.3%	26.7%	14.4%	6.6%	4.8%	1.2%

The difference between the two sets of data for the amount of ewe initiation of interactions;

Ovariectomized ewes initiated 50.0% of all interactions with the ram
Entire " " 34.5% " " " " " " "

could be the result of a breed difference, i.e. Romney ewes take a more active part in sexual behaviour than Southdown ewes do,[26] or it could be due to the treatment given to the spayed ewes.[27] That is, that 100 µg C.B. (approximately four times endogenous oestrogen levels) makes the ewes more sexually hyperactive than an entire ewe and therefore accounts for the difference found in the results. The tendency to seek the ram was considered as one type of ewe initiation of an interaction so the difference obtained between entire and ovariectomized ewes could be due to the hormone treatment given the ovariectomised ewes, for Lindsay and Fletcher (1972) showed that the incidence of ram seeking activity in ewes (ovariectomized) increased with increasing dose of oestrogen (µg C.B.).

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[26] Breed differences in sexual behaviour have been documented (Hafez,1951; 1952; Inkster,1953; Lambourne,1956) though there has been no comparitive studies done on Southdown and Romney ewes, Hulet et al. (1962a) found no significant breed affects and felt that individual differences were one of the most important factors affecting mating behaviour in rams.

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[27] A comparison of the ovariectomised ewe results with those of the entire ewes is subject to limitations because of their bi-factorial differences; those of being two different breeds plus the fact that the Romneys are ovariectomised and the Southdowns entire. This experimental structure was unavoidable as the experiment had to fit into the farm breeding programme.

CHAPTER V

A STUDY IN HORMONE LEVELS (Experiment TWO)

A. Aims

The aim of this experiment was to investigate the physiological and behavioural effects of varied Oestradiol Benzoate (O.B.) dose levels given to ovariectomized ewes to induce oestrous behaviour.

Several other studies (Lindsay,1966; Scaramuzzi et al., 1971) had investigated the effects of a varied O.B. dose level on the time taken to the onset of oestrous behaviour following an O.B. injection, and the duration of induced oestrous behaviour, but at the time of planning no information could be found regarding investigations that had examined the behavioural effects of a variation in O.B. dose levels.

B. Materials and Methods

Materials used and methods employed in this experiment were the same as for Experiment One, except for the following modifications:

i) The Experiment One ram was replaced with a second Southdown ram, aged 4½ years, of greater breeding experience. The replacement ram had not been run with ewes this season prior to his joining with the experimental flock on 9/4/73.(The commencement of a second experiment and utilization of a second ram was made necessary by the death of the ram used in Experiment One - see Chapter Four - and was not intended on the original design of Experiment One.

ii) The level of O.B. administered was altered for two of the groups of spayed ewes so that;

Group B ewes received 200 µg O.B. on 12/4,

and Group A ewes received 50 µg O.B. on 24/4,

while Group C ewes received 100 µg O.B. on 18/4, the same dose level used in Experiment One. Medroxyprogesterone acetate (M.P.A.) treatment was not changed.

The ewe flock remained unchanged and the second experiment was conducted in the same area as the first. The ram was joined with the ewe flock on 9/4/73 and removed at the conclusion of the experiment on 27/4/73. Observations continued to follow the same schedule with daylight observations taking place on 13,14,15/4 (Pd.V); 19,20,21/4 (Pd.VI); and 25,26,27/4 (Pd.VII). Night observations[28] were made

[28] Results of night observations are discussed in Chapter Six.

on the 10,15,16,18 and 23/4. (See calendar,Appendix Two). No change was made in the method of recording ewe and ram behaviour.

The methods involved in determing the onset and duration of oestrous behaviour are discussed in Chapter Four.

C. Results and Discussion

i) Time to onset of oestrous behaviour following O.B. injection and the duration of oestrous behaviour in ovariectomized ewes.

A reasonably close correlation is obtained if the hours to onset of oestrous behaviour (oestrus) following O.B. injection and the duration of oestrous behaviour in ovariectomized ewes (Table VIII) is compared with the findings of similar experiments using comparable levels of O.B. (Table III). The 200 µg O.B. dose level results concur with those of Lindsay and Fletcher (1972), who found a 15 hr interval to onset of oestrous behaviour following the O.B. (200 µg) injection, compared with the ($<$) 14.0 hr interval obtained in this experiment, and a duration of oestrous behaviour of 60 hr compared with a duration of ($>$) 59.5 hr found in this experiment.

The results for the 100 µg O.B. dose level compare well with those obtained in Experiment One ($<$ 16.5 hr to onset, $>$ 54.5 hr for duration of oestrous behaviour) and also approximate those obtained by Scaramuzzi et al.(1971), (16.6$\pm$ 1.26 hr to onset and 53.4$\pm$ 6.35 hr duration) who used a dose of 144 µg O.B.

The 50 µg O.B. results bear a close relationship with those of Scaramuzzi et al.(1971), (18.9$\pm$ 1.50 hr to onset and 34.7$\pm$ 5.18 hr duration) who used a slightly greater dose of 59 µg O.B.

Overall, the findings showed that as the level of O.B. administered was decreased, the time to onset of oestrous behaviour following the O.B. injection, is increased and the duration of oestrous behaviour is decreased and is therefore in agreement with the finding of Scaramuzzi et al.(1971). However, in this experiment the findings have certain limitations because the 200 µg 100 µg and 50 µg O.B. dose levels were conducted at different stages of the breeding season. The proceedure of dosing a group of ewes with a particular O.B. level at the same time and varying the level for each observation period was adopted (rather than the alternative of using different levels at the same time, repeated at intervals) because it eliminated the possibility of a time affect on the supposed induced 'motivational state' related to each dose level at a particular time, and also ensured that at least two

TABLE VIII. Interval to Onset of Oestrus following O.B. and Duration of Oestrus (to nearest 0.5 hours) in Ovarectomized Ewes during Observation Periods V, VI and VII.

Observation Period	Ewe Number	Level of O.B. (μg)	Hours to onset of Oestrus after O.B.	Hours to cessation of Oestrus after O.B.	Duration of Oestrus
V	8	200	16.0	> 72.5**	> 56.5
	9		< 13.0	69.5	> 56.5
	10		13.5	> 72.0	> 59.5
average			< 14.0	> 71.0	> 57.5
VI	1	100	< 15.5	> 74.5	> 59.0
	5		18.0	70.0	52.0
	6		18.0	66.0	48.0
	7		18.0	74.0	56.0
average			< 17.5	> 71.0	> 54.0
VII	0	50	< 14.0	63.5	> 49.5
	2		25.0	48.0	23.0
	3		19.5	> 49.0	> 29.5
	4		< 14.0	45.5	> 31.5
average			< 18.0	> 51.5	> 33.5

** The ram mounted and served ewe 8, 152 hours after the O.B. injection, giving a possible Oestrus duration of 136 hours. As this figure was in doubt the cessation of Oestrus was determined at > 72.5 hours, the finish of observations on the third day, so the reading remained in keeping with the others.

or three ewes would still come into heat and so represent a particular dose level at a specific time even if one or two ewes failed to respond to the treatment, whereas the alternative method could not.

Both Lindsay and Fletcher (1972) and Scaramuzzi et al.(1971), used Border Leicester X Merino ewes. This experiment utilized Romney ewes but the results obtained bear a close resemblance to the results of the other two studies, indicating that any difference in response to C.B. that occur between these breeds are probably slight, if any differences occur at all.

Because of the different criteria used to determine oestrous behaviour in the ewes between this experiment and the experiments of Lindsay and Fletcher (1972) and Scaramuzzi et al.(1971), a slightly greater time for oestrous behaviour duration could have been expected for this experiment than in the others, as well as a short interval to onset of oestrous behaviour following the C.B. injection. Any potential difference between the results caused by the use of different criteria for heat determination may have been masked by the difficulty encountered in determining the exact time of onset and termination of oestrus, or may have been virtually non-existent due to a close proximity in time between the onset of other courtship behaviour and the stage of standing and allowing the ram to mount - though Hulet et al. (1962a) found intervals in the order of several hours.

The conclusions made in Chapter Four, regarding the equivalency of the tampon (M.P.A.) treatment and the progesterone injection treatment for induced oestrus priming, and of the superiority of the tampon method in certain circumstances are upheld by the findings of this experiment.

ii) The change in the frequency and types of interaction between the ram and oestrous ewes during the oestrous period.

A decline occurred in the number of interactions between the ram and oestrus ewes as the ewe's oestrous period progressed (Table IX). Two factors were involved in this response. The first factor was the ram's loss of interest in a ewe he had recently tupped (also reported by Berman et al., 1962c), and his tendency to mate more frequently with those ewes in the most recent oestrus (also found by Hulet et al., 1962c). This accounted for the decline in ram initiation of interactions with oestrous ewes and, as was mentioned in Chapter Four, was an economical behaviour on the part of the ram, allowing him to cover a greater number

TABLE IX. Number of Interactions for Each Day of Oestrus during Observation Periods V, VI and VII in Ovarectomized and Entire Ewes and the Sex Responsible for Initiating the Interaction.

EWES	OBSERVATION PERIOD	DAY OF OESTRUS					
		FIRST DAY		SECOND DAY		THIRD DAY	
		Ram init.	Ewe init.	Ram init.	Ewe init.	Ram init.	Ewe init.
Spayed	V	28	86	18	28	6	27
	VI	30	87	17	56	3	41
	VII	26	98	24	67	3	1
Entire	V	53	55	6	3	12	0
	VI	39	48	3	1	6	0
	VII	14	23	11	29	3	0

of ewes than he would have done had he spent more time in repeated matings.

The second factor responsible for the decline in interactions over the three day observation periods was the loss of interest in the ram on the part of the ewe, as evidenced by the decline in ewe initiated contact. This was no doubt, a response to declining oestrogen levels.

If instead of the above analysis, the oestrous entire ewe results are analysed for the day on which they occurred irrespective of the day of heat (because of the experimental plan, oestrous day and day of observation coincide in the ovariectomized ewes), the total number of interactions between the ram and oestrous ewe are obtained for each day of observation (Table X).

Although showing some fluctuation, the total number of interactions between the ram and oestrous ewes were approximately the same for each observation period. The reason for this was that the decline in attention paid to ovariectomized ewes by the ram over their three day oestrous period, was compensated for by an increase in the amount of attention paid to oestrous entire ewes in the later stages of each three day observation period. This tendency will probably have affected the chances of some of the entire ewes being serviced, especially if they came into heat on the first day of the ovariectomized ewes' heat, and therefore could have an effect on ewe fertility.

The number of interactions that occurred between the ram and the overiectomized ewes for the different observation periods bore no relationship to the level of C.B. administered to the ewes.

The data in Table XI showing the categories of behavioural interaction that occurred between the ram and oestrous ewes during the three day observation periods, demonstrates the similarity in interaction types between the two breeds of ewe and the ram. A similar result was obtained in the experiment discussed in Chapter Four and, as was explained at that time, a great deal of the ram's interaction with the ewes involved investigation or "non-productive" courtship, in the sense that it did not lead to service at that time. (This does not allow for instances in which courtship occurred, contact between the ram and ewe was broken, then renewed again several minutes later and a service followed). The qualification 'non-productive' is used with caution, for each interaction between the ram and an oestrous ewe undoubtly serves to breakdown aggressive tendencies and to signal sexual intent, and therefore is fulfilling the basic purpose of courtship.

TABLE X. Number of Interactions between the Ram and Oestrous Ewes for Each Day of Observation and the Sex Initiating Them.

OBSERVATION PERIOD	DATE	Ram and Ovarectomized Ewes		Ram and Entire Ewes		TOTALS AND PERIOD TOTALS
		Ram init.	Ewe init.	Ram init.	Ewe init.	
V	13 / 4	28	86	14	8	136)
	14 / 4	18	28	33	8	87) – 323
	15 / 4	6	27	23	42	100)
VI	19 / 4	30	87	3	0	120)
	20 / 4	17	56	15	7	95) – 333
	21 / 4	3	41	30	44	118)
VII	25 / 4	26	98	11	21	156)
	26 / 4	24	67	15	22	128) – 301
	27 / 4 **	3	1	4	9	17)

** only half a day of observations.

As the above results analysed interactions between the ram and oestrous ewes only, an analysis was made of the 535 interactions recorded during observation Period VI between the ram and all ewes (both oestrous and anoestrous) for comparison with the oestrous ewe - ram interactions (Table XII).

It was found that of the 535 interactions, 33% (n=176) involved investigation only while 92.5% (n=496) involved investigation and general courtship. In 2.5% (n=13) of all interactions mounting occurred without service and only 5% (n=26) of all interactions resulted in a ewe being served. The greatest increase in the number of interactions when all ewes were considered, occurred in the Sniffing; Flehmen; Sniffing and Flehmen; and Sniffing, Flehmen and General Courtship categories. Comparing all ewe interactions with the oestrous ewe only interactions (observation Period VI) it was found that the number of interactions involving Sniffing had quadrupled, those involving Flehmen had trebled, the category for interactions involving Sniffing and Flehmen behaviours showed a sixfold increase and the Sniffing, Flehmen, General Courtship category showed a fourfold increase above its occurrence when oestrous ewe interactions only were considered. This result is somewhat expected and indicates that although the ram must spend a great deal of time searching for oestrous ewes (investigating behaviour), little other time is wasted in courting the anoestrous ewes, and certainly not to the point of mounting, (see also Chapter Three, Section A).

When the type of interaction was examined for each day of oestrus, it was noticed that the type of interaction a ewe had with the ram changed from interactions that involved a moderate degree of general courtship resulting in service on the first day, to interactions on the third day of oestrus that were predominantly investigatory with some general courtship and virtually no servicing - especially in the case of the entire ewes.

On the third day of oestrus the ovariectomized ewes showed a greater variation in the categories of interaction in which they were involved with the ram, than did the entire ewes. This was attributed to their oestrous condition being of a greater duration than the entire ewes who, in general, exhibited little or no oestrous behaviour on the third day after their heat onset.

TABLE XI. Categories of Interactions between the Ram and Oestrous Ewes for Observation Periods V, VI, and VII expressed as a Percentage of the Total Interactions for Each Day of Oestrus.

EWES	OBSERVATION PERIOD	INTERACTION CATEGORY	DAY OF OESTRUS			Category Totals for period (%)	Total Interactions
			First	Second	Third		
Spayed	V	SN & FL	7.0%	13.0%	12.0%	9.3%	193
		SN, FL & GC	86.0%	85.0%	94.0%	87.0%	
		MT	6.1%	6.5%	3.0%	5.7%	
		TP	7.9%	8.5%	3.0%	7.2%	
Spayed	VI	SN & FL	6.0%	15.0%	18.0%	12.4%	234
		SN, FL & GC	86.0%	93.0%	100.0%	91.0%	
		MT	5.1%	0.0%	0.0%	2.6%	
		TP	8.6%	6.8%	0.0%	6.4%	
Spayed	VII	SN & FL	12.0%	18.6%	25.0%	15.0%	219
		SN, FL & GC	83.0%	92.0%	75.0%	87.0%	
		MT	10.2%	1.1%	0.0%	6.4%	
		TP	6.8%	6.7%	25.0% **	6.6%	
Entire	V	SN & FL	7.4%	22.0%	58.0%	13.0%	129
		SN, FL & GC	83.0%	100.0%	100.0%	86.1%	
		MT	13.0%	0.0%	0.0%	10.8%	
		TP	4.0%	0.0%	0.0%	3.1%	
Entire	VI	SN & FL	12.6%	0.0%	100.0%	17.6%	97
		SN, FL & GC	84.0%	100.0%	0.0%	79.5%	
		MT	7.0%	0.0%	0.0%	6.2%	
		TP	9.0%	0.0%	0.0%	8.2%	
Entire	VII	SN & FL	19.0%	7.7%	0.0%	12.6%	79
		SN, FL & GC	78.0%	90.0%	100.0%	85.0%	
		MT	13.5%	7.7%	0.0%	10.0%	
		TP	8.0%	2.3%	0.0%	5.0%	

** for that day, n=4 interactions, therefore TP (1 instance) = 25%

TABLE XII. Categories of Interactions between the Ram and All Ewes (Oestrous and Anoestrous) Recorded during Observation Period VI.

Observation Period	Interaction Category	No. of Interactions	% Interactions
VI (19–21/4)	SN & FL	176	33.0
	SN, FL & GC	496	92.5
	MT	13	2.5
	TP	26	5.0
Totals		535	100.0

There was no apparent O.B. dose level affect in the response shown by the ovariectomized ewes in the nature of their interactions with the ram.

iii) Initiation of interactions between the ram and oestrous ewes.

An analysis of the sex responsible for the initiation of interactions (Table XIII) indicates that the oestrous ewes tended to initiate more of the interactions than the ram did, but the ovariectomized ewes showed a greater initiative in this respect than the entire ewes. In the investigation discussed in Chapter Four, a similar finding was made and the difference in rates of initiation of interactions between entire and ovariectomized ewes was attributed to the hormone treatment given to the overiectomized ewes, though it was explained at the time the difference could have arisen from a difference in breed behaviour of the ewes.

As Lindsay and Fletcher (1972) had found an increase in the incidence of ram seeking behaviour in ewes when the level of O.B. administered was increased, a decline in ewe initiation of interactions with the ram might have been expected as the level of O.B. administered was decreased.

This lack of correlation between ewe initiation of interactions and the amount of O.B. injected could be ascribed to a ram affect. If a ewe was particularly attractive to a ram when the ewe was on a high level of O.B., and this attractiveness declined as the O.B. dose was decreased, the result would be a decline in ram initiation of interactions. This could then interfere with a declining rate of ewe interaction initiation so that the ewe rate became static. However, there are two factors that eliminate such an affect in this instance. The first is that the total number of interactions between the oestrous ovariectomized ewes and the ram did not decline over the three observation periods, and secondly the rates of initiation of interactions for oestrous entire ewes showed a marked rise over the three observation periods. Whatever factor was responsible for causing this rise in the entire ewe initiation rate could also have suppressed a decline in the oestrous ovariectomized ewe initiation rate so that under the influence of the two opposing factors (declining O.B. level and unknown suppressing factor), the initiation rate in the spayed ewes stayed almost static.

TABLE XIII. The Percentage of Interactions between the Ram and Oestrous Ewes Initiated by Each Sex for Observation Periods V, VI and VII, and between the Ram and All Ewes (Oestrous and Anoestrous) for Observation Period VI.

Ewes	Observation Period	Total No. of Interactions	% Ram Initiated Interactions (rounded)	% Ewe Initiated Interactions (rounded)	Dose of O.B. (μg)
Spayed	V	193	27%	73%	200
	VI	234	21%	79%	100
	VII	219	24%	76%	50
Entire	V	130	55%	45%	–
	VI	97	49%	51%	–
	VII	82	36%	64%	–
All Ewes	VI	535	53%	47%	100 **

** to ovarectomized ewes 1, 5, 6 and 7 only.

An increase in the number of ewes in heat over the three observation periods could have been responsible for the unexpected stasis in the rate of initiation of interactions exhibited by the ovariectomized ewes. However, although there was some variation in the total number of ewes in oestrus on each day in each of the three observation periods, there was no clear increase in the number of ewes in oestrus with time, nor was there an increase in the number of interactions per day between the ram and the oestrous ewes over the three observation periods.

A second cause could have been ram fatigue. If the libido of the ram and his ability to court and service ewes declined during the breeding season (one of the aims of Experiment One, Chapter Four, was to detect such an effect), his rate of initiation of interactions would presumably decline also. Such an event would explain the trends evident in the ovariectomized and entire ewe initiation rates.

Some inconclusive evidence does endorse this possibility. In Experiment One, the rate of ewe initiation of interactions for ovariectomized ewes on 100 µg O.B. was 50% (compared with 79% for ewes on 100 µg O.B. in this experiment) while the entire ewes initiated only 34% of their interactions with the ram. It is possible then, that the ram rate of initiation of interactions could have been declining over the whole of the breeding season. Unfortunately, Experiment One utilized a different ram to the one used in the present experiment and some of the ewes used for recording the rates of initiation differed also, which detracts from the value of this observation.

The above argument is reliant on the supposition that the level of O.B. administered was capable of influencing the rate of ovariectomized ewe initiation of interactions, or more generally, ewe sexual 'aggressiveness' when there may be no such affect whatsoever. If however, there was no affect, the increase in the rate of initiation of interactions by the entire ewes, and the difference between the rates shown by entire and spayed ewes, remains unexplained.

CHAPTER VI

GENERAL DISCUSSION

A. Possible Origins and Functions of some Sexual Behaviour Patterns.

According to Hinde (1970) many animal courtship displays have their origins in the behaviour that occurs during conflict situations, when two or more mutually incompatible tendencies to react in a specific manner are aroused simultaneously. The two mutually incompatible tendencies that are aroused in the courtship or sexual context are;

a) the sexual attraction that exists between male and female during the breeding season, and

b) the aggressive repulsion[29] that is generated when animals come into close proximity and intrude upon the space encompassed by each animal's individual distance or personal field (McBride,1971).

In the courtship context then, the basic type of conflict that occurs is the familiar approach-withdrawal situation.

An approach - withdrawal type of conflict usually has more than a momentary existence because it is possible for the approach and withdrawal tendencies to stabilize at a point where each balances the other. At this point of balance the animal's behaviour is influenced by both sets of causal factors (sex and aggression in this case) and will remain so until the conflict is resolved.

The outcome of behaviour in conflict situations is explained by the 'behavioural inhibition concept'[30] (Hinde,1970) which postulates that behaviour associated with one of the aroused tendencies is inhibited or suppressed while behaviour associated with one of the other aroused tendencies predominates. Often only partial inhibition occurs so that a reduction in the frequency or intensity of some behaviour patterns takes place (intention movements) or a conglomerate of the expected patterns common to the aroused tendencies are exhibited (alternation, ambivalance or compromise). On the other occasions totally irrelevant behaviour (in the circumstances) may occur (displacement

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[29] The aggressive tendencies evoked are composed of two further conflicting tendencies, those of attack and flight.

[30] See Hinde (1970) for a full consideration and discussion of the mechanisms of these conflict behavioural concepts.

activity, autonomic responses, redirection activities, sexual inversion or regression) to indicate the arousal of incompatible response probabilities.

With time, many of these behaviour patterns produced in conflict situations have evolved a communicatory function through ritualisation of the conflict behaviour to form true display patterns. For instance, in courtship the ritualised displays serve to indicate sexual rather than aggressive intent (i.e. advertisement) and also may synchronise physiological processes as well as orient animals so that copulation can take place.

An examination of some of the behaviour patterns used by ewes and rams in courtship encounters indicates not only the probable function of the behaviour, but also its possible origin in conflict behaviour and development to a ritualised display.

One behaviour pattern that presents a relatively simple case was mentioned in Chapter Two. This pattern, displacement feeding (as it was termed), occurs as an abrupt, out-of-context pattern during courtship behaviour. It was most commonly observed in the ram and appeared to eventuate at a stage in courtship when a ram was attempting to avoid the attention of ewes he had already served. The possible source of conflict (mutually incompatible tendencies) for the ram in this case could have been, a) the urge to seek fresh oestrous ewes and leave the served ewe alone and, b) the tendency to respond to her insistent approaches and courtship.

Other instances of courtship display patterns that have their origins in conflict behaviour are less obvious than the displacement feeding example. None of the following instances have yet been shown to be ritualised patterns originating in conflict, but on the basis of the behaviour observed during this study, the suggested functions and origins are seen as probabilities. Several other authors have described these behaviour patterns and have asserted their suspicions as to their possible functions and/or origins.

A courtship behaviour pattern occurs in red deer (Cervus elaphus) stags in which the stag moves toward an oestrous hind and tongue flicks as he approaches (Geist,1971 and K.R.Ross,unpubl.). On reaching the female the stag begins to lick her and so Geist (1971), not unnaturally, postulated that the tongue flicking approach signals an intention to lick - that is, it is an intention movement. In sheep, tongue flicking

is an integral part of at least two sexual behaviour patterns commonly performed by the ram, the low stretch and the twist. However, the only licking that occurs in sheep sexual behaviour is during investigation of the genitalia and only rarely when sniffing or nuzzling elsewhere. No complete body licking as occurs in red deer was observed in sheep. It is possible that sheep, or a sheep-deer common ancestor, once possessed the body licking and tongue flicking approach as a part of its courtship repertoire, but that sheep somewhere along the evolutionary line have lost the body licking component, or modified the licking to nuzzling, while retaining the tongue flicking intention movement. As anogenital investigation often preceeds the tongue flicking as it occurs in the low stretch and twist, it does not appear that tongue flicking is an intention movement for anogenital investigation and its associated licking, hence the suggestion that it is not a prerequisite for this behaviour but has been associated with a more general, body licking component of behaviour that has since been lost by this line.

The low stretch itself could possibly be an intention movement for the twist as it is often followed by this display, and also contains the tongue flicking component found in the twist. It is directed from a distance (i.e. the ram refrains from contact) whereas the twist is a contact behaviour, so the ram may perform the low stretch as an intention movement for the twist, from a distance while he has reservations about approaching too close to the ewe. The similarity between the two behaviour patterns is illustrated by Geist's (1971) comment that "the twist is similar to an intensified low stretch". A second possibility is that the twist and the low stretch are basically the same display (Banks,1964, not only did not make a distinction between the two displays, but also failed to see that such a difference existed) occurring at two intensity levels. The low intensity level, the low stretch, not requiring contact and the high intensity level, the twist, requiring body contact between the two animals.

The twist itself is an interesting behaviour pattern. The element of orientation in it and the apparent necessity of body contact for its performance plus its frequent combination with the front kick indicate it may be an intention movement for the mount.

Both the chinning behaviour pattern and the front kick have been described as possible intention movements for the mount (Ewer,1968). The lifting of a fore leg is part of the act of raising off the ground

in the lifting and lunging action the ram performs when mounting. Chinning, as a means of placing weight on the rump of the ewe to test whether she will stand or not, before making the more obvious move of mounting, is a subtle means of indicating intent and testing the female reaction. Both chinning and the front kick are partial performances of parts of the mounting act.

One aspect of the front kick is intriguing. The front kick is most often directed at the udder of the ewe or the region of the milk ridge. While this may be an indirect result of the orientation assumed during the twist and the front kicks that commonly accompany it, the sensation received by a ewe from a front kick directed at her udder must be very similar to the stimulus caused by a nursing lamb when butting the udder to induce milk let-down — a behaviour that induces the ewe to stand. Geist (1971) found that the front kick was only rarely performed by ewes, and then only by dominant ones. It is useful to note that it is only dominant ewes who mount other ewes, so in this context as well, the front kick could be acting as an intention movement for (dominance) mounting.

Most of the sexual behaviour patterns exhibited by the ewes are purely investigational and do not appear to have the ritualised properties that some of the ram behaviour patterns do, except perhaps the 'looking back' behaviour pattern which, as mentioned previously, involves a degree of head turning that is not necessary to merely observe what is happening at the ewe's rear. However, one behaviour pattern common to ewes departs from this general scheme. It is the tail fanning behaviour pattern which could be the functional analogue of the Flehmen in the ram. Tail fanning, which is also common in oestrous does, is probably a pheromone dispersing behaviour and therefore a strictly functional act rather than a derived behaviour pattern as chinning has been derived from the mount. Tail fanning also occurs in nursing lambs. The ewe's response to this behaviour in her lamb is to sniff its anogenital region, probably as an identity check.

One difficulty encountered in this study was the allowance that had to be made for sexual behaviour patterns that are also used in aggressive situations. Whether to label them as aggressive patterns (as Geist,1971, tended to do), or sexual patterns that are common to another context has been a major dilemma. Whether the patterns in question (low stretch, twist, front kick etc.) are true aggressive behaviours

that have appeared as sexual patterns through a process of ritualisation of confliot behaviour, or whether the behaviours are true sexual behaviour patterns that by a process of sexual inversion, caused by conflict in aggressive situations, came to be used as aggressive behaviours, is unknown. While the true course of development is not known it is felt that the latter process of sexual behaviour patterns finding use in aggressive situations via a process of sexual inversion is more likely because, a) if the sexual context is examined, only a few behaviour patterns are ambiguous (twist, front kick, low stretch) whereas in the aggressive context almost all the behaviour patterns become ambiguous, especially mounting, which is a definite sexual behaviour pattern, and b) the fact that the response to the sexual behaviour patterns used in an aggressive context, is further sexual behaviour, such as standing for mounting and lordosis.

It is likely then, that the means by which some behaviour patterns have become common to both sexual and aggressive contexts is by a process of sexual inversion occurring in aggression - induced conflict situations. Fraser (1968) noted that the male mating pattern is not sex specific and that temporary inversions in sexual behaviour in individuals of both sex are not uncommon in many species. That these inversions are not impossible reinforces the probability that sexual behaviour patterns that occur as aggressive patterns have been assimilated by a process of sexual inversion during confliot.

It appears that the sexual behaviour patterns of sheep can be divided into two general categories. Firstly there are those patterns that primarily, have a physiological function. This category would contain sniffing, Flehmen, tail fanning, mounting and tupping. Such patterns would have communicatory functions also, but these would be subordinate to the main physiological functions. The second category would contain behaviour patterns that have signal value only. These are the ritualised, appeasement patterns that have a communicatory function, indicating state and intent, and containing the intention movements such as the front kick, chinning and twist. The behaviour patterns of both of these categories are essential to the courtship of sheep to ensure that copulation occurs between the right animals, and at the right time.

B. Experimental Findings.

This study was planned with two main aims in mind. These were a) the determination and description of the motor acts used by sheep during courtship and an analysis of the functions and possible origins of these motor acts, and b) an experiment to determine the effects of continual mating on the behaviour of the ram.

The findings related to 'a' above, are presented in Chapter Two, Three and Six, Section A. The outcome of the mating fatigue experiment and its unexpected termination is discussed in Chapter Four. Though this experiment did not run its full course, a certain amount of data was collected from it, that in conjunction with the findings of the replacement experiment (discussed in Chapter Five), indicated that the dose level of Oestradiol Benzoate (O.B.) given to ovariectomized ewes was capable of influencing at least one aspect of the ovariectomized ewes' sexual activity, the frequency with which the ovariectomized ewes initiated sexual interactions with the ram. Similar findings were made by Lindsay and Fletcher (1972).

There were also definite physiological effects caused by the varied dose levels of O.B. administered to ovariectomized ewes. It was found that as the dose level of O.B. administered was decreased, the interval from O.B. administration to the onset of oestrus was increased and the duration of oestrus decreased. Scaramuzzi et al. (1971) made a similar finding. The implications of this finding are that further experiments may be conducted that use levels of O.B. designed to induce an oestrous state of planned duration and perhaps, intensity. More work is needed to determine whether or not there are differences in breed responses to O.B.

It was not possible to determine any differences in breed performance of sexual behaviour patterns between the two breeds of ewes used in this study because the experimental structure resulted in an unavoidable physiological difference between breeds as well. General observations indicate that little, if any, differences exists between the two breeds of ewe in this respect. One analysis did show that there was little difference in the basic composition of interactions between the two breeds of ewe and the ram, but this finding was limited by the bifactorial differences between the two breeds.

During 1972 when experiments were being conducted with ovariectomized

ewes (see Chapter One) to refine management and recording techniques, a comparison was made between the progesterone intramuscular injections (i.m.i's.) and Medroxyprogesterone acetate (M.P.A.) impregnated tampons as methods of priming for an induced oestrus.[31] No difference between the two methods could be found in the two trials for the interval to oestrus following C.B. and the duration of oestrus. Nor could any differences in the performance of sexual behaviour patterns be detected between the ewes of each treatment. Following two such trials a change was made to M.P.A. impregnated tampons only for further experimental work as this allowed a reduction in the amount of ewe handling necessary in the earlier trials, and because two ewes (one in each trial) had failed to exhibit oestrus when primed with progesterone injections.

In the 1973 experiments the M.P.A. impregnated tampons were again used to prime induced oestrus in the ovariectomized ewes. Results obtained (for interval to oestrus following C.B. and duration of oestrus) were similar to those obtained by Scaramuzzi et al. (1971) who used comparable levels of C.B. but employed the progesterone i.m.i. method for priming the induced oestrus.

It appears that, at least at certain dose levels and applications, M.P.A. impregnated tampons are equivalent in affect to specific levels of progesterone i.m.i's. Because the tampon method of priming requires less ewe handling and therefore means less ewe disturbance, it is felt that in certain circumstances it is a superior method of priming to the progesterone injection method and that this finding should be of use in further experimentation.

Two aspects of the recordings that have not been examined prior to this are the results of the night observations and the effects of

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[31] 1972 progesterone and M.P.A. levels.

progesterone i.m.i - 10 mg progesterone in 1 ml peanut oil injected once per day for 5 days. (100 µg O.B. i.m.i. on day 6)
tampon - 40 mg M.P.A. per tampon inserted for 5 days (100 µg O.B. on day 6). (Levels were suggested by one of the thesis supervisors, Dr.M.F.Mc.Donald, Dept. Sheep Husbandry, Massey University). The levels employed in 1973 are given in Chapters Four and Five.

weather changes on the sexual behaviour of the sheep.

The ram was found to have three activity periods during the night. Each period was approximately 1.5 - 2.0 hours in duration and the periods tended to peak at 21.30 hr, 00.30 hr, and 03.30 hr. The times of these activity periods could possibly change throughout the year and may be subject to weather conditions also. In general, sexual activity occurred at the beginning of these activity periods and usually consisted of investigatory behaviour, though the ram was seen to court and mount ewes on several occasions. The remainder of the activity periods were usually spent feeding, while the intervals between activity periods were spent lying down. It was estimated, on the basis of these observations, that less than one quarter of the ram's sexual activity occurred at night and so the daylight observations had probably been successful in observing (approximately) 80% of the ram's daily (24 hour) sexual activity.

Changes of weather did not appear to grossly affect the sexual behaviour of the sheep, though inclement weather could cause (indirectly) minor disruptions to sexual behaviour by its affect on other behaviour patterns. Rain that came with strong winds usually induced shelter seeking, and the sheep often sought shade around noon on fine, warm days. The overall conclusion is that during this study, weather changes seemed to have only a minor affect on the sexual behaviour of the sheep observed. A similar finding was made by Hulet et al. (1962a).

C. Conclusions.

Although one of the features of this investigation was the discovery of a large amount of individual variation in the performance of sexual behaviour patterns in sheep (also found by Banks,1964; Hulet et al., 1962a; Wattner et al., 1967), Hafez (1951,1952) and Inkster (1953) were able to determine the existence of definite breed differences in the performance of sexual behaviour, over and above the individual differences noted in this and the other, above mentioned, studies.

The possibility that major behaviour differences exist between breeds could markedly affect the breeding efficiency of crossbred animals, so the possible existence of breed differences in sexual behaviour warrants further attention.

It is obvious that more investigation is called for, and not only into behavioural differences between breeds. One of the greatest problems in this field is the lack of a full ethogram for sheep. An ethogram is not only a foundation that further studies can build on but is a necessity if the breeding of stud and production stock is to realise its full potential. It is no longer sufficient to select breeding stock on the basis of morphological and physiological traits alone. As natural selection pressures for precise, correctly executed courtship have been reduced by modern husbandry methods, it has become necessary to take account of the behavioural capabilities of breeding animals when selecting breeding stock because behavioural performance is a critical factor in the reproduction of all animals.

The contribution made by this study to the field of sheep sexual behaviour should provide both a foundation and a stimulus for the further investigation that is required for the construction of an ethogram for sheep. The results of the hormone treatments have indicated both alternative experimental methods for inducing artificial oestrus, and the benefits to be realised by the continuance of sexual behaviour studies outside the natural breeding season.

CHAPTER VII

SUMMARY

1. Preliminary observations of sheep sexual behaviour were conducted during the 1972 breeding season and during the remainder of 1972 and January 1973. These observations were used to determine the sexual motor patterns of the sheep and to refine observation and management techniques. Findings indicated that previous studies on the subject had either presented a simplified account of sheep sexual behaviour patterns or had ignored these behaviour patterns altogether.

2. During the 1973 breeding season, observations were conducted on a mixed flock of entire and ovariectomized ewes running with a Southdown ram. Behaviour patterns observed during interactions between the ram and ewes were recorded and analysed. The sexual behaviour patterns that were recorded are defined, illustrated and discussed in Chapters Two and Three.

3. As it was possible to conduct an experiment within the observation programme for the breeding flock, an attempt was made to investigate the effects of ram fatigue, caused by mating large numbers of ewes, on the behavioural interactions between the ram and ewes. Unfortunately, the experimental ram died before completion of the investigation. Data collected before the ram died, however, was of interest and is discussed in Chapter Four. This includes a comparison of the sexual behaviour of entire and ovariectomized ewes which established different rates of initiation of interactions with the ram, for entire and ovariectomized ewes, and the physiological responses of the ovariectomized ewes to the hormone treatment.

4. A substitute experiment was designed to involve a replacement ram. This investigated the behavioural and physiological effects of different dose levels of hormone on the ovariectomized ewes, It was found that as the dose of O.B. was decreased, the interval to onset of oestrus following O.B. was increased and the duration of oestrus decreased. Indirect evidence of a ram fatigue effect became evident in this experiment.

5. In the final section of the thesis, the possible origins of some of the sheep sexual behaviour patterns are outlined and some functions are suggested. It was considered that many of the courtship display patterns of sheep have arisen from behaviour occurring in conflict situations. It appears that the development of a full ethogram for sheep

would be a great aid to the selection of breeding stock, which at the moment is selected, in the main, on its morphological and physiological merits while the behaviour of the animal is considered only indirectly. The consequences of behavioural parameters in sheep breeding programmes are discussed.

APPENDIX 1.

Sample Recording Sheet for Sheep Sexual Behaviour Patterns.

Date	21/4	Weather	fine, mild.

Time	#	↓↑	Behaviour Under Observation
3°41p.		↓	sn. fl. sn. fd.
	19	↑	fd. lk. ma. fd.

EXPLANATION. At 3.41 p.m. on 21/4/1973, the ram approached (↓) ewe 19 (#) who was feeding (fd.). He sniffed her flank (sn. fl.) and then her perineum (sn.). The ewe looked back (lk) at the ram, then moved off (ma) to resume feeding (fd) elsewhere. The ram commenced to feed (fd).

This is an example of a simple interaction involving investigation of a ewe by the ram.

APPENDIX 2. Observation Calendar for Experiments One and Two

Date	Group A	Group B	Group C	Observation Period
5/3/1973	tampons in			
6				
7				
8				
9				
10				
11		tampons in		
12	Flock mixed	Flock mixed	Flock mixed	
13				
14				
15	Ram 1 in	Ram 1 in	Ram 1 in	
16	tampons out			
17	tampons in			
18	tampons out			
19	O.B. imi		tampons in	
20	Oestrus			I
21				
22				
23				
24		tampons out		
25	tampons in	O.B. imi		
26		Oestrus		II
27				
28				
29				
30			tampons out	night observation
31		tampons in	O.B. imi	
1/4/1973			Oestrus	III
2				
3				
4				
5	tampons out			night observation
6	O.B. imi		tampons in	
7	Oestrus			
8	Ram 1 out	Ram 1 out	Ram 1 out	IV
9	Ram 2 in	Ram 2 in	Ram 2 in	
10				night observation
11		tampons out		
12	tampons in	O.B. imi		
13		Oestrus		V
14				
15				night observation
16				night observation
17			tampons out	
18			O.B. imi	night observation
19			Oestrus	VI
20				
21				
22				
23	tampons out			night observation
24	O.B. imi			
25	Oestrus			VII
26				
27				

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