PART A

CHAPTER 1

LITERATURE REVIEW

INTRODUCTION

The Australian Merino is a lowly prolific breed and over the last 40 years considerable research effort has been expended which aimed to increase, by genetic means, the prolificacy of this breed. Due to the unique fibre characteristics of the Merino, attention has focussed on within-breed methods of selection. Prolificacy is sex-limited in its expression, and in the past selection programmes have been largely restricted to female selection. With sheep breeding, however, because of the male to female mating ratios which are utilised, individual male selection has relatively greater impact on flock improvement than selection of individual females. Increasingly sheep breeders are wishing to identify the genetic merit of their sires for reproductive performance traits.

The review of literature, below, examines the general areas of i) traits of the male which may be related to flock reproductive performance; ii) current methods of selection for prolificacy, iii) the use of male traits as indirect selection criteria for improving prolificacy, and iv) identification of male carriers of the Booroola F gene.

1.1 MALE REPRODUCTIVE PERFORMANCE TRAITS

1.1.1 GONADAL GROWTH AND FUNCTION.

Attainment of mature or adult gonadal function implies production of spermatozoa which are capable of fertilizing the female germ cell. In the male sheep this status is preceded by a complex and relatively lengthy sequence of morphological changes which begin early in foetal development.

It is convenient to divide gonadal development into three stages as identified by Courot (1971).

The impuberal (or pre-pubertal) stage begins from the time of sex

differentiation (approximately the 35th day of embryonic life; Sapsford, 1962) and is characterised by the seminiferous tubules maintaining a constant structure with gonocytes at the centre of the tubules and supporting cells at the periphery. The total number of both cell types increases continuously. Likewise, during this phase, the interstitial component of the testis shows continuous differentiation and volumetric growth. No Leydig cells can be recognised (Sapsford, 1962), but the seminiferous tubules, which occupy about 50% of testicular volume at birth, increase in proportion relative to the interstitial component.

The pubertal stage of development is a period of rapid testicular growth during which spermatogenesis is established. Spermatogenesis involves the transformation of undifferentiated stem cells (type A spermatogonia) into highly differentiated immature spermatozoa. This process takes place whilst the germ cells are embedded in the cytoplasm of the Sertoli cells. Specific details of the development from spermatogonia to spermatozoa have been described elsewhere for the ram (reviewed by Amann, 1970) and will not be considered in detail here.

Each stage of development involves a specific and constant association of germ cell types and occurs in a co-ordinated manner, such that localised portions of seminiferous tubules can be observed to be in the same stage of the spermatogenic cycle. In the ram, these stages follow each other in succession along the length of a tubule, which, on a whole testis basis results in a continuous and relatively constant production of spermatozoa (Courot, Hochereau-de-Reviers and Ortavant, 1970).

At the time the first spermatozoa are released into the lumen of the seminiferous tubules, a large proportion of the differentiating germinal cells degenerate, but gradually the yield of the various stages of spermatogenesis improves (Courot et al., 1970). From the beginning, however, the absolute rate of differentiation is identical to that of the adult (Courot, 1971).

The post-pubertal stage is an on-going period of slow testicular growth during which the animal maintains an adult rate of spermatogenesis (Hochereau-de-Reviers, 1981).

1.1.2 FACTORS AFFECTING GONADAL GROWTH AND DEVELOPMENT

1.1.2.1 Age and Liveweight

Most of the studies on gonadal growth and development have concentrated on the pubertal stage, with relatively few workers tracing development through all three stages identified above. In those investigations which have covered all phases, the most common approach has involved serial castration of samples of animals at different agesduring the development period. The few investigations where gonadal development of individual animals has been followed, have been restricted to external measurement of gonadal dimensions, since serial biopsy is not practical in the ram.

1.1.2.1.1 Testicular size or weight.

Detailed studies of the relationship between testicular development, age and liveweight have been reported by Watson, Sapsford and McCance (1956); Courot (1962); Skinner, Booth, Rowson and Karg (1968) and Colyer (1971). In general testicular size was more closely related to liveweight than to chronological age.

Watson et al. (1956), who studied development in Merino lambs aged between one and 64 weeks of age, noted that the weight of the testes at any one age varied widely between animals. However, the general pattern of development was sigmoidal. These authors found that as bodyweight increased from 23 to 27 kg, the relative increase in the weight of the testes was much greater than at higher or lower bodyweights. Upon treating the data separately within three bodyweight classes, linear regressions on liveweight counted for 96% of the variation of testicular weight. Colyer (1971) observed a linear increase in testicular weights up to a bodyweight of 20.9 kg in Clun Forest rams. This was followed subsequently by a significantly greater rate of increase at higher bodyweights. This study was concluded at

21 weeks of age when the rams had average liveweights of 12kg, and a third and slower phase of growth was not observed.

1.1.2.1.2 Seminiferous tubule function.

The relationship between age and liveweight and the development of seminiferous tubule function has been investigated by histological studies of testicular tissue following castration (Carmon and Green, 1952; Watson et al., 1956; Sapsford, 1962; Courot, 1962; Skinner et al., 1968; Dyrmundsson and Lees, 1972 and Hawker, 1976). Histological characteristics vary widely at any one age but are closely related to the weight of the testes and thus to the liveweight of the ram.

Watson et al. (1956) observed that the semininferous tubules were present as solid or only slightly vacuolated cords in all rams less than 21 kg liveweight. Spermatozoa were not seen in any animals weighing less than 27 kg but were noted in almost all rams greater than 28 kg liveweight. Dyrmundsson and Lees (1972) in their study of Clun Forest rams concluded that the first appearance of the spermatozoa occurred when they had reached 35-45% of mature liveweight. They further suggested that rams need to reach a certain degree of body growth and testicular size before spermatozoa are formed, and there is a minimum age below which this stage is not reached. They were not, however, able to define specific values for these critical events in their study of Clun Forest rams.

1.1.2.1.3 Attainment of mature gonadal function.

The rate of attainment of mature gonadal function is of considerable practical importance and there are many reports in the literature of the age and liveweight at which rams attain this stage of development. In most studies, the criterion used to define this stage of development has been the first appearance of spermatozoa, established either by repeated ejaculation of individual rams or through periodic castration of groups of rams. The length of the time intervals between successive samplings in many studies casts some doubt upon the precision of results, as does the practice of

defining age simply from the mean birth date of the overall flock. However, whilst there are large differences between studies in the ages and liveweights at which spermatozoa are first detected, the major feature of these reports is the considerable variation between animals within studies.

The quality of semen and quantity of spermatozoa produced by rams during the pubertal stage of development is far below that produced by adult rams. Semen from pubertal rams is of low motility, and abnormal and dead sperm are more numerous than in ejaculates from adult rams (Louw and Joubert, 1964; Skinner and Rowson, 1968 and Courot, 1976). Louw and Joubert (1964) using electro-ejaculation techniques, quantified the rate of improvement in these parameters in Dorper rams over a period of 13 weeks following the first appearance of spermatozoa. During this relatively short period, they found a rapid improvement in ejaculate volume (0.20 to 1.20 ml), spermatozoa numbers (75.6 to 3,359 million sperm per ml), motility rating (0.7 to 5.0) and percent live sperm (27% to 83%). In some studies sperm production continues to increase with age beyond this initial level(Lightfoot, 1968; Colas and Zinszuer, 1975), but Knight (1977), found no relationship between age and sperm production in Merino rams aged from one to four years and Romney rams aged two to five years.

1.1.2.2 Nutrition

Direct information on the effect of nutrition on gonadal development in rams is limited. Dun (1955), Watson *et al*. (1956) and Skinner and Rowson (1968) all concluded that nutrition was one of the major factors affecting rate of gonadal development. However, in those studies, the variations in levels of nutrition were of a seasonal nature and hence confounded with changes in photoperiod. In an attempt to directly study the effects of nutrition, Pretorius and Marincowitz (1968) fed South African Merino ram lambs, from three days of age on *ad libitum* diets containing 110, 140 and 170% (L, M and H respectively) of maintenance energy requirements. Feed intakes were such that the M and H lambs grew at similar rates. Appearance

of first sperm in ejaculates (collected weekly by electro- ejaculation) was attained at a significantly earlier age and liveweight by the M and H rams than by the L rams.

In mature rams, undernutrition has been shown to adversely affect testicular size and is accompanied by correlated changes in the spermatozoa producing activity of the testis (Setchell, Waites and Lindner, 1965; Moule, Braden and Mattner, 1966 and Parker and Thwaites, 1972). These effects have also been confirmed in the converse type of experiment, where rapid increases in testicular size, seminiferous tubule diameter and sperm production have been recorded following both energy and protein supplementation above maintenance requirements (Salamon, 1964; Lindsay, 1976 and Oldham, Adams, Gherardi, Lindsay and Mackintosh, 1978).

1.1.2.3 Photoperiod

Whilst there have been many reports on the effects of photoperiod on gonadal function in the adult ram, there have been relatively few studies of the effect of photoperiod on gonadal growth prior to adulthood.

Courot, de Reviers and Pelletier (1975) have shown that season of birth affects testicular growth in ram lambs, with the testes of animals born in spring growing more slowly than those born in autumn. In contrast, Alberio and Colas (1976) found that development of the testis of lambs in their study was independent of the season of birth. Howles, Webster and Haynes (1980), who maintained Suffolk and crossbred ram lambs in constant short (8 hours) or constant long (16 hours) photoperiod from four to 20 months of age, found no differences between these treatments in the patterns of testicular growth. However constant photoperiod whether short or long, produced a different developmental pattern compared with rams kept in simulated natural environments.

In mature rams, seasonal effects on each step of the spermatogenic process have been shown, resulting in a higher quantitative sperm production in autumn compared with spring (Courot, 1976). In a study of Ile-de-France

rams in France, Hochereau de Reviers, Loir and Pelletier (1976) found that testicular weight, volume of inter-tubular tissue, seminiferous tubule length, Sertoli cell size, spermatogonia numbers and yield of spermatogonial divisions were all increased significantly in autumn compared with spring. However, the same authors noted, that in rams of the Prealpe-du-Sud breed, there were much smaller variations in testicular weight between seasons.

Whilst spermatogenic activity was initially thought to be regulated purely by the numbers of hours of daylight, with maximum activity occurring whilst daylight decreases, more recent research suggests that the photo-periodic control of seasonal changes in spermatogenic activity may involve an interaction between the pineal gland and the generation of a circadian rhythm in the brain, regulated in its timing by the daily cycle of light and darkness (Lincoln, Almeida and Arendt, 1981).

1.1.2.4 Genetic Effects

The literature contains few reports of studies with sheep specifically designed to examine between and within-breed variation in male gonadal traits. Considerably more research has been carried out with beef and dairy cattle due largely to the widespread use of Artificial Insemination (AI) in this species. Efficient AI programs require objective assessment of each individual's potential usage and depend on males with repeatable gonadal output. Thus variation between males in gonadal production traits is more routinely identified.

1.1.2.4.1 Between-breed studies.

In the sheep, between-breed-studies have been conducted by Carmon and Green (1952), Land and Carr (1975), Land and Sales (1977), de Reviers *et al.* (1980), Louda, Doney, Stolc, Krizek and Smerlia (1980) and Dacheux, Pisselet, Glanc, Hochereau de Reviers and Courot (1981).

In their comparison of Hampshire and Southdown ram lambs, Carmon and Green (1952) observed differences in testicular growth relative to age but no difference relative to liveweight. At any specific age, testicular

weight was greater in Hampshires, though seminiferous tubule diameter showed a more rapid increase with testicular weight in Southdowns. Land and Carr (1975) identified breed differences in testicular size, testicular growth rate and the degree of hypertrophy of the remaining testis following hemi-castration. The relative increase in testicular growth following hemi-castration at 12-16 weeks of age was greatest in Merinos, (72%), least in Finnish Landrace, (42%), and intermediate in Scottish Blackface, (57%). The authors suggested that these differences may have been due to breed differences in the sensitivity to negative feedback from the testes. A subsequent study by Land and Sales (1977) established that in comparison with Merino rams, the diameter of the testes of Finnish Landrace and crossbred ram lambs at six months of age was a greater proportion of their diameter at 18 months, The Merino rams also showed an earlier increase in testicular diameter at the beginning of the sexual season than Finns or crossbreds.

Romanov and Finnish Landrace sexual development has been compared by Louda et al. (1980) who found that at 13 months of age testicular dimensions were greater in the Romanov and, whilst Romanov rams did not show seasonal variation, rams of the Finnish Landrace breed showed a reduction in testicular volume as the breeding season progressed.

Breed differences in sperm production have been shown by Dacheau et al. (1981) and these differences were associated with differences in the flow rates of rete testis fluid following cannulation.

1.1.2.4.2 Within-breed studies.

Many of the between-breed reports on gonadal growth and development in ram lambs have also shown considerable within-breed variation, but in none of these studies have the sources of this variation been systematically identified and partitioned.

Genetic parameters for testicular size and semen traits have been reported by Goerke, Thrift and Dutt (1970), Fogarty, Lunstra, Young and

Dickerson (1980), Thorsteinsson, Thorsteinsson and Dyrmundsson (1982), and Hanrahan and Quirke (1982).

Goerke et al. (1970) calculated heritability estimates for semen traits, from data collected over a 12 year period from a small flock of Southdown sheep selected for early lambing. These estimates were based on only 22 degrees of freedom for sires, and this is reflected in the large standard error of the estimates. Moderately high heritabilities for semen volume (0.43 $\pm$ 0.23) and percent abnormal sperm (0.42 $\pm$ 0.23) at yearling age were obtained, but the data were not corrected for systematic environmental effects and there was a change in the method of semen collection (from artificial vagina to electro-ejaculation) during the course of the study.

Testicular diameter and scrotal circumference at 17-21 weeks of age in 1553 rams of various breeds were analysed by Fogarty et al. (1980). The fixed effects included in the model were breed, year, season, type of birth and rearing, age of dam, ram age and interactions, with and without liveweight as a covariate. All fixed effects were a significant source of variation. Heritability estimates were relatively low for adjusted 140-day scrotal circumference and testicular diameter, being 0.14 $\pm$ 0.08 and 0.13 $\pm$ 0.08 respectively (130 degress of freedom for sires). Adjustment for liveweight reduced these estimates.

A relatively high heritability estimate of 0.47 $\pm$ 0.15 for testicular weight at 129 days of age and 36.3 kg average liveweight has been reported by Thorsteinsson et al. (1982). This estimate was derived from the records of 695 ram lambs (44 degrees of freedom for sires) adjusted for year, birth type and age and weight at slaughter and is of similar magnitude to estimates for testicular size in other species. Coulter and Keller (1979), for example, report the heritability of scrotal circumference of yearling beef bulls completing a 140-day growth performance test to be 0.69 $\pm$ 0.15 whilst Islam, Hill and Land (1976) quote the heritability of testicular size

in mice to be 0.5.

Genetic correlations (r_g) between various male gonadal traits and between these and other production criteria have not been reported except from the study by Goerke et al. (1970). Their estimates had large standard errors, and given the experimental design inadequacies already indicated, are of little predictive value.

1.1.3 EPIDIDYMAL AND PENIAL DEVELOPMENT

The epididymis has several functions; it serves as the duct conveying spermatozoa from the testes to the vas deferens and is also the location for the maturation of immature spermatozoa and for the storage of those already mature. A comprehensive review of epididymal anatomy and function is provided by Orgebin-Crist (1969).

In the ram lamb epididymal development has often been studied as an adjunct to investigations of testicular growth and in general the patterns of growth and cellular differentiation are closely correlated.

As with testicular size, at any one age, epididymal weight varies considerably between animals but there is a closer relationship with liveweight. A still closer relationship exists between epididymal and testicular weights, particularly during and after the pubertal phase of sexual development (Watson et al., 1956; Colyer, 1971; Dyrmundsson and Lees, 1972). Colyer (1971) found that the familiar biphasic pattern of growth of the testis was matched by that of the epididymis and noted that in the first growth phase, the rate of development of the epididymis was significantly greater than that of the testis. This suggests, that epididymal development may to some extent be independent of the testis during the pre-pubertal period. In Colyer's study, the increased rate of epididymal growth during the second phase was associated with histological changes in the ductus epididymis, principal among them being an increase in tubular diameter. Seasonal factors appear to have a lesser impact on epididymal size than is the case with the testis (Dyrmundsson and Lees, 1972).

Genetic studies of epididymal size in sheep are limited to that of Thorsteinsson et al. (1982) who estimated heritability (half-sib) of epididymal weight at weaning (129 days of age) to be 0.38 ± 0.13 compared with 0.47 ± 0.15 for testicular weight and 0.48 ± 0.15 for testicular plus epididymal weight calculated from data on the same animals.

Many researchers have attempted to define the point where ram lambs have reached mature gonadal function in terms of easily measured and non-destructive morphological parameters. In numerous studies, the development of the penis has been used as a criterion for such classification. Johnston (1948), Wiggins and Terrill (1953) and Dun (1955) monitored the development of the ovine penis and noted that the breakdown of the adhesions between adjacent cell layers of the preputial mucosa, which in the post-natal ram lamb envelops the glans penis and processus urethrae, was associated with testicular development. Complete separation of the prepuce from the glans penis occurred just prior to the onset of spermatogenesis in a large proportion of animals.

As with testicular development, penial development is more closely related to liveweight than chronological age. Dun (1955) working with Merinos found that age at penial maturity ranged from 182-213 days whilst liveweight ranged from 24 to 38 kg; Hawker (1976) using the same criterion and breed noted an age range from 115-310 days. Skinner and Rowson (1968), who studied penial development in Suffolk rams noted that the penis had separated from the prepuce at a much earlier age (63 to 70 days) but at similar liveweights to those in other studies.

Also in common with testicular development, a low level of nutrition considerably retarded penial development in Merino ram lambs when compared to medium and high levels of nutrition (Pretorius and Marincowitz, 1968).

1.1.4 ENDOCRINE CONTROL OF GONADAL DEVELOPMENT AND MAINTENANCE OF SPERMATOGENESIS IN THE RAM

Evidence for the endocrine control of testicular development and

maintenance of spermatogenesis in the ram has mainly been derived from studies utilizing the following techniques:

i) the effect on testicular development of hypophysectomy combined with subsequent hormone replacement therapy,

ii) characterisation of hormone concentrations and patterns of release and determination of the relationship between changes in these parameters and testicular development,

iii) characterisation of changes in the sensitivity of the pituitary to gonadotrophin-releasing hormone (Gn-RH), and

iv) the effect of castration and cryptorchidism on the patterns of gonadotrophin and androgen secretion.

Courot (1971) used foetal and neonatal hypophysectomy to establish that the pituitary has a profound and rapid effect on the late foetal (> 110 days after gestation) and neonatal testis in the sheep. Ablation of the pituitary causes a rapid decrease in testicular weight and regression of both interstitial tissue and seminiferous tubule dimensions. The number of supporting cells decreases rapidly and germinal cell differentiation ceases. Courot (1965) also showed that of the anterior pituitary hormones, only lutenizing hormone (LH) and follicle-stimulating hormone (FSH) can reverse this effect in the sheep with LH being the more active. When LH and FSH are administered to hypophysectomised lambs together, there is a strong synergistic effect on the weight of the testes and on the activity of the seminiferous tubules.

Subsequent research in various species has established that LH and FSH are released from the pituitary under the influence of the hypothalamic hormone, Gn-RH (Reeves et al., 1970; Foster et al., 1972).

LH acts on the Leydig cells (Catt and Dufau, 1976), while the supporting cells and their differentiated product, the Sertoli cells, which are located within the seminiferous tubules, have been shown to be the target site for FSH (Means et al., 1980). Testosterone, a steroid hormone

has a major role in the maintenance of the secondary sex organs and spermatogenesis is implicated along with other steroids in the initiation and control of sexual behaviour (Mattner, 1980).

Plasma concentrations and the secretory patterns of FSH, LH, testosterone and prolactin in the developing ram have been studied by Skinner et al. (1968), Courot (1971, 1975), Blanc and Terqui (1976), Walton et al. (1978), Foster et al. (1978), Lee et al. (1976a, 1976b, 1981), Schanbacher and Crouse (1980) and Sanford et al. (1982). There are differences between these studies in hormone assay methods, breeds of sheep utilized, nutrition and photoperiod under which the sheep were raised, but there is an encouraging degree of agreement between studies in the general conclusions reached.

Plasma FSH levels in the ram lamb which are low at birth, increase progressively to reach a maximum level at five to eight weeks of age, and thereafter stabilize or progressively decrease to the levels found in the adults (Lee et al., 1976a, Blanc and Terqui, 1976). FSH release at all ages appears to be relatively non-pulsatile and not associated with the peaks of LH (Sanford et al., 1982).

Plasma LH levels, like those of FSH, are low at birth and remain low until an abrupt increase at four to six weeks of age, an event which Foster et al. (1978) have shown to be associated with the commencement of a pulsatile secretory pattern. Subsequently, plasma LH levels slowly decline or remains static until a secondary rise occurs after 30-40 weeks of age (Lee et al 1976a, 1981).

Prior to, or associated with the abrupt increase in plasma LH, there is a substantial elevation in the levels of circulating testosterone, which has been steadily increasing from very low levels at birth (Lee et al 1976a, Bremner et al., 1981 and Lee et al., 1981). This rapid rise in testosterone concentration is thought to be due either to an increased sensitivity of the testicular Leydig cells to LH (Lee et al., 1981) or more likely to the rapid

increase in Leydig cell number which both Sapsford (1962) and Hochereau de Reviers and Courot (1978) have shown to occur at this stage of development.

Lee et al. (1976b) have shown increased levels of FSH and LH in plasma at 6-8 weeks and 2-3 months of age respectively. They suggest that these changes reflect an alteration in the sensitivity of the hypothalmus or pituitary gland which facilitates the beginning of spermatogenesis. The relative fall in FSH after this period, may reflect the initiation of secretion of a non-steroidal FSH-inhibiting hormone which has been named inhibin (Setchell et al. 1977; Walton et al., 1980).

The existence of a non-steroidal feedback mechanism regulating FSH release from the pituitary is supported by the study of Blanc and Terqui (1976) who used surgical cryptorchidism in ram lambs at two weeks of age to prevent seminiferous tubule development. The treatment did not affect subsequent testosterone production when compared to lambs left entire, but did result in significantly elevated FSH levels at 5-8 weeks. The authors suggested that the difference in FSH levels was due to the beginning of inhibin synthesis in the entire males and that this did not occur in the cryptorchids due to disruption of Sertoli cell differentiation. Similar conclusions have been drawn by Walton et al. (1978, 1980) who provided evidence that the hypertrophy of a remaining testis following hemicastration is associated with an increase in plasma FSH levels rather than a generalised increase in total gonadotrophin secretion.

The evidence for a quantitative association between gonadotrophin levels, testicular function and sperm production has been more thoroughly studied in adult sheep. These studies have largely concentrated on associations within animals between seasons or between periods under differing artificial light regimes.

As has been shown earlier, testicular size and sperm production in adult rams show rhythms which are closely associated with photoperiod. Investigation of the circulating levels of the gonadotrophins and

testosterone in adult rams has revealed that LH and testosterone levels parallel the variation in testicular size, but that the association with FSH levels is much less clear (Purvis et al., 1974; Sanford et al., 1974; Schanbacher and Ford, 1976). Courot and Ortavant (1981) have shown that a linear relationship exists between FSH levels and testicular size up to a maximum FSH level after which no further effect on the gonad is evident. A clearer relationship between these two parameters was also evident when FSH levels, six weeks prior to testicular measurements, were compared. These authors suggested that FSH control of the testis is therefore being directed at the early stages of spermatogenesis.

The precise target cells for FSH, LH and testosterone have not been specifically identified in the ram. However, Courot and Ortavant (1981) suggest, rather than FSH and/or LH acting directly on germ cells, their action is more likely mediated through the action of FSH on Sertoli cells and LH on Leydig cells. Sertoli cells have been shown to possess FSH receptors (Steinberger and Steinberger, 1977) and, in response to FSH stimulation, secrete Androgen Binding Protein (ABP) which has been implicated in the support of meosis and spermiogenesis in the rat (Means, 1977; Jegou, Dacheau, Garnier, Terqui, Colas, and Courot, 1979).

The seasonal changes in pituitary secretion of gonadotrophins may arise from changes in feedback sensitivity. Such a hypothesis is supported by the studies of Pelletier and Ortavant (1975) and Schanbacher (1980) which have shown that the pituitary is more sensitive to steroid negative feedback during the spring. Lincoln (1977, 1979a) in his work with the highly seasonal Soay breed, has shown that increased numbers of Gn-RH pulses are released from the hypothalmus as daylength shortens. He has also shown that exogenous Gn-RH administration during long days can stimulate changes in gonadotrophins, testicular growth and testosterone production which are comparable to the changes induced by the onset of short days.

Hypothalmic control of gonadotrophin secretion is thought to be

mediated by the pineal gland, since pineal inactivation by surgical means causes a cessation in the seasonal rhythms of gonadotrophin secretion and testicular size (Barrell and Lapwood, 1978, Lincoln, 1979b). There is at present a great deal of research being directed at understanding the role of the pineal gland and its major secretory product, melatonin. However, the results of these investigations in the ram are not yet conclusive (Lincoln and Short, 1980).

1.2 LIBIDO AND SERVING CAPACITY

1.2.1 GENERAL

Wodzicka-Tomaszewska, Kilgour and Ryan (1981) have stated that the term "libido" was first used by Freud in 1894 to refer, in a human context, to the force by which sexual instinct is represented in the mind. In the context of domestic sheep production, libido has been defined by Raadsma (1981) as the "desire of a ram to mount and achieve one or more services (ejaculations) with the available oestrous ewes".

Serving capacity on the other hand is the ability of a ram to achieve a number of services in a given period of time. This measure therefore incorporates components of libido and mating dexterity and thus measures the efficiency with which an animal achieves intromission.

Associated with the concepts of libido and serving capacity is an elaborate courtship ritual which involves behavioural interaction between male and female. Banks (1964) has characterised in detail this ritual for domestic sheep.

1.2.2 MEASUREMENT

In the context of natural mating (as distinct from artificial insemination), libido and serving capacity should ideally be measured in a field mating situation, where the ram has available to him sufficient oestrous ewes to enable his maximum capacity to be expressed under

conditions where interaction between rams occurs. However, such paddock observations are extremely laborious and liable to error in the differentiation between mounts and services. This has led to the development of test procedures aimed at predicting paddock mating performance. In general, these tests all involve an artificial mating situation, where observations on various measures of libido and mating dexterity, are recorded over a set time period. Such tests have involved three basic approaches: subjective assessments; measurement of reaction time to first mount or ejaculation or between successive ejaculations; quantification of numbers of mounts, serves or mount to serve ratio during a set time period.

1.2.2.1 Subjective assessment

Early attempts to evaluate rams involved allocation of scores based on the subjective assessment of the behaviour of rams attempting to serve an artificial vagina which was either hand held or fitted to a dummy sheep (Yeates, 1949; Ahmed, 1955). Whilst this technique takes account of all visible behavioural signals, it is subject to observer bias. The relative effectiveness of such scoring systems have not been tested by relating scores to field mating performance.

1.2.2.2 Reaction times

Several researchers have utilised the concept of reaction times to differentiate between the libido of rams, and the most widely measured parameters have been time to first mount or time to first ejaculation. Wiggins, Terrill and Emik (1953), and Mattner, Braden and George (1971) reported negative relationships between time to first service and measures of paddock performance. However, Kilgour (1981) found this parameter to be of low repeatability (0 to 0.18) and Wodzicka-Tomaszewska _et al_. (1981) concluded that, although reaction times identify males which get excited and ejaculate quickly, they are of little value for predicting the ram's ability to ejaculate repeatedly.

1.2.2.3 Number of mounts and services during a specified time period

The basis of the techniques used for research on numbers of mounts or services during a specified time period, was the method developed by Mattner, Braden and George (1971). This was the first investigation which aimed to evaluate different parameters as predictors of paddock mating performance. These workers designed an individual ram pen-test procedure, which utilised five oestrous ewes enclosed in pens 30-50 m^2. Each ram was tested for 20 minutes on three separate occasions, seven to 10 days apart. The parameters measured were i) number of mounts without service, ii) number of services, iii) mount to service ratio, and iv) reaction time to first mount and serve. The measure most highly correlated with subsequent service activity in paddock mating was the mean number of services in the three 20-minute pen-tests.

In a further series of studies, Kilgour and Whale (1980), modified the procedures of Mattner et al (1971) in an attempt to determine whether different test conditions and test times would allow rams to better express their flock-mating potential. They found that the mean number of services during two one-hour pen tests was highly correlated with the number of ewes inseminated during a paddock joining ($r = 0.88$), and that tests of 20-minutes duration were not of sufficient length to distinguish accurately between rams. The above study also revealed that the number of services performed by rams in each of the two one-hour tests was significantly correlated ($r = 0.77$). Kilgour (1981) has also shown that tests of one-hour were as efficient as tests of three hours duration in distinguishing between rams.

Single ram pen-tests as described above are time-consuming and labour intensive and take no account of the effect of the social interactions between rams which occur in paddock matings involving more than one ram. These tests also require a source of oestrus-induced ovariectomised ewes or entire ewes in natural oestrus. This has led to the evaluation of multiple

ram pen-tests and the use of restrained non-oestrous ewes in procedures similar to that developed by Blockey (1976) for libido testing of cattle.

Rival and Chenoweth (1982) have shown ram performance in such tests to be repeatable and to result in a range of scores adequate for comparison between animals.

1.2.3 RELATIONSHIP BETWEEN MEASURES OF SERVING CAPACITY AND FLOCK REPRODUCTIVE PERFORMANCE

Several studies during the 1970's in Australia and New Zealand, investigated the relationship between serving capacity, as assessed by pen-tests, and paddock mating performance as indicated by observations of mating activity, ewes detected in oestrus and ewes pregnant (Cahill, Blockey and Parr, 1975; Fletcher, 1976; Walkley and Barber, 1976 and Allison, 1978). All these investigations utilized 20-minute pen-tests to assess ram serving capacity and as suggested by Kilgour (1980), such tests may not adequately distinguish between rams. Relatively high ram to ewe ratios were used to assess paddock mating perfomance in several of these studies, and this may have limited the full expression of the capacity of individual rams. Haughey (1959), for example, found that individual rams were capable of impregnating up to 250 ewes during paddock matings lasting the length of one oestrous cycle.

The results of trials where rams have been assessed for serving capacity on the basis of one-hour pen-tests and where rams were subsequently challenged with a high number of oestrous ewes during a paddock joining period, have shown that serving capacity measures are related to flock fertility parameters (Kilgour, 1980 and Kilgour and Whale, 1980). However, such relationships have only been found when paddock mating periods were restricted to one oestrous cycle in length. Where mating periods typical of commercial joining have been used (two or more oestrous cycles in length), the number of ewes inseminated or pregnant has not been related to measures of serving capacity. This is because the number of oestrous ewes available

to mate after the first seventeen days are insufficient to allow high serving capacity rams to continue to perform at their maximal level (Kilgour, 1980).

In all the studies mentioned above, the rams were joined in paddock mating trials to either mature or a mixture of mature and maiden (non-parous) ewes. Maiden ewes have a shorter oestrus period (12.6 vs 20.5 hours) and their courtship and harem forming behaviour is less developed than in mature ewes (Blockey and Cumming, 1975). Thus, the influence of ram serving capacity on maiden ewe reproductive performance could be more important than that for mature ewes. Whilst there is no published work to support this contention, Blockey (1983) cites unpublished results of I.D. Killeen which show a significant advantage in pregnancy rates of maiden Merino ewes joined with rams of high serving capacity.

There have been suggestions (Blockey, 1983) that the serving capacity of rams can have a direct effect on flock prolificacy (lambs born per ewe lambing). Whilst it has been shown that ewes served two or more times in the one oestrous period have a better chance of becoming pregnant than ewes served only once (Mattner and Braden, 1967), the work of Restall, Brown, Blockey, Cahill and Kerins (1976), suggests that fertilisation is an all or none process and that very few multiple ovulating ewes exhibit partial fertilisation. Thus any effect of high serving capacity rams on lambs born per ewe joined operates through the effect of such rams on pregnancy rates, rather than a direct ram effect on prolificacy.

1.2.4 SEXUAL INHIBITION

In almost all studies of ram sexual behaviour reported in the literature, a varying percentage of tested rams showed no sexual activity in the presence of oestrous ewes or could not be trained to serve an artificial vagina (e.g. Hulet,Blackwell, and Ercanbrack, 1964; Pretorius 1967; Mattner et al., 1973; Fletcher, 1976; Walkley and Barber, 1976 and Kilgour and Wilkins, 1980). The proportion of such rams in any group varies

considerably (range 3.3% to 67% in the above reports) and may be at least partly dependent upon the amount of prior heterosexual mating experience. (Kilgour, 1981). However, Fletcher (1976) did not find any effect of previous contact with ewes when rams were pen-tested at 76 weeks of age, but, the animals used in this study displayed a very low level of sexual inhibition(4.9%).

Hulet et al. (1964) and Mattner et al. (1973), found that 83% and 88% of rams which were initially sexually inactive in pen-tests, began mounting and serving when constantly exposed to oestrous ewes. The time taken to commence such activity varied from one to three or more days in the case of the former study, whilst Mattner et al. (1973) found that it varied from three hours to 33 days. In both studies some rams remained sexually inactive during the study period. Although Hulet et al. (1964) reported that the libido of those rams initially inactive, appeared normal when they did begin to mount and serve, Mattner et al. (1973) noted that the initially sexually inactive rams marked fewer ewes, and of the ewes marked, fewer lambed when compared to rams that were initially active in pen-tests. These latter authors concluded, however, that under paddock mating conditions with a joining period of five weeks, relatively high ram percentages and with mature ewes, the presence of up to 50% of sexually inactive rams would not depress lambing rates.

1.2.5 FACTORS AFFECTING LIBIDO AND SERVING CAPACITY

1.2.5.1 Age

From a very early age, ram lambs exhibit signs of sexual behaviour with pre-pubertal mounting, both hetero- and homosexual in nature, being a common occurrence (Banks, 1964). Whilst pubertal lambs show clear signs of mating ability, development of the full range of behavioural patterns associated with courtship and mating dexterity appears to occur as a consequence of mating experience rather than of chronological age (Dyrmundsson, 1972). Young inexperienced rams tend to serve less ewes than mature sexually

experienced rams (Lindsay, Gherhardi and Oldham, 1976). However, observations by Mattner et al (1971, 1973) and Mattner and Braden (1975), suggested that the libido and mating performance of individual young Merino rams does not undergo marked changes relative to that of their peers during the following one to two years.

1.2.5.2 Dominance

As with many other species of animals, when a group of male sheep are confined together a dominance order is quickly established by acts of aggression and fighting (Lambourne, 1956) and this order generally remains stable for relatively long periods of time (Schreffler and Hohenboken, 1974; Fowler and Jenkins, 1976). In general, mature animals are dominant to young rams (Hulet et al. 1962b) but within groups of similar age and heterosexual experience, dominance order is not consistently related to physical size (Marincowitz, Pretorius and Herbst, 1966 and Schreffer and Hohenboken, 1974).

The effect of dominance order on libido and serving capacity can be quite different in pen and paddock mating situations. In confined areas, dominant rams have been shown to suppress the sexual performance of subordinate rams (Lambourne, 1956; Marincowitz et al. 1966 and Lindsay et al., 1976). Thus, in pen-tests where visual contact between rams is allowed, or where rams are tested in groups, a ram's serving capacity may be affected by his dominance rank. Lindsay et al. (1976) termed the inhibition of a subordinate ram's performance by a dominant ram watching from nearby, the "audience" effect, and its influence has been shown by Kilgour (1980) to lower the repeatability of pen-test serving capacity.

Although some studies have shown that dominant rams can suppress the flock mating activity of subordinate rams, in general, these studies were conducted in small paddocks where ram contact was relatively frequent (Lambourne, 1956; Bourke, 1967., Lindsay et al., 1976 and Edey, Kilgour and Bremner, 1978). In contrast, under open pasture conditions where paddock size was more typical of commercial properties (in Australia, at least)

little evidence has been found of dominant rams adversely affecting the performance of subordinates (Lindsay and Robinson, 1961 and Mattner et al., 1967).

1.2.5.3 Nutrition

The level of nutrition is vitally important in the sexual development of the ram lamb (Dyrmundsson, 1973), and the rate of sexual development is highly related to the growth rate of the animal (Watson et al, 1956). Thus, undernutrition can markedly delay the full development of libido. However, there is no firm evidence to link such delays in sexual development with sub-optimal mature mating performance.

The results of investigations into the effect of nutrition on libido and serving capacity in mature rams are conflicting. However, in several of the studies where no effect on sexual performance was found, either the treatment effects (deficiencies in certain components of the diet, etc) were relatively mild or the precision of the libido and serving capacity tests used was probably not sufficient to adequately distinguish between the performance of the test rams.

Gross deficiencies of nitrogen in the diet of rams did not affect libido as measured by reaction time at 14-day intervals (Warnick, Meacham, Cunha, Loggins, Hentges and Shirley, 1961), but such a result is perhaps not surprising in view of Kilgour's (1981) work which shows that reaction time has a very low repeatibility. Similarly, Tilton, Warnick, Cunha, Loggins and Shirley (1964) found that nutritional stresses which gave rise to severe losses in bodyweight, did not affect reaction time. In contrast Mattner and Braden (1975) found that undernutrition, which led to a liveweight loss of 0.5 to 0.6 kg per week, caused a decline in libido within five weeks. Likewise Parker and Thwaites (1972), who studied groups of mature rams fed diets at maintenance, 75%, or 50% of maintenance levels over a 15-week period, observed that underfed rams required longer to ejaculate, showed more mounting activity but ejaculated less frequently than their adequately

fed controls. The effect on mating behaviour appeared to be mediated through general muscular weakness and reduced libido rather than simply through the latter.

Attempts at enhancing libido and serving performance by feeding high energy diets, have been largely unsuccessful, despite causing significant increases in liveweight (Mattner and Braden, 1975). Such treatments can cause obesity, which has been shown to severely reduce sexual performance, particularly if associated with hot weather (Okolski, 1975).

1.2.5.4 Photoperiod and Season

There are many reports of seasonal changes in the libido of mature rams, with the level of mating activity tending to parallel the variation in ewe sexual activity. However, the majority of reports suggest that unlike the ewe, rams do not show seasonal periods of complete sexual inactivity (Pepelko and Clegg, 1965; Lindsay and Ellsmore, 1968; Lincoln and Davidson, 1977; and Sanford, Simaraks, Palmer and Howland, 1982). Amir and Volcani (1965) and Lees (1965) however, found that rams of breeds in which ewes experienced long periods of anoestrus (> 4 months), show seasonal periods of almost complete sexual inactivity.

Several studies with artificial light regimes have revealed that photoperiod corresponding to short days (usually 16 hours dark : 8 hours light) stimulates increased libido as evidenced by increased numbers of services in pen-tests, when compared to rams maintained in a long day light regime (Schanbacher, 1979; Tulley and Burfening, 1983).

1.2.5.5 Genetic Effects

Whilst breed differences in various measures of libido and serving capacity have been found in several studies, these differences have generally been established on the basis of very small numbers of each breed and in most cases breeds have not been compared at the same stage of sexual maturity. Land and Sales (1977), for example, found that a significant proportion of Finnish Landrace (21 of 23) and Finn-Merino crossbred (23 of

28) males mated at six months of age, whilst all of 9 Tasmanian Merinos did not do so until their second breeding season at about 18 months of age. The Merino ram lambs at six months of age, however, weighed approximately 20 kg while the other two genotypes, were approximately 30 kg. Thus, these differences may reflect mainly breed differences in rate of attainment of sexual maturity. Kilgour and Winfield (1977) likewise found that mature experienced rams of four breeds (Romney, Border Leicester, Cheviot and Dorset Down) did not significantly differ in observed pen-mating behaviour scores nor in fertility as measured by ewe returns to service after a controlled joining during the breeding season. Differences in these parameters were found in comparisons of 15 month-old rams from four "exotic" breeds (Finnish Landrace, East Friesian, German Whiteheaded Mutton and Oxford Down) at that time recently introduced to New Zealand.

Merino, Border Leicester and Dorset Horn rams of unstated age and experience were compared by Lindsay and Ellsmore (1968). There were indications of seasonal differences in sexual activity between breeds, but the authors noted that, given adequate and constant stimulus from oestrous ewes, most rams of all three breeds worked at all times of the year.

There are no reports in the published literature of investigations aimed at estimation of within-breed genetic parameters for measures of libido and serving capacity in sheep. Kilgour (1981), in an unpublished thesis, reported a heritability estimate for serving capacity of 0.30 $\pm$ 0.62, the standard error of which reflects the inadequacy of the data set for such a calculation. Mattner, Braden and George (1973-1974) have reported that sons of sires of high "libido" rams had a higher libido score than sons of low libido rams. However, a detailed account of this finding has not been subsequently published.

Variation in serving capacity of beef bulls has been shown to have a high genetic component. Blockey, Straw and Jones (1981) have reported a half-sib heritability estimate of 0.67 $\pm$ 0.19 for serving capacity of

Hereford and Angus bulls, whilst Hultnas (1959) observed variation between half-sib groups of bulls to be greater than variation within each group.

1.3. SELECTION FOR IMPROVED REPRODUCTION RATE IN SHEEP FLOCKS

1.3.1 GENERAL

The subject of improvement of reproduction rate in sheep has received extensive attention from reviewers during the past two decades (e.g. Turner, 1968; Bradford, 1972; Bindon and Piper, 1976; Land, Gauld, Lee and Webb, 1982 and Piper and Bindon, 1984). The passage of time, represented by the dates of publication of the above reviews, has been marked by considerable advances in the understanding of the physiological and endocrinological basis of many of the components which determine the quantitative expression of the complex trait, reproduction rate. These advances in the understanding of the reproductive process have led to increasing use of non-genetic techniques for improving reproduction rate and Piper and Bindon (1984) list synchronisation of ovarian cycles, techniques to promote fertility outside the normal sexual season, techniques to increase prolificacy, improvement of lamb survival and the technique of artificial insemination, as being areas where advances have been made. In general, however, non-genetic manipulation involves added costs and in most cases the benefits do not accrue to future generations. Interest, therefore, remains in improvement of reproduction by genetic means.

1.3.2. BETWEEN-BREED VARIATION IN REPRODUCTION RATE

Between-breed variation in reproduction rate is considerable and has been shown to be largely a function of differences in prolificacy (number of lambs born per ewe lambing) (Bradford, 1972; Hanrahan, 1974). In turn, variation in prolificacy between breeds reflects differences in ovulation rate (Land, Pelletier, Thimonier and Mauleon, 1973 and Hanrahan, 1980) with little evidence being found of significant between breed variation in embryo

survival (Hanrahan, 1979, 1982).

A review of the literature on between-breed variation in survival from birth to weaning by Cundiff, Gregory and Koch (1982) showed that there are significant additive genetic differences among breeds for direct transmitted and maternal effects on lamb survival, whilst Ricordeau (1982), concluded that a similar situation exists for variation between breeds in the length of the breeding season, its date of onset and cessation and in the length of post-partum anoestrus.

In a comprehensive review of the literature on heterosis in components of reproduction rate, Nitter (1978) found significant positive heterosis in most components except for ovulation rate, where the unweighted mean heterosis estimate from a number of studies was not different from zero.

Utilization of between-breed variation in reproduction rate is now widespread in many countries, through techniques of breed substitution, the formation of synthetic populations and regular systems of crossbreeding (Jacubec, 1977; Ricordeau et al., 1978, and Rae and Land, 1981).

1.3.3. WITHIN-BREED VARIATION IN REPRODUCTIVE RATE

Until the development of the technique of fibre optical laparoscopy for quantification of ovulation rate (Thimonier and Mauleon, 1969), most attention, in studies of within-breed variation in the components of reproduction rate focussed on prolificacy, or on lambs born per ewe joined (the product of fertility and prolificacy). Land, Atkins and Roberts (1983) have summarised from the literature, repeatability and heritability estimates for fertility and prolificacy. Whilst repeatability estimates range from 0 to 0.13 (average 0.06), heritability estimates range from 0 to 0.17 (average 0.07). Corresponding estimates for prolificacy were 0.04 to 0.19 (average 0.15) and 0.04 to 0.15 (average 0.10). The results of several long-term experiments on selection for prolificacy or fertility and prolificacy accord well with the above estimates of heritability, with average annual response of approximately 1.5% lambs per ewe lambing being

achieved (Clarke, 1972; Turner, 1978: Hanrahan and Timon, 1978 and Atkins, 1980).

Hanrahan (1982) has reviewed the evidence for genetic variation in the two components of prolificacy, namely ovulation rate and embryo survival. He concluded that genetic variation in prolificacy was largely a function of variation in ovulation rate with little or no contribution attributable to genetic variation in embryo survival. Heritability estimates of ovulation rate vary considerably, but in general are higher in the moderately and highly prolific sheep than comparable estimates for litter size. In a Finnish Landrace population, the heritability of ovulation rate and litter size were estimated as 0.45 and 0.10 respectively, whilst in Galway sheep the values were 0.57 and 0.06 (Hanrahan, 1980). Piper et al. (1980), however, reported a much lower estimate of 0.05 for ovulation rate in 18 month old Merinos, while for mixed age (3-5 year old) ewes, from the same population, heritability estimates of 0.08 and 0.07 for ovulation rate and litter size respectively, have recently been reported (Piper et al., 1984).

Other components of overall reproduction rate, which have been shown to display potentially useful genetic variation, are the number of occurrences of oestrus during the first breeding season (Baker and Morris, 1982), the age at first oestrus during the second year of life and the number of subsequent occurrences of oestrus prior to joining at approximately 18 months of age (Piper, 1982). Whilst these traits are closely related to age at attainment of puberty, it has not yet been established whether their use as selection criteria would be reflected in worthwhile increases in lifetime reproduction rate.

Evidence for genetic variation in the maternal component of lamb survival has recently appeared (Haughey,1983; 1984), and Cundiff et al. (1982) in reviewing studies on this subject, concluded that the average heritability of the maternal component of survival was double that of the individual component (0.08 vs 0.04). This and other considerations, led

Piper (1982) to suggest that selection for reproduction rate might be more effective if lambs weaned was the selection criterion rather than lambs born.

1.3.4 INDIRECT SELECTION CRITERIA FOR IMPROVING REPRODUCTION RATE

Factors contributing to the relatively slow reponse to selection for improved reproduction rate have been identified by Bindon and Piper (1976). The use of ovulation rate as the selection criterion overcomes several of the limitations associated with mating and lambing performance as selection criteria. The ram is not required for the normal expression of ovulation rate and repeated records can be obtained during the one breeding season, which allows opportunities for reduction of the generation interval. Hanrahan (1980) calculated that response in prolificacy to selection based on ovulation rate, could be three times greater than from direct selection on prolificacy. There remains however, the disadvantage that ovulation rate is expressed only in the female and is also influenced by the age of the ewe (Ricordeau *et al.*, 1982). In lowly prolific sheep breeds, like the Merino, there is the added disadvantage that the heritability is low and similar to that of prolificacy. Such problems have served to stimulate investigation of other indirect selection criteria for the improvement of reproduction rate and of ovulation rate.

1.3.5 MALE PHYSIOLOGICAL INDICATORS OF REPRODUCTION RATE

1.3.5.1 Studies in Laboratory Animals

The initial stimulus for investigations into the possibility of utilizing male physiological traits as indicators of female reproductive merit was the hypothesis advanced by Land (1973) that gonad function in males and females is mediated through the same hormonal control pathways and hence, gene complexes. Land based this proposition, initially, on evidence from studies by Purser (1965) and Land and Falconer (1969) where the transmission of genes for female reproductive performance through males was demonstrated by differences in the reproductive performance of daughters of different sires.

Further support for this suggestion was given by Land (1973) in the form of results of selection in mice for high and low natural and induced ovulation rate. Selection had resulted in correlated changes in testicular weight in the same direction as ovulation rate. Subsequently Eisen and Johnson (1981) quantified correlated responses in testicular weight arising from selection for litter size and liveweight in mice. They calculated the realized genetic correlation between testicular weight and litter size to be 0.60 $\pm$ 0.04 and the realized partial genetic correlation when liveweight was held constant, to be 0.42, which suggested the existence of pleiotropic loci affecting testicular weight and litter size independently of bodyweight. Conversely, selection on male sex traits, has also been shown to result in correlated responses in reproductive parameters of the female. Islam, Hill and Land (1976), who selected mice for testicular weight and over 5 generations changed this trait by 60% (3 standard deviations) of the base value. Correlated responses in ovulation rate yielded estimates of genetic correlations, independent of bodyweight, between testicular weight and ovulation rate of 0.50 $\pm$ 0.18 for primiparous and 0.25 $\pm$ 0.20 for nulliparous ovulation rate.

Wolfe *et al.* (1981) have presented evidence that the type of selection practiced in the above studies is likely to have acted at the cellular level in the gonads of both sexes and that gonadotrophin levels were probably not a target of selection. These workers found that selection of mice on the basis of differential number of ovulations in response to PMSG/HCG treatment resulted in the development of two strains differing in both ovarian and testicular responsiveness to gonadotrophins. The differences in biological responses to gonadotrophic stimulation in these mice appeared to be due to differences in gonadal FSH receptor levels.

1.3.5.2 Studies in domestic animals

The major emphasis in the investigation of genetic relationships between male and female reproductive traits in domestic animals has been

resticted to the comparison of breeds differing in prolificacy. This has been especially so in the sheep, a species showing considerable between-breed variation in reproduction rate and its major components (Bradford, 1972).

There are many reports of between-breed comparisons which show strong relationships between male and female reproductive traits of the same breed. These studies have been reviewed by Land (1974, 1978 and 1981). Relationships include associations between rate of attainment of mature gonadal function and sexual behaviour, gonadal activity (indicated generally by testicular size in males) and endocrine profiles in males and females of breeds differing widely in reproductive rate (Land and Carr, 1975; Land and Sales, 1977; Hanrahan et al., 1977 and Land, 1978).

Unlike the situation in laboratory animals, however, the relatively few studies in domestic animals, of within breed genetic covariation between male and female reproductive traits, have not yielded consistent findings. To a large degree the inconsistency, both between studies in the same species and between animals within studies, reflects inadequacies in experimental design and the use of inappropriate statistical techniques.

In beef cattle Brinks et al. (1978) have reported estimates of genetic correlations between age at puberty in heifers and scrotal circumference and semen traits in half-sib yearling bulls. Whilst estimates of genetic correlations between the semen traits and heifer age at puberty showed favourable relationships (absolute values 0.09 to 0.37),the correlation between the female trait and scrotal circumference was calculated as -0.71. These estimates were based on the half-sib progeny of only 21 sires from 11 lines of cattle, and although standard errors were not calculated for the genetic correlations, they could be assumed to be as large as the estimates.

Proud et al. (1978), compared testicular growth in eighth generation selected and control line boars to determine whether there were correlated changes in testicular development associated with the ovulation rate

increase of three corpora lutea, produced by selection on this trait in the female. Testicular growth was more rapid in selected line boars after 91 days, resulting in larger testicular weights at 154 days of age. Although only 21 sires were represented in this comparison, analysis of variance revealed highly significant sire effects on the male gonadal parameters, but genetic correlations between male and female traits were not calculated.

Within-breed studies in sheep have been more numerous than for the other domestic farm species. Ricordeau et al. (1979) in an examination of male and female half-sib progeny of 14 sires of the highly prolific Romanov breed, found a non-significant correlation (0.43) between progeny group mean ovulation rate at 9 months of age and liveweight-corrected testicular growth from 70 to 100 days of age. There was no evidence of a relationship between ovulation rate and measures of lutenising hormone (LH) in half-sib ram lambs. In contrast, Bindon (1973) and Trounson et al. (1974) found that young male lambs from a line of Peppin Merinos selected for the increased incidence of multiple births, had higher LH levels than males from a line selected against this trait.

In an investigation by Thorsteinsson et al. (1982), the genetic relationship between testicular weight at weaning and lambing performance (lambs born per ewe mated) of ewes at 1,2 and 3 years of age was examined in 13 groups of half-sibs of an unstated breed. Although a favourable relationship was suggested from the data, the small number of sire groups examined and the method of estimating the genetic covariances (calculated from the regression of unweighted sire progeny-group means), mitigate against firm conclusions being drawn from the results of this study.

Contrasting results of three sheep selection experiments are also found in the literature. Burfening and Tulley (1982), examined testicular size, ram libido and mating dexterity in lines of Rambouillet sheep which had been selected for high and low prolificacy for approximately three generations. Although consistent results were not obtained, male progeny from the line

selected for prolificacy generally showed higher libido and had larger testes than those from the line selected against prolificacy.

From a second selection experiment with Finnish Landrace sheep, Hanrahan and Quirke (1982), have reported that divergent selection based on ovulation rate, has resulted in a significant ($P < 0.05$) correlated response in testicular diameter at 10 and 14 weeks of age . Genetic correlations, between ovulation rate and testicular diameter at these ages, calculated from the divergence between these lines after one generation of selection, were estimated to be 0.41 and 0.35 respectively. In contrast to these two results, Land et al. (1983), have found no correlated responses in ovulation rate and lambing performance, arising from selection for testicular diameter. In this latter experiment the population under selection was derived from a Finnish Landrace-Dorset Horn cross, and the selection criterion was liveweight-corrected testicular diameter at 6 to 14 weeks of age. The authors have, however, noted correlated responses to selection, in mature liveweight of females and time of onset of the breeding season, with females of the line selected for increased testicular size being of lighter mature liveweight but having an earlier onset of the breeding season when compared to the females of the line selected against testicular size. It is noteworthy that the correlated responses in testicular size resulting from selection on ovulation rate found by Hanrahan and Quirke (1982) were not associated with line differences in lamb liveweight.

1.3.6 PRACTICAL IMPLICATIONS OF INDIRECT SELECTION CRITERIA FOR REPRODUCTION RATE

Falconer (1960) defines the merit of indirect selection, relative to that of direct selection, as the ratio of the expected correlated response of character X, (CR_x), resulting from selection on character Y, over the

expected response to direct selection on character X,(R_x). This is a function of:

$$r_a \cdot \frac{i_y \cdot h_y}{i_x \cdot h_x}$$

where r_a is the genetic correlation between X and Y, i_y and i_x the appropriate selection intensities, and h_y and h_x the square roots of the two heritabilities. If the selection intensity in selecting for character Y is the same as when selecting for X then the correlated response will be greater than the direct response if $r_A.h_y$ is greater than h_x. Therefore, indirect selection can only be expected to be more efficient than direct selection, if the secondary character has a higher heritability than the desired character, and the genetic correlation between the two is high.

Walkley and Smith (1980) have quantified the theoretical advantages of using indirect selection criteria for improving prolificacy in sheep. They compared three selection schemes: direct selection on prolificacy, indirect selection using a correlated physiological trait, and selection using an index based on both prolificacy itself and the physiological trait. This study showed that there are substantial gains to be made from indirect selection, especially when the heritability of an individual measurement of the direct selection trait is low. The most important parameter, however, is the genetic correlation between the physiologial trait and prolificacy. As the genetic correlation rises above 0.3, the gains in response can become as large as 50 to 100%. However, these authors also offer the reminder that unreliable genetic parameter estimates can markedly affect the prediction of correlated responses as was shown by Sales and Hill (1976).

1.4.THE GENETIC, PHYSIOLOGICAL AND ENDOCRINE BASIS OF THE HIGH PROLIFICACY OF THE BOOROOLA MERINO

1.4.1. ORIGINS.

The Booroola Merino (henceforth simply referred to as the Booroola) originated from a multiple-birth selection flock established by two private breeders, the Seears brothers of Cooma, N.S.W. The detailed history of this flock has recently been documented by Turner (1982). Whilst the exact date of commencement of this flock is not recorded it is thought to have been somewhere around 1943 to 1947.

The multiple-birth flock was begun by the choice of a ewe which had produced triplets in the Seears' main flock, which was based on sheep from the "Egelabra" bloodline of the medium-wooled non-Peppin (MNP) Merino strain. Subsequently all ewes seen with multiple births were transferred to this special flock, whilst lambs born as singles in the selection flock were returned to the main flock, but their dams retained.

Turner (1982) states that selection was practiced only on the female side with all rams being bought without regard to birth type from studs of the "Egelabra" bloodline, the breeding policies of which, did not include selection for multiple births.

By 1958 this special flock had built up to contain between 200 and 300 breeding ewes and had a lambing percentage of between 180-190%.

1.4.2. CSIRO BOOROOLA SELECTION FLOCK.

Over the period 1958-1960, CSIRO acquired from the "Booroola" multiple-birth selection flock, 12 ewe lambs born as either triplets or quadruplets, one ewe lamb born as a sextuplet, a 2-year old ewe which had given birth to triplets at her first lambing and two quintuplet-born ram lambs (Turner, 1978). Upon dispersal of the Seears brothers' flock in 1965, CSIRO purchased 91 ewes aged 2-6 years which had all been born as multiples

but in unknown litter sizes. These animals formed the basis of the CSIRO Booroola selection flock.

Turner (1978) has described the ram and ewe selection procedures and experimental management of this flock which operated up until 1974, whilst Piper and Bindon (1982b) have described the procedures which have operated since. This latter report also contains reproductive performance statistics of both the Booroola selection flock ewes and of a control flock of Peppin Merino ewes which was established in 1968. Based on analysis of three lambings (1977 to 1979) the average litter size for CSIRO Booroola ewes aged 2 to 7 years was 2.30 and ranged from one to six, whilst the comparative figure from the control Merino flock was 1.30 with a range of one to two. Piper et al (1984) quote mean ovulation rate and litter size statistics for the Booroola flock in 1982 of 4.2 (range 1-10) and 2.5 (range 1-7) respectively.

1.4.3. GENETIC BASIS OF THE BOOROOLAS' HIGH PROLIFICACY.

The observation that the high prolificacy of the Seears brothers' Booroolas had been obtained without any emphasis on prolificacy in sire selection, led Piper and Bindon (1982a, 1982b) to suggest that, despite the considerable amount of selection on the female side, the high lambing percentage and greater proportion of litters of three or more, produced by selection at Cooma, could not have resulted from gradual increases in the frequency of many genes of small effect. The continual introduction of genes from rams unselected for prolificacy, suggested to Piper and Bindon that the increased prolificacy had arisen from the gradual accumulation, within the Seears' selection flock, of ewes carrying a single gene (or duplication, deletion or closely linked group of genes) with a major effect on prolificacy.

The evidence to support the segregation of a major gene affecting prolificacy, as presented by Piper and Bindon (1982a, 1982b), was initially based on the lifetime records of the 14 foundation CSIRO ewes and of 19 of

their daughters. The segregation criterion adopted, was the occurrence of at least one set of triplets, or higher order birth in a ewes' lifetime lambing record. Using this criterion, it was shown that the lambing records were in good agreement with the segregation expectation. Further studies in Australia with the CSIRO Booroola selection flock and with Booroola x ordinary MNP Merino crossbreds (Piper and Bindon, 1982c), and in New zealand with crosses from imported Booroolas (Kelly et al., 1980 and Davis et al., 1982) have all been consistent with the major gene theory.

Assessment of ovulation rate in Booroola populations, both in Australia and New Zealand has further clarified the mode of action of this gene. Piper and Bindon (1979) found no evidence of heterosis for ovulation rate in crosses between Booroolas and ordinary MNP Merinos and this led them to propose that the gene had an additive action on ovulation rate (Piper and Bindon, 1982c). Agreement with this proposal was found in data from Booroola x New Zealand Merino crosses and back-crosses examined by Davis et al. (1982). These authors proposed ovulation rate (OR) classification criteria for non-carriers (no OR record > 2), heterozygotes (at least one OR record > 3 but < 5) and homozygous carriers (at least one OR record > 5) with a Merino genotype. They also proposed the symbol F for representing the major gene and the symbol + for the wild-type in accordance with the nomenclature rules documented by Lyon (1977). The symbol F was chosen after discussion between CSIRO and New Zealand research workers because of early indications (Piper and Bindon, 1982b), that the gene might be completely dominant for fecundity (prolificacy). The nomenclature of FF for homozygous-carriers, F+ for heterozygotes and ++ for non-carriers of the Booroola F gene, will henceforth be used in this review.

Whilst the effect of the Booroola F gene has consistently been found to have an additive effect on ovulation rate, its action on prolificacy appears to depend on the level of this trait in the ++ genotypes of the populations in which the gene is segregating. Thus Piper et al. (1984), in examining

lifetime prolificacy records of ewes from the CSIRO Booroola flock, found a significant dominance deviation [F+ - (FF + ++)/2] of 0.27 ± 0.10, with the first and second copies of the gene adding 0.9 and 0.4 of a lamb respectively. However, exclusion of the "genotype ascertainment record", which could be suspected to bias the dominance estimate, resulted in a non-significant dominance deviation for prolificacy. This led the authors to suggest that the effect of the F gene may be nearly additive in populations with prolificacy levels similar to, or less than, the ++ Booroola genotype (1.5 lambs born per ewe lambing). However they also suggested that due to the non-linear relationship between ovulation rate and prolificacy, found by Hanrahan (1982), the gene's effect on prolificacy in breeds with higher ovulation rates will be to show partial or even complete dominance. Davis et al. (1984) have recently reported partial dominance in the effect of the F gene on prolificacy in a Booroola x Romney Marsh crossbred population.

1.4.4. PHYSIOLOGICAL AND ENDOCRINOLOGICAL CHARACTERISTICS OF BOOROOLA EWES.

Bindon (1984) has published an exhaustive review of the large number of studies which have been carried out since the early 1970's aimed at describing the endocrinology and physiology of the Booroola female, and the extent to which these animals differ from other Merinos. To a large degree, these studies have utilised animals from the CSIRO Booroola selection flock and three CSIRO Peppin Merino flocks which have been selected for (T flock) and against (O flock) prolificacy or randomly bred (C flock). Turner (1978) has given complete descriptions of the origin, selection and management of these flocks.

In addition to the previously mentioned differences in ovulation rate litter size, Booroola ewes also differ from ordinary Merinos (of both the Peppin and MNP strains) in several other of the components of reproduction rate. In their second year of life Booroola ewes reach puberty signifi-

cantly earlier than "C" Merinos and have slightly more oestrous cycles between puberty and their first joining at 18 months of age (Bindon et al., 1982). In comparison to "O" ewes, Booroola ewes experience about 40% more oestrous cycles per year, and 60% of Booroola ewes ovulate in all months of the year, whilst most "O" ewes do not ovulate for 4 months of the year (Bindon and Piper, 1976). In comparison to "C" Merinos, it is estimated that the Booroola ewe ovulates about 7.5 hrs earlier, following the onset of oestrus (Bindon et al., 1984a).

Aspects of the reproductive physiology of the Booroola ewe which do not differ from ordinary Merinos include i) the proportion of ewes reaching puberty in their first year of life, ii) the duration of oestrus and length of oestrous cycle, iii) uterine capacity and iv) timing of resumption of ovarian cycling post-partum (Bindon, 1984).

It should be noted that in all the above comparisons between Booroolas and ordinary Merinos, the F gene status of the Booroola ewes was either unknown or not taken into account in comparative analyses.

Studies on the reproductive endocrinology of Booroola ewes have concentrated on establishing the endocrinological basis of the Booroolas' exceptional ovulation rate. Several studies of LH secretion have failed to demonstrate a quantitative relationship between LH plasma levels or LH pulse frequency and prolificacy when both Booroola ewes differing in F gene status and Booroola and control Merinos have been compared (Scaramuzzi and Radford, 1983 and Bindon, 1984). This contrasts with a finding by Webb and England (1982), that prolific Finnsheep had lower LH levels in the pre-ovulatory period than Suffolk ewes. Booroola ewes were also shown to differ from other prolific breeds in that they have an LH discharge which occurs at the same time after the onset of oestrus, as that of ordinary Merinos.

Bindon and Turner (1974), found that pre-pubertal Booroola ewe lambs had higher concentrations of plasma LH than ewe lambs from the CSIRO O and T Merino selection-lines, but this was largely a reflection of a litter size

effect on LH concentrations, with higher order multiples having higher LH levels than singles and twins.

Cahill et al. (1981) have suggested that peri-ovulatory FSH concentrations influence the ovulation rate of the next cycle, and studies with the highly prolific Romanov by these authors, and with the D'Man breed by Lahlou-Kassi and Marie (1985), have revealed higher FSH levels on day 2 of the cycle in these breeds, when compared to lowly prolific breeds. Booroola ewes have similar day 2 FSH patterns to those of other prolific breeds (Bindon, 1984). Booroola ewes (FF and F+) have higher plasma FSH concentrations, both during the 24 hours preceding the pre-ovulatory LH discharge, and at the time of the second FSH peak which occurs about nine hours after the LH discharge. In the pre-pubertal ewe, basal FSH levels and the peaks induced by administration of Gn-RH , are higher in Booroolas up to 45 days of age, but are not different from O and T Merinos at 60 days of age. Bindon (1984) suggests that this may reflect an ovarian feedback deficiency in the young Booroola ewe.

Robertson et al. (1983) have demonstrated that Booroola ewes have a greater pituitary content of FSH than ordinary Merinos, whilst unpublished data quoted by Bindon (1984) shows comparable differences in immunoreactive FSH in urine.

Evidence that the non-steroidal hormone, inhibin, contributes to the feedback regulation of FSH is accumulating (Tsonis et al, 1983), and several investigations with Booroola genotypes have indicated that the higher FSH levels found in these genotypes, when compared to ordinary Merinos, may be substantially a reflection of their lower inhibin production (Scott et al., 1980, Cummins et al., 1983). This in turn may reflect lower granulosa cell number in Booroola follicles (Cummins et al., 1983).

1.4.5. REPRODUCTIVE BIOLOGY AND ENDOCRINOLOGY OF BOOROOLA RAMS

Although considerable commercial importance is attached to the quantification of differences in physiological and endocrinological traits

between male Booroola F gene carriers and non-carriers, relatively few investigations of the Booroola male have been conducted.

Gonadal size, which because of its close association with spermatozoa production rate, quantitatively reflects testicular activity (Knight, 1977), has been examined in several CSIRO flocks. Booroola rams do not appear to differ in testicular growth rates or testicular size when compared with rams from other Merino flocks (Bindon and Piper, 1976), nor do Booroola x British breed rams differ from ordinary Merino x British breed rams for the same traits (Curtis et al., 1980, Purvis et al, 1983). This situation contrasts to that of the Finnsheep, which has been shown to have faster testicular growth rates than lowly prolific genotypes. Unpublished data of P.E. Mattner and A.W. Braden (quoted by Bindon et al, 1982) demonstrates that Booroola rams to not differ from ordinary Merinos in total daily sperm production. In the above comparisons, only the study of Purvis et al (1983) identified the F gene status of individual Booroola rams.

Comparisons between control Merinos and Booroola rams have established that they do not differ in plasma LH, FSH and testosterone levels, nor in their sensitivity to exogenous Gn-RH (Findlay and Bindon, 1976 and Stelmasiak et al., 1978). Unpublished data of Hillard, Bindon and Piper, quoted by Bindon (1984), also showed no difference in gonadotrophin response to castration, between adult Booroola and control Merino rams. In none of these studies was the F gene status of the Booroola males established.

1.5. CONCLUSIONS

This review of the literature on male reproductive performance traits, the relationships between these traits and measures of female reproductive performance, and on current methods of selection for improved reproduction rate has focussed on the domestic sheep, Ovis aries.

Although the physiological and endocrine aspects of male gonadal growth

and function in sheep, have been extensively studied, in many breeds and environments, the quantitative inheritance of measures of male reproductive function have received relatively little research attention. Estimates of genetic parameters are relevant, theoretically, only to the population and environment from which they are estimated. There are no estimates available of genetic parameters for male reproductive traits, which have been obtained from Merino sheep, maintained under pastoral conditions typical of those found in the areas where the Australian Merino sheep breeding industry is centred. Consideration of the literature on ram reproductive behaviour reveals a similar gap in our knowledge, as to that for male physiological reproductive traits.

It is more than a decade, since R. B. Land (1973) first suggested the possibility of utilising male physiological traits as indicators of female reproductive performance in domestic animals. Although many between-breed studies have given qualified support to this suggestion, there are still no reliable estimates of the magnitude of genetic relationships between male and female reproductive traits in sheep. Given the potential advantages of using appropriate "marker " traits in sheep selection programmes (Walkley and Smith, 1980), such a deficiency needs to be rectified. This requirement is especially marked for the Australian Merino breeding industry, where the current methods of genetic improvement of reproduction rate are clearly limiting.

The possible exploitation of the Booroola Merino F gene to rapidly increase prolificacy in lowly prolific sheep populations, is currently restricted by our inability to recognise, by some feature of the male phenotype, the presence or absence of the F gene. Further comparative studies of physiological and endocrine traits in carriers and non-carriers of the F gene may identify "marker" traits which can successfully predict the F gene status of a ram at an early age.

PART B. - EXPERIMENTAL

INTRODUCTION

The review of literature (Part A) established that although it has been more than a decade since R.B. Land (1973) first suggested the use of male physiological traits as indirect selection criteria for female reproductive performance in domestic animals, there have been no studies with sheep which have reported reliable estimates of the magnitude of genetic relationships between male and female reproductive traits.

The primary objective of the first part of the experimental studies reported in this thesis, was to estimate genetic correlations between ovulation rate and various male reproductive traits in a large random-breeding Merino flock. However, before such an investigation was begun it was considered important to have a detailed knowledge of the environmental and genetic sources of variation influencing these traits. Piper et al. (1980) had already reported preliminary results of an ongoing project aimed at estimating the heritability of ovulation rate in this flock. The aim of the studies reported in Chapters 3 and 4, therefore, was to measure various male gonadal and sexual behaviour traits, identify the sources of variation influencing these traits, and estimate appropriate genetic parameters.

Another deficiency in our ability to effect maximal genetic improvement in the reproductive performance of sheep flocks was shown in the review of literature, to be due to our failure to be able to identify at an early age, male Booroola F gene carriers. The studies described in Chapter 6 utilised crossbred Booroola and control Merino rams to examine whether various morphological and endocrine traits were indicative of a ram's F gene status.

CHAPTER 2

MATERIALS AND METHODS - GENERAL.

2.1. INTRODUCTION.

This Chapter contains general descriptions of the genetic background and management of the flocks from which animals, used in the experimental studies described in Chapters 3-6, were drawn. Also included are descriptions of the environmental conditions experienced by the animals at the two locations at which these studies were conducted.

Whilst details of specific measurement and statistical techniques are presented in the appropriate section of each experimental Chapter, this Chapter contains general descriptions of statistical methodology common to the 4 experimental Chapters and describes the conventions used throughout the Thesis.

2.2. ANIMALS AND ENVIRONMENT.

2.2.1. Trangie D flock.

2.2.1.1. Background.

The Trangie D flock, which is maintained at the Trangie Agricultural Research Centre (hereafter referred to simply as Trangie), was formed in 1974-75. The initial aim in establishing this flock, was to develop through selection, a Department (D) of Agriculture fertility flock. However, this aim was changed following the realisation that there was very little information on the variation in reproductive traits, both between and within Merino strains and families (bloodlines) in NSW. It was therefore decided to form the D flock at Trangie on the basis of it being representative, in terms of the genotypes included, of the structure of the Merino industry in NSW and to maintain this feature by within genotype random breeding. The D flock was therefore established, with 14 sub-flocks which were representative of:

2 fine wool non-Peppin families;

2 medium wool non-Peppin families;

9 medium wool Peppin families; and

1 South Australian strong wool family.

A full description of each of the strains sampled is given by Carter (1955).

Each sub-flock was formed with the purchase of 100 ewes from stud or commercial flocks, and each year since then, 3 (in rare instances, 4) rams have been purchased from a major stud representative of that family.

2.2.1.2. Management.

The ewes of the 14 sub-flocks were maintained as one management unit at all times, except at joining (mating) and lambing. Sub-flock ewe numbers were kept at 100 by the annual culling of 6.5 year old ewes and their replacement (where numbers permitted) with randomly chosen 18 month old progeny of the same sub-flock. The only selection practiced, in the choice of ewe replacements, was against phenotypic evidence of unsoundness for breeding or the presence of severe wool faults.

The rams, purchased each year from a major stud of the relevant family, were chosen by Department of Agriculture Officers, with reference only to their soundness for breeding. They were aged between 18 months and 2 years and arrived at Trangie during a period of 1 to 4 months prior to mating in late February of each year. The rams were single-sire mated to approximately 33 ewes each, for a period of 5 to 6 weeks, in paddocks of between 5 and 10 hectares. Lambing occured in a drift system, which has been described by Dun and Eastoe (1970). Within 12 hours of birth, the dam, liveweight and litter size of each lamb was recorded. Tailing and mulesing occurred 2 and 4 weeks after the end of lambing, and weaning was at 4 to 5 months of age. After weaning, ram lambs were maintained as a single mono-sexual year group, whilst the ewe lambs were also maintained separately from their dams, until approximately 15 months of age.

All D flock animals were shorn in October of each year, whilst the ram hoggets were also shorn in May. Normal husbandry procedures, as described by Dun (1964), were utilised for this flock. Supplementary feed in the form of oat grain or lucerne/grass hay was provided to animals on an ad. hoc. basis when the body condition of the animals suggested the need.

2.2.1.3 Environment.

Trangie Agricultural Research Centre lies on the western edge of the Central Western Plains (Lat. 32.4^{o} S; Long. 148^{o} E), approximately 550 km by road north-west of Sydney. The station consists of 3900 ha of flat country which has been extensively cleared and is now only sparsely timbered with an open savannah type of Eucalypt forest (E.populnea). Rainfall averages approximately 475 mm per annum, is non-seasonal, and is characterised by considerable variability and unreliability. Soil types vary from sandy loams to heavy black alluvials.

In general, sheep are grazed on native pastures, paddocks of dryland lucerne or crop stubble. The dominant native pasture species have been described, for the area generally, by Biddiscombe et al. (1954). The dominant species vary with the season. Various Stipa, annual and perennial Chloris and ephemeral species are predominant in summer, whilst in winter, barley grass (Hordeum sp.), burr clovers (Medicago spp.) and some Stipa species are dominant. Whilst late winter pastures are of good quality, they are killed off quickly by the high temperatures of late spring. Temperatures are high in summer, with maxima commonly above 35^{0}C between November and March, whilst winter is mild, with only rare and light frosts being experienced.

The only common health problems are associated with blow-fly (Lucilia cuprina) strike, which commonly occurs in the spring and autumn, and can be the cause of significant production losses. Spring problems with grass seed injury can also cause losses, especially in young lambs.

Rainfall records for the Trangie Agricultural Research Centre, specific to

Table 2.1. Monthly rainfall (mm) at Trangie ARC during the period 1979 - 1983.

Month	Year				
	1979	1980	1981	1982	1983
July	25.8	21.4	73.0	5.2	
August	13.8	16.8	10.2	0.0	
September	66.8	0.4	8.8	21.6	
October	45.4	23.0	78.4	15.8	
November	28.4	4.4	54.2	4.6	
December	0.6	25.6	5.0	20.4	
January		66.6	13.8	60.8	76.2
February		24.2	70.2	22.0	21.0
March		21.8	2.0	80.6	42.8
April		11.0	7.8	15.6	28.0
May		111.0	50.8	14.2	177.2
June		35.8	55.8	3.4	18.2
Totals		300.4	259.6	221.6	

the years during which the experimental studies described in Chapters 3, 4 and 5 were conducted, are presented in Table 2.1.

2.2.2. CSIRO AB42 Booroola Crossbred Flock.

2.2.2.1 Background.

The CSIRO AB42 flock was established in 1976, with the dual purpose of providing information on the suitability of female Booroola-cross genotypes as components in the Australian prime lamb industry and of providing a source of experimental animals for investigations of the physiological and endocrinological basis of the Booroola's exceptional prolificacy.

The AB42 flock consists of 100 Booroola and 100 control Peppin Merino ewes. Ewes of the Booroola genotype are selected each year from the 18 month old progeny of the Booroola selection flock and are the next highest ranking ewes to those selected as replacements for that flock. The Peppin (Control)

Merino ewes are randomly chosen, at 18 months, from a larger random breeding Peppin flock maintained at Longford Field Station (see Section 2.2.2.3).

The 200 ewes are mated each year to 8 new Border Leicester rams, obtained from the registered stud run by the NSW Department of Agriculture at Glen Innes, NSW.

2.2.2.2 Management

In February/March of each year, ovarian cycles of the ewes were synchronised with either 14 day insertion of progestagen-impregnated vaginal pessaries ("Repromap"; 60mg of 6- -methyl-17-acetoxyprogesterone; Upjohn Ltd.) or with 2 intra-muscular injections, each of 125ug of prostaglandin analogue ("Estrumate"; ICI Ltd.), 10 days apart. Ewes were not mated at the synchronised oestrus but were single-sire joined with the Border Leicester rams at the second oestrus following the synchronisation treatment.

During pregnancy the AB42 ewes are grazed as part of a flock of approximately 1000 ewes and are subject to the normal Longford Field Station management procedures (Turner, 1968) throughout gestation. Ovulation rate at mating is determined by laparoscopy approximately 7 days after the commencement of mating.

On day 144 (from the day on which most ewes were served in the 4-day synchronised joining), ewes received an intra-muscular injection of 16mg dexamethazone (9 -fluoro-16 -methylprednisolone; Sigma Chemical Co.). Lambing generally commences on day 146 in individual pens in a lambing shed and lasts 3-4 days. Assistance with lambing is given to alleviate birth difficulties when required and small lambs may be helped to begin suckling. At approximately 4 months of age lambs are weaned from their dams.

2.2.2.3 CSIRO Field Station - "Longford"

For the study described in Chapter 6, observations and measurements were recorded between January 1983 and June 1984 at the CSIRO Field Station, "Longford" (Lat 30 20°S.; Long. 151 27°E), which is situated 37km, by

road, north-west of Armidale, in the Northern Tablelands of NSW. The average altitude of the Station is 1189 metres.

"Longford" comprises 947 ha of undulating, lightly timbered country, with the predominant soil type being yellow solidic/podzolic. Animals graze improved perennial pastures which are supplemented by a variable growth of annual clover species depending upon the magnitude of the late winter and spring rainfall. The area experiences a cool temperate climate with predominant spring summer rainfall of approximately 800mm. Winters are cold, with frosts common and summer temperatures are normally mild and seldom rise above 30 ^{o}C.

2.3 STATISTICAL - GENERAL

The major statistical procedure utilised in the analysis of data was Least Squares analysis of variance. Analyses were conducted using the statistical program "LSML76" which has been described by Harvey (1982). Polynomial regression analysis, in Chapter 3, was conducted using routines from the NAG Library (Numerical Algorithm Group), whilst in Chapter 5, Restricted Maximum Likelihood (REML) analysis of variance was conducted using software developed by Dr. L. R. Schaeffer, University of Guelph, Canada and Dr. J. Lax, CSIRO, Division of Animal Production, Prospect, NSW, Australia. This software was based on procedures described by Schaeffer, Wilton and Thompson (1978).

Duncan's Multiple Range test (Steel and Torrie, 1981) was used to determine the significance of specific linear contrasts among "treatment" means, but was only applied when the variation due to that "treatment" was significant in the analysis of variance. Levels of significance of effects in analyses of variance and for comparisons between means are indicated in the text.