THE CONSTRUCTION OF A SELECTION INDEX COMBINING A MAJOR GENE AND QUANTITATIVE TRAITS

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MENG JIAO SHI

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ABSTRACT

The Massey University Booroola-cross flock was initiated by crossing Booroola Merino x Romney cross rams with Perendale ewes at the Tuapaka hill country farm in 1980. Records were annually kept of the reproductive performance [expressed as number of lambs born (NLB), foetal number (NF) and ovulation rate (OR)], body and fleece weights, and wool quality characteristics.

Segregation criteria were used for sheep with lifetime lambing records (6 lambings), to assign them to one of the three genotypes. Any ewe with all records of NLB, NF or OR smaller than 3 was defined as being the ++ genotype, for ewes with at least one record of 3 or 4 as the F+ genotype and for ewes with at least one record larger than 4 were assigned as the FF genotype. For ewes with 3-5 lambings and reproductive records less than 3, special requirements were set to define sheep into the ++ genotype. For the remaining unclassified sheep, discriminant analysis was employed to estimate their probabilities of being either ++ or F+ genotypes. The FF category was ignored due to only a small number of FF ewes identified in the present study. The method of discriminant analysis was found to be satisfactory, and it overcame some of the problems that occurred when the segregation criteria were used.

A selection objective (H) for lifetime performance for animals in the Massey Booroola flock was defined as:

$$H = 53.79NLW+2.39WW+42.87CFW-8.75MFD+0.29MSL+3.15SCG,$$

where, NLW = number of lambs weaned, WW = weaning weight,

CFW = clean fleece weight, MFD = mean fibre diameter,

MSL = mean staple length, and SCG = scoured colour grade.

Economic weights for wool quality traits were calculated directly from the regression of auction price on level of the traits. For other traits, economic weights were calculated using the marginal profit method. The relativities between the calculated economic weights were generally in good agreement with those of previously published estimates.

For the selection objective defined, various selection indices were examined. It was found that MFD, CFW and hogget liveweight (HLW) were the most important traits, whereas MSL, SCG and WW were almost of no value in the index. The F-locus was chosen to be the selection criterion of NLW, since reproductive rate of the Booroola sheep is largely controlled by the F-locus.

A method for combining the information on the F-locus into the selection index was developed. Under the assumption that there were no correlations between the F genotpye and any of other selection criteria, an index (I) of the form:

$$I = I_F + I_Q,$$

was proposed to select the genetically superior sheep.

Here, I_F was the major gene selection index, set to be half of the dam's breeding value of the individual concerned for the F-locus (BV_F), adjusted by the economic value for the F-locus.

I_Q was the quantitative selection index, composed of the remaining selection criteria. Different selection indices for lambs, ram and ewe hoggets were derived.

Sensitivity analyses to changes of genetic and phenotypic parameters, and the economic weight of CFW were undertaken. Generally, there was little effect on the relative importance of traits in the index or in the rate of change in the objective.

An alternative method to incorporate the information on the F-locus into an index was proposed for situation where the correlation between I_F and I_Q is found to be significant.

In conclusion, it was found that the methods examined for categorising animals into various genotypes (discriminant analysis) and for combining quantitative and qualititative traits into a single index were successful and worthy of consideration for similar situations in other breeds or species.

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INTRODUCTION

Many traits of economic importance to the animal producer such as liveweight and clean fleece weight, show continous variation between two extremes. These traits are usually refered to as quantitative or metric characters (Falconer,1981) and are normally assumed to be controlled by many genes , each with a small effect on the trait. Accordingly, animal breeders designed their breeding programmes based mainly on the concepts and methodology of quantitative genetics, which were developed on the above assumption. The polygenic interpretation of continuous variation has been found to be satisfactory and traditional breeding methods based on quantitative genetics have achieved considerable improvement of animal production, typically at a rate of 1-3% of the mean per year over many years for most commercial traits in farm livestock (Smith, 1984).

However, for some quantitative traits an appreciable amount of the variability of the trait may be due to the segregation at one or a group of closely-linked loci, each with a large effect on the trait. Genes at these loci are called major genes and the traits affected by these genes are inherited in a simple Mendelian pattern.

Since recognising that some metric traits in farm animals may be controlled largely by major genes, the interest of many animal breeders has centred on the effects that the individual loci have on the metric traits and the possible ways to utilise them efficiently. Because the different genotypes can be identified when traits are

controlled by major genes, more efficient breeding methods rather than the traditional ones are warranted to increase the frequency of the major gene in the animal population of interest. Some studies have been undertaken to exploit major genes in breeding programmes (Neimann-Sorenson & Robertson,1961; Soller,1978; Smith,1967, 1985; Smith & Webb, 1981; Smith & Simpson, 1986). However, these studies were either theoretical or only involved selection on one trait.

In the present study, the two primary objectives were to first, examine possible ways of distinguishing between genotypes at the F-locus for sheep without lifetime reproductive records, and secondly to incorporate the F-locus into a selection index including quantitative traits for the Booroola-cross sheep.

C H A P T E R T W O

REVIEW OF LITERATURE

2.1 Major Genes in Sheep

A number of major genes have been shown to affect a variety of characters in sheep. These traits include:

(a) wool characters, such as medullation, pigmentation of wools and lustre,

(b) morphological traits, such as presence or absence of horns, lethals, semi-lethals and abnormalities, and

(c) biochemical and physiological traits, such as haemoglobin type, potassium ion concentration in blood, fecundity of sheep.

Some breeds of sheep, e.g., Drysdale, Tukidale, Booroola, Poll Dorset, have been developed based on some of the above major genes.

2.1.1 Wool characters

2.1.1.1 Medullation

It was initially assumed that the degree of hairiness in a fleece was under polygenic control (Rae, 1956). However, subsequent observations led to the conclusion that carpet-wool expression in some Romney or Romney-cross flocks were based on a small number of major genes, with the possible involvement of unspecified modifiers (Dry, 1955a; 1955b; Rae, 1956; Wickham, 1985; Sides & Banks, 1987).

At least three major loci have been found to have a major impact on the level of medullation in wool (Wickham, 1985). Two of them, called N- and nr-loci, were initially detected in New Zealand (Dry, 1955a; 1955b; Rae, 1956; Wickham, 1978, 1984). Four alleles have been reported at the N locus, (N^d, N^t, N^j and n), whereas the nr-locus has only two, (nr and +nr). Among the four alleles in the N-locus, N^d was the first major gene to be found to affect the level of medullation in the fleece (Dry, 1955a; Rae, 1956; Wickham, 1978). It was shown to be inherited as an incomplete dominant. The effects of N^t and N^j are similar to the N^d, and both of them are completely dominant for hairiness (Wickham & Rae, 1977). Suggestions were given that they might be identical, but it is clear that they arose from different mutations (Wickham, 1984; 1985). Therefore, it is safer to assume that they are different until more evidence accumulates (Wickham & Rae, 1977; Wickham, 1978).

Three carpet wool breeds, Drysdale, Tukidale and Carpetmaster, have been developed based on the major genes N^d, N^t, N^j, respectively. In New Zealand, the Drysdale is the most numerous of the carpet breeds, since Tukidale and Carpetmaster stock were not available until the Drysdale was well established (Wickham, 1985). In addition, it is difficult to distinguish between homozygous and heterozygous genotypes in Tukidale and Carpetmaster breeds which makes it difficult to establish a true-breeding flock (Wickham, 1978; 1985; Wickham & Rae, 1977)

The third locus carrying a major gene to promote hairiness was found in Tasmanian sheep and led to the development of the Elliottdale breed. Research in Tasmania (Sides & Banks, 1987) suggested that the Elliottdale gene (E-gene) was different from the N-gene, since the E-gene did not induce horn growth in ewes. Wickham (1985) suggested that the E-gene might be an allele at the nr-locus.

Table 2.1 summarises the effects of the various loci which affect medullation in sheep.

2.1.1.2 Colour

Wool colour resulting from melamin pigmentation ranges from totally white through various shades of brown to black. Furthermore, the distributon of coloured fibres can range from a small number of isolated fibres to completely coloured. Consequently, coat colour tends to be described in terms of colour types (Rae, 1956; Ryder & Stephenson, 1968) and colour pattern (Rae, 1956). Adalsteinsson (1982) proposed eight loci for the determination of coat colour. However, the genetic basis for the colour types and colour patterns is not simple, since more than one pair of genes tend to be responsible for any particular colour and pattern (Ryder & Stephenson, 1968). Furthermore, genetic modifiers are always involved in the formation of colour (Adalsteinsson, 1982). Extensive reviews about this topic have been undertaken: e.g., Rae (1956), Ryder & Stepherson (1968), Ryder (1980).

Table 2.1 Major genes affecting medullation in sheep

Gene	The mode of inheritance	Effects		Origin	Breed based on
		Medullation	Horn		
N^t	completely dominant	hairiness or medullation of primary fibres in all regions of the body	horned in both sexes	Romney	Tukidale
N^j	completely dominant	similar to N^t	horned in both sexes	Border Leicester x Romney	Carpet-master
N^d	semi-dominant	hairy in both birthcoat and adult fleece in N^dN^d, with variation in the extent of hairiness and no hairiness in the should-patch position in N^dn lambs	Rams fully horned, ewes small horns	Romney and Cheviot-cross	Drysdale
n	recessive	non-medullated fleece	no horns in eithet sex	Romney and other breeds	Romney and other non-medullated breeds.
nr	recessive	nrnr produces a phenotpye similar to that of N^dn	Rams horned ewes polled	Romney	
+nr	dominant	similar to n	polled in both sexes		
E	semi-dominant	similar to N^d	no horns in ewes, vary from polled to 3/4 horned in rams	Romney of Tasmanian origin	Elliott-dale

Some colour genes act as lethals. For example, the gene for dominant grey colour in Karakul, R, is semi-lethal in homozygous form; the gene for dominant white or Afghan pied in Karakul, Wh, is most lethal when combined with R (Adalsteinsson, 1982; Rae, 1956).

2.1.1.3 Lustre

Two independent examples of a major gene affecting lustre in sheep have been noticed in the 1930s and 1950s, one in Merinos from Texas, UAS (Warwick et al, 1960), and one in Australian Merinos (Short, 1958; McGuirk & Short, 1967). Recently, several independent examples of lustre mutations have been reported in New Zealand (Blair, 1989). In all cases, the lustre gene was shown to be inherited as a simple dominant, and the phenotypic effects of the gene were remarkably similar in the various examples. In terms of fleece characteristics, sheep carrying this gene produced a light yellow fleece with a distinct lustre, similar to wools grown by the lustre-wool breeds (Lincoln, English Leicester). Scouring removed the yellow colour but not the lustre. The birthcoat of mutant animals lacked staple crimp but there were about 1 to 4 crimps per inch in staples from adult fleeces. The fibres from mutant fleeces felted very rapidly. In other aspects, the lustre-type animals also had lower body weights and survival rate, reduced follicle density and wool production, compared with normal Merino sheep of the same strain.

Research is now being undertaken to study the potential uses of the gene, but it is not yet possible to judge whether the gene can be

utilized commercially (Blair, 1989).

2.1.1.4 Bulk

It is possible that a major gene affecting wool bulk may exist in some Perendale sheep. Bigham et al (1985) estimated the heritabilities of loose wool bulk in both Romney and Perendale sheep flocks, and found a value of about 0.35 for Romney but a range of 0.42 to 0.93 for Perendale flocks. With this high heritability of bulk, as well as evidence of large between-breed variation and great variation within the Perendale breed (Elliott, 1981). Bigham et al (1985) suggested that the expression of loose wool bulk might be due to the action of one, or at most, relatively few genes. However, the result of a recent study by Sumner et al (1989) failed to support the major gene hypothsis in Perendale or related breeds.

2.1.2 Morphological traits

2.1.2.1 Horns

In sheep, presence or absence of horns in different breeds depends primarily on a series of three alleles, P, p' and p, in decreasing order of dominance (Dolling, 1964, 1970; Hutt & Rasmusen, 1982). The various genotypes and phenotypes resulting from these 3 alleles are shown in Table 2.2. It appeared that the effects of this series of alleles were different in different sexes.

Table 2.2 A summary of the effects of the various horn/poll alleles in sheep (From Hutt & Rasmusen, 1982; Dolling, 1970).

Genotype	Phenotype		Breed
	Ram	Ewe	
PP/Pp	Polled	Polled	Suffolks, Southdown and Polled Merinos
p'p'	Horned	Horned	Dorset Horn
Pp'	Small horns	Polled	
pp	Horned	Polled, but with knobs or scurs	Merinos and Rambouillets
p'p	Horned	Horned	Merinos

Polledness is considered to offer some management advantage over horned animals, including relative freedom from fly strike on the head, ease of handling, and possibly a lower death rate from accident (Turner & Young, 1969). Therefore, some polled breeds of sheep have been preferentially bred, e.g., the Poll Merino and the Poll Dorset, by selecting for P allele as well as other important characters (Dolling, 1964; 1970). The poll allele has been present in the Merino breed for long time (Dolling, 1970), but, for the Poll Dorset, P was introduced from the Ryeland and Corriedale breeds to result in the Poll Dorset (Dolling, 1964).

2.1.2.2 Lethal genes

A number of lethal or semi-lethal characters have been reported in sheep (Rae, 1956; Stormont, 1958; Ryder & Stephenson, 1968; Hutt, 1982). Rae (1956) described eleven such traits for which there is some evidence suggesting a simple genetic control.

2.1.2.3 Inherited abnormalities

Abnormalities may be defined as traits that are not found in the normal animal, but are not lethal or semi-lethal to individuals possessing them. Some may be detremental while others may have no obvious deleterious effects. Inherited abnormal traits and the suggested modes of inheritance had been discussed by Rae (1956).

Besides single gene control, many genetic modifiers are always involved in the inheritance of the above listed traits, consequently forming a complex genetic backgroud for the variation in a trait (Ryder & Stepherson, 1968).

2.1.3 Biochemical and physiological traits

Several major genes bave been shown to be involved in the inheritance of blood characteristics (Ryder & Stepherson, 1968; Tuner & Young, 1969).

It is well established that a single allelic gene pair exists to differentiate sheep with high and low levels of potassium ion concentration in the erythrocytes. The gene responsible for high potassium (HK) is recessive to the gene for low potassium (LK). However, there may be modifiers affecting the potassium level in the red blood cells, in addition to the major genes (Tuner & Young, 1969).

Sheep may also be classified according to haemoglobin types into A, B and AB groups. It appeares that this seperation is also due to the action of single genes, without dominance.

Studies have also been undertaken to investigate the relation between blood characteristics and the productivity or adaptation of sheep. Detailed reviews on these studies can be found in Ryder & Stepherson (1968) and Ricordeau (1982).

The fact that a major locus exists in Booroola-Merino is already well known (Piper & Bindon, 1982a, b; Piper et al, 1985; Piper & Bindon, 1988). Many studies have been done to investigate the mode of inheritance of the gene, effects on fleece characters and physiology, and the possility of incorporating it into animal breeding programmes. This gene will be studied in detail later. Furthermore, Booroola-type major genes were also found in other breeds, such as Javanese sheep (Bradford et al, 1986), Iceland sheep (Jonmundsson & Adalsteinsson, 1985) and Cambridge sheep (Hanrahan, 1986). However, whether these genes are allelic to the Booroola-gene or not is not known (Hill, 1987).

2.2 Methods of Detecting Major Genes

The definition of a major gene is quite arbitrary. Following Morton and Maclean(1974), a major locus is refered to as one having an effect of at least one standard deviation of the metric trait, as measured by the difference between the two homozygotes($2a>=\sigma$).

A variety of methods have been proposed to aid in the identification of single genes of large effects. Reviews of this area have been given by Hanset (1982), Roberts & Smith (1982), Nicholas (1984), Hill & Knott (1987), Meikle & Wickham (1987) and Pirchner (1988). Various simple and more elaborate methods are summarised in Table 2.3.

Despite the many methods proposed, the discovery of major genes in farm animals has been fortuitous in nearly all cases (Pirchner, 1988). Few of the major genes discussed in livestock have been discovered following a systematic statistical investigation, unless one considers investigations of blood groups. For example, a major gene affecting reproductive rate in Booroola sheep was suspected when exceptional individuals appeared during selection (Piper & Bindon, 1982a,b), and loose wool bulk in Perendale was suggested to be under major gene control when the estimate of heritability of bulk was very high (Bigham et al, 1985). Pirchner (1988) suggested that in domestic animals, research succeeded in finding major genes in two rather different ways: via observation of Mendelian segregation, e.g., segregation of N^d gene or the Booroola gene in sheep (Dry, 1955a; Piper & Bindon, 1982a), or via performance of marker phenotypes, which comprise blood groups, plasma proteins, lymphocyte antigens, restriction fragment length polymorphisms (RFLP), and possibly colour and morphological traits. It is argued that methods based on likelihood calculations such as segregation analysis are most likely to be appropriate, despite complex computation, for analysis of both crosses between populations and individual random mating populations

Table 2.3 Methods for identification of major genes

Technique	References
1.Cell level.	
(1)effective number of genes	Wright(1952) Lande(1981)
(2)chromosomal analysis	Thoday(1961) Wehrhahn & Allard(1965) McMillan & Robertson(1974)
2.Methods using population differences	
(1)segregation in crosses and backcrosses	Wright(1952) Steward(1969) Lande(1981)
(2)repeated backcrossing and selection	Wright(1952)
(3)use of markers	Geldermann(1975) Hill & Knott(1987) Pirchner(1988) Lander & Botstein(1989)
3.Within population analysis	
(1)departures from normality	
a.heterogeneity of variance	Merat(1968), Penrose(1969) Fain(1978)
b.skewness & kurtosis	Hammond & James (1970)
(2)structured exploratory data analysis(SEDA)	Karlin et al (1979) Famula(1986)
(3)maximum likelihood methods	
a.complex segregation analysis	Morton(1974), Morton & Maclean (1974) Elston(1981), Elston (1987) Hoeschele(1988)
b.simple segregation analysis	Davie(1979) Nicholas(1984)
(4)rate of genetic response to selection	Piper & Bindon (1982b) Hanset (1982)
(5)genetic parameter	Smith & Webb (1981)

(Hill & Nott, 1987). Roberts & Smith (1982) suggested that the techniques proposed might be of more value in confirming suspicion of a major gene from other evidence, rather than in establishing the presence of such a gene where none had been expected.

While each of the statistical methods may find particular applications, the statistical power of all these methods depends greatly on the magnitude of the effect of the gene and on its frequency in the population, and the genetic backgroud of the population. The detection power of these methods declines rapidly as the magnitude of the effects falls (Smith & Webb,1981). In livestock, other non-genetic factors such as seasonal, nutritional and non-random environmental factors also affect the detection of major genes. These factors are likely to lead the overlap of phenotypes with different genotypes at the major locus and cause misclassification. In general, despite the many methods and proposals available, the detection of major genes in domestic livestock still presents methodological problems (Roberts & Smith,1982). In practice,several methods are always combined to identify the major genes.

2.3 Effects of Major Genes on Genetic Parameters

The presence of a major gene may affect the heritabilities of the traits concerned (Smith & Webb, 1981; Smith & Roberts, 1982; Hanset, 1982). The changed value of heritability was derived by Smith & Webb (1981).

For simplicity, assuming that all the variance due to the other loci is unaffected by the introduction of the major gene, and that the environmental variance also remains unaffected. Then following the notation of Falconer (1981), the properties of the major locus are shown as:

Genotype	A1A1	A1A2	A2A2
Frequency	p^2	2pq	q^2
Genetic value	a	d	-a

If V_A and V_P represent the additive genetic and phenotyptic variances, respectively, then the heritability (h^2) in the presence of the major gene becomes:

$$h^2 = \frac{V_A + 2pq\alpha^2}{V_P + 2pq\alpha^2 + (2pqd)^2} ,$$

where: $\alpha = a + d(q-p)$.

If a major gene affects two traits, the genetic correlation (r_A) between these traits is augmented by the major gene in a manner analogous to the effect on the heritability (Roberts & Smith,1982). The formula then becomes:

$$rA = \frac{CovA_1A_2 + 2pq \times \alpha_1 \times \alpha_2}{/(V_{A1} + 2pq\alpha_1^2)\ (V_{A2} + 2pq\alpha_2^2)} ,$$

where: the numerical subscripts refer to the two traits.

From the above two formulae, it can be seen that both heritability and genetic correlation estimates are affected by both the major gene effect and its gene frequencies in the population.

Smith & Webb (1981) studied the influence of various values of a and d over the full range of gene frequencies (0-1), and concluded that the effect of a major locus generally increased the heritability of the trait concerned; the only exception is in the presence of overdominance at the locus with a limited range of gene frequency (0.6-1.0).

2.4 The Optimum Use of a Major Gene in a Breeding Programme

The detection of major genes offers opportunities for new developments and breeding systems. It is important not to be constrained by conventional thinking or practices, but to consider all ways to exploit the genes; thereby enabling progress towards some objective to proceed as rapidly as possible.

2.4.1 Information required for the utilization of major genes

A substantial amount of prior information is necessory before any firm recommendation about the use of a major gene in a breeding programme can be made with any confidence (Smith, 1967)

The mode of inheritance, degree of penetrance of the genotypes and gene frequency are the first requirements, followed by a means of ascertaining the genotype of individuals. Then, it is essential to have reliable information on the effects of the different genotypes (at the major locus) on all traits of economic importance, since in farm livestock normally more than one trait will combine to determine the overall performance or economic merit of an individual or a

breeding group. It is frequently found that a major gene has positive effects on some economically important traits but deleterious effects on others. This problem was shown by Webb & Jordan (1979) when the benefit from improved carcass quality in halothane-positive pigs could be outweighed by the gene's negative effects on viability and fertility. Thus it is the net effect of the major gene on overall performance, rather than its effects on one trait, that will determine its usefulness (Smith, 1967, 1985). Roberts & Smith (1982) suggested that the economic value (A) of genotype K at a major locus is:

$$Ak = \sum ai(Xik - \bar{Xi}).$$

where: ai = the economic value of a unit change in trait i, and

Xik = the performance of genotype k (at the major locus) for trait i, with a mean over all genotypes of $\bar{Xi}$.

This expression could be adapted to allow for traits with intermediate optima and possibly non-linear economic weights. Smith & Webb (1981) applied this method to calculate the economic values of halothane genotypes in pig.

2.4.2 Manipulation of major genes

With a balance sheet on the effects of a major gene, decisions can be taken about how to manipulate it to best advantage for the breeders (Smith, 1985). Smith (1967) suggested six methods of selection to manipulate an identified locus (referred to as 'known' locus by Smith, 1967) and listed the expected genetic response to each method as in Table 2.4.

Table 2.4 Methods and responses expected to different methods of selection (after Smith, 1967)

Method	Expected genetic response ($h^2\sigma$ unit per period)
1. Individual perfomance (mass selection)	$i_1 c_1$ [a]
2. Known genetic loci	$i_2 c_2 / \overline{R/h^2}$ [b]
3. A selection index of (2) and (1)	$i_1 c_1 [1+(1/2)(R/h^2)]$ [c]
4. Two-stage selection, first on (2), then on (1)	$i_1 c_1 [1+(i_4/i_1)/\overline{R/h^2}]$
5. Indirect selection on relatives	$i_5 c_5 (r/w)$
6. An index selection of (2) and (5)	$i_5 c_5 (r/w)[1+(1/2)(R/h^2)(w^2/r^2)]$ [c]

a i--selection differential.
c--reciprocal of the generation interval. For family selection multiply by $[1+(n-1)r]/nr$, where w2 equals $[1+(n-1)t]/n$, the variance of the mean of n tested relatives; t is the correlation among tested relatives and r is the genetic relationship of the selected individual with its tested relatives.

b R--the proportion of the additive genetic variance controlled by known loci.

c Approximately.

In general, known genetic loci that affect metric traits may be useful in livestock improvement. Their value depends on the proportion (R) of the total additive genetic variation due to the known loci relative to the heritability of the trait concerned and on the form of selection practised. Information on known loci is likely to be of most value in improvement when normal selection methods are not very effective such as when the heritability is low or when indirect selection on relatives is necessary. Some advantage may also be gained if a more intense or an earlier selection is possible by using known loci (which is generally possible). Normally, if the

proportion (R) of the additive genetic variance controlled by known loci is not large relative to the heritability (h^2), the information on known loci will be used most efficiently if combined with performance records, as in a selection index (Smith,1967). Smith (1967) stated the method of index selection is, in any case, never less efficient than mass selection or selection on known loci (Fig. 2.1)

2.4.2.1 The index method

Some methods have been proposed to combine the information from the known factors into a selection index in animal selection.

In the 1950's, studies on poultry indicated that there might be some relationship between blood groups and production capacity, or fitness of poultry. Based on these findings, Neimann-Sorenson & Robertson (1961) investigated the possible association between blood groups and six production characters in dairy cattle. Suppose the information from the blood groups leads to a prediction (B) of the breeding value (H) of an animal for, say, milk yield, and a cow has a performance record of P with a heritability of h^2. Then the information on performance and from blood groups is combined into a selection index (Hazel,1943) to maximize the correlation, R_{IG}, of the resulting index with the breeding value of the cow for yield. If a_1 and a_2 are the regression coefficients in the prediction of breeding

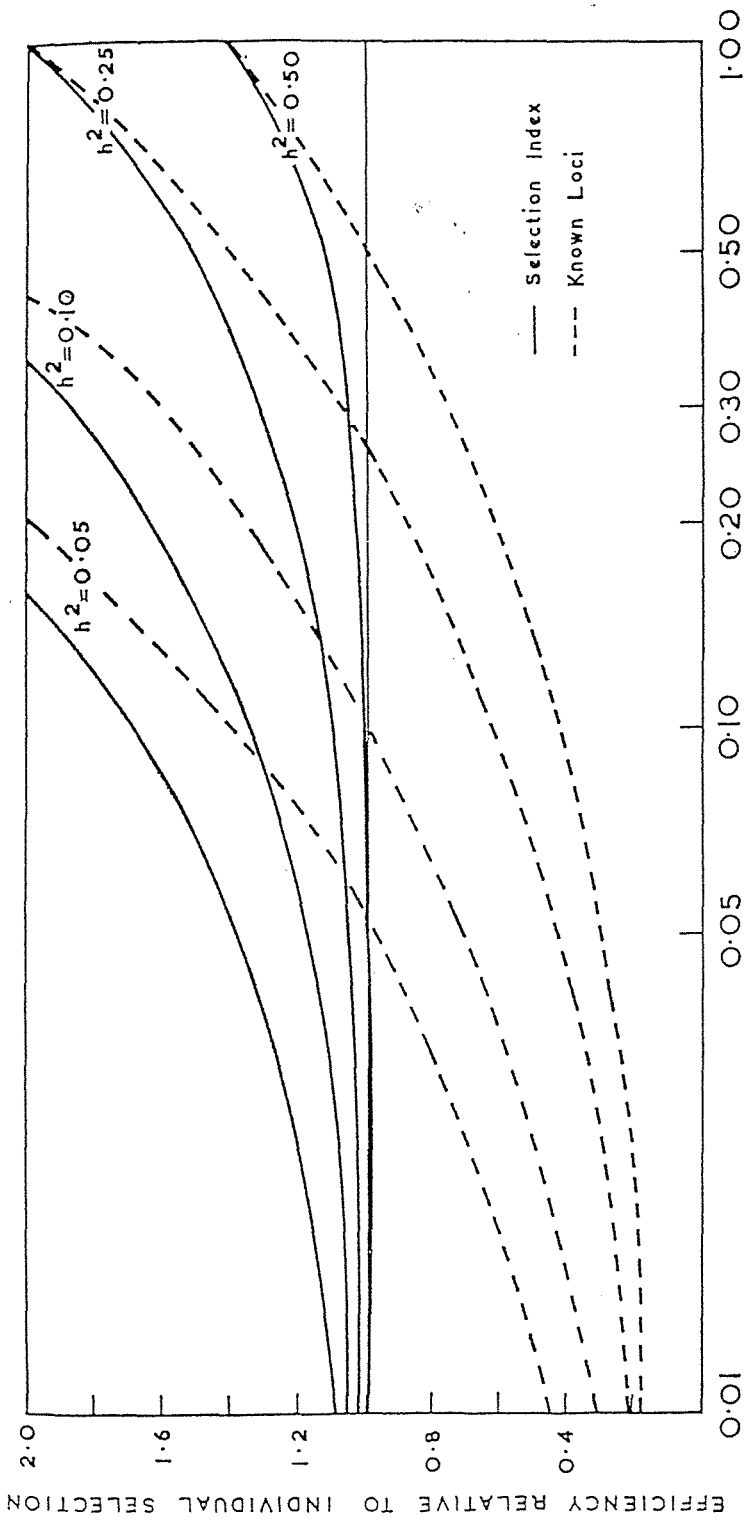

FIG. 1. The efficiency of selection on known loci alone and in a selection index, relative to individual selection.

value, then the breeding value of the cow could be predicted as follows:

$$G = a_1B + a_2P,$$

where: a1 and a2 can be derived from the following simultaneous equations:

$$a_1\sigma^2_B + a_2CovBP = CovBG$$
$$a_1CovBP + a_2\sigma^2_P = CovPG$$

Here, $\sigma^2_B = CovBP = CovBG$ (since B is a constituent of B, P and G).

The correlation between the selection index (I) and the breeding value G is then given by:

$$R^2_{IG} = h^2 + \frac{h^2_1(1-h^2)^2}{h^2(1-h^2_1)}$$

Where $h^2_1 = \sigma^2_B/\sigma^2_P$ (=R in the term given by Smith, 1967). If h^2_1 is small, this will simplify to:

$$R_{IG} = h\left(1 + \frac{1}{2} * \frac{h_1^2}{h^4}\right)$$

$$= h\left(1 + \frac{1}{2} * \frac{r_{BG}^2}{r_{GP}^2}\right)$$

Since the amount of genetic improvement expected from selection is proportional to R_{IG}, the relative gain expected from the additional blood group information is $r_{BG}^2/2r_{GP}^2$.

Using an approach similar to that used by Neimann-Sorenson & Robertson (1961), Soller (1978) developed an index to select for young males on known-loci. The index comprised of the breeding value of a young male at the known locus (A) and on the residual breeding value of the young male as estimated from the breeding value of his dam (B), after correction for her known-locus genotype. A and B were assumed independent, and for simplicity, B was estimated from a single production record. Then:

$$I = A + B,$$

where: A is discontinous, taking values of $2q\alpha$, $(q-p)\alpha$ and $-2p\alpha$, with frequencies p^2, $2pq$ and q^2 for the A_1A_1, A_1A_2 and A_2A_2 genotypes, respectively, and $\alpha=d+(q-p)h$, and

B is normally distributed with mean zero and standard deviation $(1/2)h'^2_t\sigma$; h'^2_t and σ are the heritability and phenotypic standard deviation of dam production records after removal of the known locus portion of the genetic variance. For a single known locus of moderate effect, h'^2_t and σ are approximately equal to the corresponding total population parameters, h^2t and σ_p.

Smith & Simpson (1986) extended the selection index stated above into the situation where more than one trait were selected. Although they did not give the formula of the index directly, the selection index based on the information of the individuals own record, its

relatives records and identified QTL (Quantitative trait loci, i. e., the loci affecting a quantitative trait) was shown as:

$$I = b_1X + b_2X_F + b_3X_H + b_4A' + b_5A'_F + b_6A'_H,$$

where: bi is the index coefficient from information of its own, full-sib and half-sib at quantitative genetic background and the identified QTL, respectively, X, X_F and X_H are the performance of the individual, its full-sibs and its half-sibs, respectively, and

A', A_F' and A_H' are the breeding values on the identified QTL of its own, its full-sibs and its half-sibs, respectively.

The same structure of index can be applied to the case where more than one trait is selected. In the multi-trait situation, both the additive genetic variances of the major locus for each trait (A'_i) as well as the additive genetic covariances between all pairs of traits are required. The parameters required to derived a selection index for just two traits using information on QTL and performance records were shown by Smith & Simpson (1986).

2.4.2.2 Other possible ways to utilize a major gene

Another simple way to utilize a major gene in breeding is to manipulate the gene directly and make the population homozygous for the best allele (Smith,1967, 1985). This will take only one or two generations of selection if the favourable gene is recessive, or if the genotypes of individuals can be ascertained. If the initial frequency of the allele is low and when selection is mild several

generations will be required. With complete dominance of all gene effects, progeny testing is required. However, with this method, the duration of response to selection for known loci may be rather short. Smith (1967) stated that the response from fixing the better allele at a locus is normally less than the response from selecting on all available information.

A possible problem with this approach is that the effect of a major gene in homozygote form may be too large, as in calving difficulty with the double-muscled gene and perhaps litter size with the Booroola gene. In such cases, the best combinations of traits could then well be found in the heterozygote and the optimum strategy might then call for sire and dam lines to be fixed for different alleles, the commercial product being the heterozygotes (Smith, 1967; 1985). To have different alleles fixed in different lines also applies to the case of an overdominant locus (Smith, 1967). An alternative to crossing lines may be to select for background effects which modify the effects of the major gene. However, even if this were possible, it would take some time to achieve and would be restricted to the line concerned (Smith, 1985).

Frequently a major gene is detected in one breed or line and exploited in another breed or line. This can be undertaken by introgression, i.e., backcrossing (Smith, 1985). For example, the very high incidence of calving difficulty with the recessive double-muscled gene would rule out its use in normal production, or in selection with an index which included calving ease. However, this gene might be used by introducing it into the Jersey breed, which is

noted for its ease of calving, and so produce a small, efficient, lean, milking, dual-purpose breed (Smith, 1985). The same principle can be used in exploiting the Booroola gene. The high incidence of fleece-rot and foot-rot of the Booroola Merino in high-rainfall areas reduces the gene's potental use, but if the Booroola Merino is crossed with some long-wool breeds, the Booroola gene could be more effectively utilized in these environments.

2.5. The Booroola-cross

2.5.1 The history of Booroola sheep

The highly prolific Booroola Merino was initially developed by two commercial sheep breeders, the Seears brothers of 'Booroola', Cooma, New South Wales, Australia. It is now well documented that in the Seears' breeding programme, selection for increased multiple birth was only applied on the female side. Rams used in the multiple birth flock were always purchased (without regard to birth type) from outside studs whose own breeding programmes did not include any selection for increased litter size (Turner, 1982). The date at which multiple-birth selection commenced is not clear, but it was at least as early as the year of 1959 (Turner, 1982).

From the Seears'flock, CSIRO obtained 14 multiple-born ewes or ewes which had multiple-births and 2 quintuplet-born rams during 1958-1960. In 1965, a further group of 9 multiple-born ewes was purchased. These sheep later formed the CSIRO Booroola flock at Armidale (Turner,1978, 1982; Piper & Bindon, 1982a). Selection of

multiple-born male and female sheep was practised in the CSIRO flock, with marked response in terms of lambs born (Turner,1982).

In 1973, three purebred Booroola rams were given by CSIRO to the NZ Ministry of Agriculture and Fisheries (MAF). In subsequent years, further imports from a commercial source in Western Australia occured. Most of the later animals were not purebred Booroolas (Clarke, 1982; Lewer & Allison, 1980). Using these animals, quantitative genetic research relavent to their evaluation and utilisation through crossbreeding in New Zealand was initiated.

2.5.2 Evidence of a major gene in Booroola sheep

In sheep, reproduction rate has been successfully increased by within-breed selection; but the rate of incease is unlikely to exceed 2% per year, even if lifetime reproduction records are available (Turner,1979). Therefore, from the viewpoint of breeding improvement, given a non-closed flock and selection only on the ewe side based largely on birth type, it would not have been possible for the Seears to raise the mean lambing percentage from normal Merino levels (approximately 80-110% in the Cooma district) to their 1958 level of 170-180% by gradual accumulation of favourable genes of small effect (Piper & Bindon, 1982b; Robertson, 1982; Turner, 1982). The continual migration of genes through the introduced, unselected rams also precludes that result. Therefore, the only way for the observed increase to have occured was by a gradual increase in the frequency of individuals carrying a gene (or a closely linked group of genes) with a large effect on litter size (Piper & Bindon,1982a, b).

With the hypothesis that a major gene for fecundity existed in Booroola sheep and the evidence that litters of three or more were rare in normal Merinos but were relatively common of the multiple births (18%, Turner, 1982) in the Seears, high fertility flock, Piper & Bindon (1982a, b) proposed that any ewe with one or more set of triplets in its lifetime lambing records was heterozygous for a major gene. The distribution of litter size at birth of Booroola and control Merino ewes given by Piper & Bindon (1982a) supported the above segregation criterion (Table 2.5)

Table 2.5 Distribution (%) of litter size at birth in mixed age Booroola (2-7 years) and control (2-6 years) Merino ewes (from Piper & Bindon, 1982a)

Flock	n	litter size						Mean
		1	2	3	4	5	6	
Booroola	522	24	37	30	7	2	1	2.29
Control	835	78	22	-	-	-	-	1.22

With this criterion, segregation analysis has been applied to validate the proposed single major gene hypothesis.

(1) In the foundation CSIRO Booroola flock.

The lifetime lambing records of the 14 foundation CSIRO Booroola ewes and 19 of their daughters sired by the 2 foundation Booroola rams were studied by Piper & Bindon (1982a, b). The results are shown in Table 2.6.

Table 2.6 Number of ewes (mean litter size) with different reproductive performance

Group	Total ewes	number of ewes with litter size >= 3	< 3
Foundation Booroola ewes	14	8 (2.42)	6 (1.37)
Daughters from ewes with at least one litter size record >= 3	11	6 (2.52)	5 (1.35)
Daughters from ewes with no litter size record >= 3	8	0	8 (1.35)

Under the breeding policy utilised by the Seears brothers (rams used were introduced from outside), the major gene theory would lead to the predicttion that only half of ewes in the flock could be heterozygous, whereas the other half would not inherit the putative allele at all. The data in Table 2.3.2 showed that the segregation of both the ewes and their daughters under the assumed criterion was in good agreement with the segregation ratio of 1 to 1 (8 to 6, and 6 to 5 for the ewes and their daughters, respectively) on the basis of a major gene hypothesis. The results in Table 2.3.2 also indicated that neither of the foundation rams were carriers of the gene.

(2) Crosses between the Booroola and conventional Merinos in Australia.

Piper et al (1985) reported trial matings between the Booroola and Medium non-Peppin (MNP) Merinos. Measurement of ovulation rate and litter size were recorded, and the results are shown in Table 2.7.

Table 2.7 Frequency ± s.e. of ewes carrying the putative allele in several Booroola (B) x MNP Merino genotypes

Genotype	No. of ewe	Frequency of carriers	
		Observed	Expected
F_1 (B x MNP)	136	0.72±0.04	
F_2 (B x MNP)^2	124	0.55±0.04	0.59
Backcross [(B x MNP) x MNP]	82	0.35+0.05	0.36

The expected frequencies of the carriers in the F_2 and backcross generations have been calculated by Piper et al (1985), using a random mating, single locus (2 allele), hypothesis and with the knowledge that the F_1 carriers cannot be homozygous. It is obvious that the observed and expected frequencies are in good agreement.

(3) Crosses between the Booroola and conventional Merinos in NZ.

In New Zealand, Davis et al (1982b) analysed the lifetime records of ovulation rate (OR) and litter size of Booroola x Merino (F_1), Booroola parent backcross (3/4 Booroola) and Merino parent backcross (1/4 Booroola) ewes. 'Carriers' of the putative gene were defined as those animals that had at least one litter size or OR record >= 3 during their lifetime. The observed proportions of carrier ewes were tested against the expected values appropriate for particular progeny groups by the X^2 goodness of fit test. The results were consistent with the presence in the Booroola of a major gene affecting fecundity.

(4) In the progeny test records of F_1 sons of progeny tested Booroola rams.

Previous segregation studies have been limited to only the female progeny (F_1 and F_2) of a Booroola parent of unknown genotype (Piper & Bindon, 1982a, b; Davis et al, 1982b). Davis & Kelly (1983b) extended the work to both the F_1 female and male progeny of Booroola rams.

Oulation rate records from female progeny of 3 Booroola-type rams in a commercial flock in NZ suggested that among the three rams, one was homozygous FF, one heterozygous F+ and one normal ++. Thus, the expectations of the progeny test results for F_1 sons (Booroola x local breed) of each of these rams would be different. All for FF, half for F+, and none for ++ ram of the sons should be heterozygous for the putative allele. The progeny test results of the sons were in excellent agreement with the expectation of a major locus segregation, after adjustment for the proportion of carriers based on one observation (Davis & Kelly, 1983b).

(5) Repeatability of OR in the Booroola and Booroola-cross ewes.

Estimates of the repeatability of OR differ according to the F-locus genotype of the flock. The estimates from the flocks containing all three genotypes (FF, F+ and ++) were much higher (around 0.6-0.9, Bindon, 1975; Lewer & Allison, 1980; Davis et al, 1982a; Owens, 1986) than the estimates from the separated homozygous (FF, F+ or ++) subpopulations (around 0.10-0.24) (Davis et al, 1982a; Owens, 1986). The high repeatability in the combined Booroola flock results from

the high variability in OR between the three genotypes, and supports the conclusion of the segregation of a gene having a large effect on OR in the Booroola (Davis et al, 1982a; Owens, 1986).

In summary, the major gene hypothesis to account for the exceptional prolificacy of the Booroola Merino was first advanced in 1980 (Piper & Bindon, 1982a, b). Since then, a considerable research effort has been directed towards testing the theory, and the results strongly support the presence of a major gene determining the high fecundity of the Booroola Merino. Reviews of the evidence of the gene have been given by Robertson (1982), Piper et al (1985) and Piper & Bindon (1988).

2.5.3 The segregation criteria and problems in the segregation analysis

2.5.3.1 The segregation criteria

Both Piper & Bindon (1982a, b) and Davis et al (1982b) defined the 'carriers' of the putative gene as those animals which had at least one litter size or ovulation rate record equal to or greater than three during their lifetime. To distinguish between heterozygous and homozygous individuals, Davis et al (1982b) further defined a ewe with an ovulation rate ≥5 in its lifetime as being homozygous for the major gene. This level was chosen because very few ewes (7.8%, Davis et al, 1982b) had ovulation rate records of 5 or more in the F1 generation, where only heterozygotes could exist.

Davis et al (1982b) suggested that the distribution of progeny classified on ovulation rate was more consistent with the single gene segregation than that on litter size. In genetic terms, the variation in litter size was largely a reflection of variation in OR (Hanrahan, 1982). However, litter size became an increasingly inaccurate indicator of OR as mean OR increased since embryo loss rate was directly proportional to OR (Hanrahan, 1980). In cases where ewes were lambing in flocks, the precision of classification on litter size was likely to be further reduced because of errors in identification of lambs to their dams.

Another advantage of classifying genotypes on OR is that, with the development of laparoscopy in sheep, it is possible to have a number of OR records within one breeding season, and consequently distinguish genotypes earlier.

However, some problems remain unsolved by the use of these segregation criteria (Piper et al, 1985; Elsen et al, 1988).

2.5.3.2 Problems

(1) Genetic background.

The above suggested criteria appear appropriate to distinguish the three genotypes at the F locus when the base breeds is Merino such as in the studies of Davis et al (1982b) and Piper & Bindon (1982a, b). However, these criteria will clearly be much less useful in segregation studies involving breeds with higher average

prolificacy because the proportion of naturaly occurring triplet births increase markedly when the mean OR exceeds 1.7 (Davis et al, 1983a; Piper et al, 1985). Piper et al (1985) mentioned that the F-gene would increase OR by about 1.2 in heterozygotes and this value appeared to be independent of the prolificacy of the base breed.

(2) The number of observations required.

In the study of lifetime OR records (3-6 per ewe) of F_1 Booroola x Conventional Merino ewes in NZ, Davis et al (1982b) found that only 64% of the F-gene carriers had a record of three or more at any single observation. There were no significant age or year of birth effects on this proportion. Therefore, the expected frequency of carriers identified after n ovulation records would be given by $1-(1-0.64)^2$. Thus, after three records 95%, after four records 98% of carriers would be expected to have been identified. However, this is an overestimate because it assumes the repeatability of OR to be zero, when actually the estimated repeatabilty of OR was about 0.31 (Davis et al, 1982a).

The incidence of carrier ewes identified under the suggested criteria at any one time is not always 0.64, even when the background genotype is wholly Merino. In the experiment of Piper & Bindon (1982a) where Booroola rams were mated with conventional medium non-Peppin Merinos in Australia, only 32% of F_1 carrier ewes had an ovulation record of three or more at any one time. While this proportion was not affected by age of ewe, there were highly significant ($p<0.01$) differences between different years of

measurement. For litter size records, the overall probability of expressing the F-gene was only 20%, and though year of measurement effects were not significant, the effects of age were ($p<0.01$), with 2-year-old carriers having only 30% as many triplets births as their adult counterparts.

Therefore, the proposition that using OR as a segregation criterion may have the putative genotypes distinguished earlier would not necessarily work under Australian conditions because of the highly significant year of measurement effects. Whether it would work under NZ conditions is not clear from the analysis of Davis et al (1982b), because the year effects studied were the year of birth rather than the year of measurement (Piper et al, 1985).

(3) Recognizing male carriers of the F allele.

Since prolificacy is expressed only in the female, the F locus genotype of males must be determined by progeny test. The difficulties associated with progeny test procedures have resulted in a considerable effort being directed toward finding traits directly measurable and correlated with the F locus genotypes in male. A number of studies have been undertaken (Bindon & Piper, 1976; Bindon et al, 1982 ; Beetson, 1982) and summarized by Bindon (1984) and Piper & Bindon (1988). The general conclusion is that the testis growth rate, testis size and total daily production of spermatozoa of the Booroola ram are similar to those of normal Merinos. Comparative hormone (androgen and gonadotrophon) profiles of Booroola and Control Merino males have also been studied in a few experiments, but

so far no differences have been discoved (Piper & Bindon, 1988). Recently studies suggested that rams carrying 0, 1, or 2 copies of the F gene might be distinguishable by sperm characteristics, e.g., sperm swimming speed and sperm mortality index (Moore, et al, 1989), but these results were based on only 2-3 rams for each genotype.

2.5.3.3 Alternative statistical approaches

Owens et al (1985) proposed the use of cluster analysis techniques to separate the Booroola-Merino genotypes based on ewes OR. The results were similar to those derived from the classification by the criteria of Davis et al (1982b). Cluster analysis incorporates all OR records for each ewe, and therefore is less affected by the occurence of a single high OR record in the lifetime of an ewe. It is particularly useful when classifying genotypes in flocks with genetic background of OR differing greatly from the Merino breed.

The technique of Owens et al (1985) has been criticized by Elsen et al (1988), who pointed out that Owens et al (1985) did not take into account other error sources such as age, season, and individual genetic-background deviation. As an improvement, Elsen et al (1988) suggested a mixed model, taking into account environmental factors, to classify sires and daughters for their genotypes at the major locus in a progeny test design. The trait examined by Elsen et al (1988) was normally distributed, and the case of a discrete trait was studied in the same way by Foulley & Elsen (1988).

2.5.4 Characteristics of the F gene

The Booroola gene could have arisen as a mutant in the Seears' flock or in one of the stud flocks supplying replacement rams. However, the gene was most likely to be introduced to Australia in 'Bengal' or 'Cape' sheep, which were stated to be prolific (Turner, 1982).

2.5.4.1 Name of the gene

Since the gene affects the fecundity of its carriers, 'F' was adopted as the symbol of the gene (and the locus). The recommended alternative of '+' was used to indicate the wild type or the normal allele (Davis et al, 1982b; Piper & Bindon, 1988).

2.5.4.2 Mode of gene action of the F gene

In the segregation analysis, Piper & Bindon (1982b) suggested that the F gene had an additive effect on OR, but might be almost completely dominant for litter size, whereas Davis et al (1982b) and Robertson (1982) stated that the effect of the F gene on litter size was only partially dominant. Further studies (Owen et al, 1985; Piper et al, 1985; Piper & Bindon, 1988) confirmed the conclusion of Davis et al (1982b) that the effects of the F gene on OR is additive (at least on Merino background), but might be very nearly additive for litter size in breeds with levels of prolificacy similar or less than 1.5 (Piper et al, 1985) (Table 2.8). However, Piper et al (1985) suggested that, if the relationship between litter size and OR

proposed by Hanrahan (1982) holds, the effects of the gene on litter size in breeds of higher average prolificacy may well be dominant.

Table 2.8 F gene dosage effects on ovulation rate (OR) and litter size (LS)

Genotype	Davis et al (1982b)			Owens et al (1985)		Piper & Bindon (1988)	
	n	OR	LS	n	OR	OR	LS
FF	22	4.51	2.71	33	4.08	4.38	2.66
F+	88	2.78	2.25	72	2.56	2.82	2.17
++	66	1.49	1.36	71	1.32	1.40	1.48

2.5.4.3 Characteristics of the F gene in crossbreeding trials

A series of trials under production conditions throughout Australia and N. Z. have evaluated the role of the Booroola in improving the reproductive rate of other Merino strains or sheep breeds.

The Booroola (B) was mated with medium non-Peppin Merinos (MNP) in Australia. Piper & Bindon (1982a) showed that the half-Booroola mixed-age ewes had much higher OR (about 80%) and litter size (about 50%), but lower overall lamb survival (64% vs 85%) with a resultant increase of 16% at weaning. For any wool or body trait, differences between B x MNP and ordinary MNP offspring were small and rarely significant from weaning through to 4 years of age. Growth to weaning of lambs from half-Booroola ewes was slower than lambs from MNP ewes but the differences were much reduced when the data were adjusted for litter size at birth. This is consistant with the earlier result of Piper et al (1979).

When Booroolas were crossed with stong-wool Merino strains, McGuirk et al (1982) and Piper et al (1979) found that the Booroola-cross ewes produced about 0.4 Kg less clean wool per head, but 20-28% more lambs weaned. Beetson (1982) reported the mean liveweight of the half Booroola was also lower than the Control at 18 months of age.

Booroolas have also been mated with Romney ewes in New Zealnd. Kelly et al (1980) and Allison et al (1982) reported that 2 to 4 year-old Booroola- cross ewes shed 0.7-0.9 more ova per ewe than the Romneys, resulting in about 0.5 more lambs present at tailing. Fleece weights and liveweights of hoggets were similar, but Booroola-cross ewes produced up to 0.5 Kg less greasy wool per ewe at later ages. Allison et al (1982) stated that B x R fleeces were finer, bulkier, with shorter staples and lower yields than Romney fleeces.

In summary, the Booroola-cross progeny have a much higher OR, larger litter size at birth and relatively higher weaning percentage when compared with the control breeds. These increases were generally achieved without losses in wool production and quality, and body weight at first joining when the cross was made with finer-woolled Merino strains. However, crosses with coarser-woolled sheep showed some reduction in fleece weight and body weight at 18 months of age (Ch'ang et al, 1979). With these results, potential exists to exploit the Booroola gene in other strains or breeds. It was recognised that multi-breed synthetics might be a better long-term prospect for successful exploitation of the Booroola gene (Clarke, 1982). Possible crossbreeding programmes have been suggested by Robertson (1985) and

Smith (1985). The essential management changes in farms following cross-breeding with the Booroolas have been studied by Davis (1983), Davis & Hinch (1985) and Robertson (1985).

2.5.4.4 Other aspects

The discovery of the Booroola gene has stimulated a great deal of research aimed at understanding the nature of the genetic change of the Booroola. The reproductive biology and endocrinology of the Booroola Merino sheep has been studied intensively. Some differences have been found between the reproductive biology of carrier and non-carrier ewes. Detailed reviews could be found in Bindon (1984) and Piper & Bindon (1988). Smith (1985) stated that knowledge of the physiological nature of the effects of a major gene was not necessary for its utilization; however, it might be useful to understand the factors involved to help im predictions of effects in other situations or to overcome sex limitations.

C H A P T E R T H R E E

THE MASSEY BOOROOLA FLOCK

3.1 The Origin of the Massey University Booroola-cross Flock

The Massey University Booroola-cross [(Booroola x Romney) x Perendale] flock originated at the Tuapaka hill country farm in 1980. The original objective was to develop an interbred-crossbred type of sheep which would be suitable for North Island hill country conditions and produce more lambs and finer wool than the Romney and Perendale sheep which dominate in this farming system. Another part of the objective was to compare the performance and rate of genetic gain in the sheep of this flock with that of the Perendale sheep flock which had been run at Tuapaka for many years. However, changes in the personel supervising Tuapaka led to changes in priorities. At the beginning of 1986, the removal of the Perendale flock was followed shortly afterwards by a decision that the Booroola-cross flock would not be carried at Tuapaka.

Since 1975, a similar flock of 100 ewes had been run on the Pahiatua block of the Animal Science Department Research and Development unit. This flock had been generated by mating Perendale rams with superfine Merino x Romney ewes and were called the Merper flock. The flock had performed well, but when the Booroola-cross flock was being shifted from Tuapaka, it was felt that the Booroola-cross animals had more potential research uses. Consequently, the Merper flock was disposed of in 1986 and 250 of the Booroola-cross

ewes were transfered from Tuapaka to the Research and Development unit.

3.2 Mating Systems

Crossbred matings to generate the Booroola-cross flock took place at Tuapaka in 1980 and 1981. In 1980, three Booroola Merino rams, obtained from the Tara Hills Reseach Station, were mated to 100 Romney ewes to generate rams for use in 1981. Subsequent studies indicated that two of these rams were FF while one had the F+ genotype.

In the same year (1980), 700 Perendale ewes were also mated to six Booroola x Romney rams which were surplus to requirements at the Invermay Research Station. Information on progeny from these six rams suggested that all were F+.

In 1981, about 600 of the same Perendale ewes used in 1980 were mated to 12 ram lambs. These rams, generated from the mating of Booroola Merino rams and Romney ewes as mentioned above, were selected for a combination of good liveweight, high lamb fleece weight and freedom from footrot. Because of shortage of paddocks, there were 6 mating groups, with about 100 ewes per group. Each group was mated with two ram lambs, the ram lambs used in each group being half brothers. These rams took turns in running with the ewes. An attempt was made to recognize which ram sired the lambs by:

(a) using different coloured mating crayons (however, many ewes lambed without showing marks),

(b) leaving a gap of a day between removal of a ram and releasing its replacement, and

(c) relating date of birth to the ram run with the ewe 147 days earlier.

This system has been described more fully by Alwan (1983). Unfortunately it left a degree of doubt as to which of the two half brothers sired some lambs. The mating groups were kept seperate at lambing to ease identification problems. Analysis of subsequent fecundity records of the progeny suggests that all except one of the 12 ram lambs were F+. All progeny thought to be sired by the ++ ram were culled.

In the years from 1982 to 1985, interbred matings were carried out at Tuapaka. At this stage emphasis was on the selection of animals likely to carry the F-gene and the culling of those unlikely to have the gene. During the years 1983, 1984 and 1985, approximately 500 ewes were mated each year to 5 two-year old rams. The 5 rams were selected as following: first about 25-30 out of 250-300 lamb rams were selected according to their dams' fecundities, then 5 two-year old rams chosen on the combination of their dams' fecundities, their own hogget clean fleece weights and mean fibre diameter, with some attention on the colour of the fleeces and horns. The same method was used for selection of sires in later years.

In 1986, the 250 ewes moved to the Research and Development unit were mated to 5 rams, one of which had also been used in the previous year.

In 1987 and 1988, only 4 sires (all 2 years old) were used. The same method described above was used to select for sire

3.3 Performance Records

Due to management constraints, it was not been possible to maintain a consistent recording system, throughout the development of the Booroola-cross flock.

In the year from 1980 to 1986, the need to conform to the philosophy that Tuapaka was a commercial unit and that staff would only carry out normal commercial operations, apart from a few exceptions, limited recording efforts. Upon transfer to the Research and Development unit, the level of recording became more intensive, but it was still limited by competing demands on the time of farm staff and Department of Animal Science staff.

3.3.1 Lamb production of ewes

Fecundity of the ewes was assessed in several ways:

1. hogget ovulation rate. This has been recorded in most years except 1985, 1986 and 1988. The observations have been made via laparoscopy with all hoggets being observed at one common time late in June or early in July irrespective of whether the hoggets had a previous oestrous or not. This system did not provide such accurate records as laparoscopy at a fixed time

after observed oestrous, but labour supply problems did not allow a more accurate system,

2. ewe's ovulation rate. This was observed as part of the study by Rangel (1987). An initial set of ovulation rates were recorded and the ewes which could be most clearly identified as being F+ or ++ according to the criteria of Davis et al (1982b) were placed in experimental groups. Some animals were treated with PMSG and the ovulation rate was recorded again. Some embryo transplantation also took place as part of this work,
3. foetal counts. In the years of 1983-1985, X-ray scans of ewes were carried out at about 100-130 day stage of pregnancy to determine how many foetuses were present. Subsequently (1986-1988), foetal counts were carried out at about 40-70 day stage of pregnancy using a realtime ultrasonic scanner, and
4. lambs born or tagged and pedigree. In 1980, during the initial crossbreeding, ewes mated to different rams were lambed down in seperate paddaocks and the lambs were not identified as being singles or twins or being from a particular ewe. Sire was the only pedigree information recorded. Dam information from 1981 (Perendale ewes) was also limited. In the years from 1982 to 1985, lambs and ewes were mustered at docking time and then allowed to 'mother up' so that the ewe and her offspring could be recognized and recorded. Since docking typically occurred 2 to 3 weeks after birth, it was not possible to determine the number of lambs born since a proportion would not survive to docking.

Since transfer to the Research Farm, lambs have been tagged and their dams recorded within 2 days of birth.

3.3.2 Other traits

Liveweights were recorded at weaning, sometimes in autumn and at hogget shearing.

Shearing was once yearly in the October-November period, except for lambs which were shorn in late December-early January. Fleece weights were recorded each time.

Midside samples were removed from the fleeces at shearing and wool characteristics were assessed on these midside samples as described by Leyva (1986).

C H A P T E R F O U R

DISCRIMINANT ANALYSIS

4.1 Introduction

As stated in Section 2.5.3, problems exist when attempting to identify the genotypes at the putative F-locus by the segregation criteria proposed by Piper & Bindon (1982a, b) and Davis et al (1982b). Consequently, other methods are sought to solve (at least some of) the problems. One appropriate method is the discriminant function analysis.

Discriminant function analysis is a topic in the general area of multivariate analysis, i.e., dealing with the simultaneous variation of two or more variables. It is frequently important in biological work, on examining the multiple measurements of a single individual or a small sample of individuals, to be able to decide in which of the previously recognized groups the individual or small sample belongs. In such cases, it is always reasonable to combine the several characters into one proper linear compound (i.e., an index), and by this linear compound to classify futher individuals into one of the known groups.

In almost every way, discriminant analysis parallels multiple regression analysis, except in the former the number of dependent variables is equal to the number of groups whereas in the latter, the number of dependent variables is equal to the number of individuals.

4.2 Principles and Approaches

Discriminant functions were first proposed by Fisher (1936) to seperate two taxonomic species of plant (iris) by four measurements: sepal length, sepal width, petal length and petal width (x1, x2, x3 and x4, respectively). Fisher (1936) first combined the above four measurements into a linear function:

$$Z = a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4,$$

where: a_i = the discriminant function coefficent of the ith variable in the discriminant function.

He then suggested that the particular linear function (Z) which best discriminated between the two species could be found by maximising the ratio of the squared differences between the sample means of the two species $[(\bar{Z}_1-\bar{Z}_2)^2]$ to the within species variance of Z (V_Z). Therefore, the various a_i values can be estimated by maximizing the ratio:

$$(\bar{Z}_1-\bar{Z}_2)^2/V_Z.$$

Once the discriminant function coefficents are estimated, the mean discriminant score for each group ($\bar{Z}_1$ and $\bar{Z}_2$, respectively) can be calculated. If for example, group 1 mean ($\bar{Z}_1$) is bigger than group 2 mean ($\bar{Z}_2$), then the discriminant rule will allocate an individual $\underline{x}$ (vectorof its measurements) to group 1 if the discriminant score Z (=a'x) of the individual exceeding the mid-point $(\bar{Z}_1+\bar{Z}_2)/2$, i.e.:

$$a'x > (\bar{Z}_1-\bar{Z}_2)/2.$$

Otherwise, the individual will be classified into group 2 (Kendall, 1975; Morrison, 1976).

The theory of Fisher's linear discriminant functions was later extended to more general situations. This allowed for more than two groups to be involved, and possibly the situation where the prior probabilities of each group were known (Rao, 1952; 1973; Anderson, 1984; Lebart et al, 1984; Manly, 1986).

In the general cases where the number of groups (g) > 2 and p variables are measured for each individual, the discriminant function coefficents $\underline{a}$ (= a_1, a_2, ..., a_p) can be estimated by maximising the ratio of the between-group variance to the within-group variance (Lebart et al, 1984; Manly, 1986), i.e., maximizing the ratio of:

$$\underline{a}'\underline{B}\ \underline{a}/\underline{a}'\underline{W}\ \underline{a},$$

where: $\underline{B}$ and $\underline{W}$ are the between-groups and within-groups matrices of the sums- of-squares and cross-products, respectively. The values of $\underline{a}$ can be shown to be the eigenvector of $W^{-1}B$ corresponding to the largest eigenvalue.

Once the linear discriminant function has been calculated, an observation $\underline{x}$ (which is a vector containing the variables of an observation) can be allocated to one of the g groups on the basis of its 'discriminant score' ($a'\underline{x}$). Let the sample means $\bar{x}_i$ have score $a'\bar{x}_i=\bar{y}_i$ for group i, then an individual $\underline{x}$ is allocated to that group whose mean score is closest to $a'\underline{x}$; that is, allocate $\underline{x}$ to j if:

$$1\ a'\underline{x}-a'\bar{X}_j\ 1 < 1\ a'\underline{x}-a'\bar{X}_i\ 1 \quad \text{for all } i=/\ j.$$

Or equally, an observation $\underline{x}$ is placed in the jth group from which it has the smallest generalized squared distance. The generalized

squared distance from an observation $\underline{x}$ to group j is (from SAS, 1984):

$$D_j^2(x) = g_1(x,t) + g_2(t),$$

where: $g_1(x,t) = (x-U_j)'s_j^{-1}(x-U_j) + \text{Log}_e|s_j|$

if the within-group covarince matrices are used, or

$g_1(x,t) = (x-U_j)'s^{-1}(x-U_j)$

if the pooled covariance matrix is used; and

$g_2(t) = -2\text{Loge}(p_j)$

if the prior probabilities of groups are not all equal, or

$g_2(t) = 0$

if the prior probabilities are all equal.

Here: x = a vector containing the variables of an observation,

U_j = the vector containing means of the variables in the group j,

s_j = the covariance matrix within group j,

$|s_j|$ = the determinant of s_j,

s = the pooled covariance matrix, and

p_j = the prior probability for group j.

The posterior probability of an obervation $\underline{x}$ belonging to group j can consequently be calculated, after simplification, as following (Rao, 1973; Anderson, 1984; SAS, 1984):

$$P_j(x) = \frac{\exp[-D^2_j(x)/2]}{\sum\{\exp[-D^2_i(x)/2]\}} .$$

An observation is classified into group i if setting j=i produces the largest value of $P_j(x)$ {i.e., the smallest value of $D^2_j(x)$}.

4.3 Definition of Groups

In the present study, discriminant analysis is used to assign some sheep into one of the three genotypes (FF, F+ and ++, respectively). However, before applying the discriminant analysis, the known groups have to be first defined.

According to the segregation criteria proposed by Piper & Bindon (1982a, b) and Davis et al (1982b), sheep having at least one record in their lifetime of either: three or more lambs born, three or more foetuses, or three or more ovulations, but less than five, were assumed to be F+ genotype and were therefore classified into the F+- group. There were only three sheep identified to be FF genotype if the criteria of Davis et al (1982b) was used. Because of this small number, the FF-group was not created. The criteria for classifying an animal into the ++-group was not easy to define for the flock investigated here, since most sheep in this category were culled before they had the chance to have lifetime reproductive records. In addition, no sheep had all three traits recorded together in every year. Although NLB was available in each year, it is commonly accepted that the young of highly prolific sheep always have high mortality (Hanrahan, 1980). Therefore, some criteria needed to be defined for assigning a ewe having more than two lambings into the

++-group according to previous experience. The criteria were defined as:

(1) sheep having at least three lambings,

(2) the largest value of records for any of the reproduction traits was less than 3,

(3) no 2-tooth having 2 foetuses or 2 NLB,

(4) not having an OR or NF or NLB of 2 twice or more, except for sheep having five or six lambings, and

(5) for sheep having five or six lambings, the value of 2 was not to be repeated more than three times for any one of the three traits.

All other sheep which did not satisfy the above criteria were assumed to have an unknown-genotype and were assigned into an unknown-group. Because there were different amounts of information available for sheep born in different years, this unknown-group was sub-divided into smaller sub-groups within which all sheep had their records of reproductive traits (NLB, NF and OR, respectively) match each-other in terms of age and number of records. For example, many sheep born in 1981 were culled after lambing in 1983. These sheep could not be divided into the same unknown-subgroup with the sheep born in the same year (1981) but culled one year later (1984) since the former had only one lambing record while the latter had two lambings. But both of them had less than three lambings, therefore they had to be classified into the unknown-group.

4.4 Analysis

For each unknown-subgroup, the corresponding F+-group and ++-group could be found. The records for different years of an individual were treated as different variables and the three traits, i.e., NLB, NF and OR, were treated equally. The distribution within each group was assummed to be approximately multivariate normal.

Based on a set of reproductive records, the discriminant function was estimated through the use of the Discriminant Procedure in the SAS computer package (SAS, 1984). The Discriminant Procedure in SAS develops a number of discriminant functions (classification criterion) equal to the number of groups previously given and classifies the ewes into one of the two groups with a certain probability. The classification criterion is based on either the individual within-group covariance matrices or the pooled covariance matrix; it also takes into account the prior probabilities of the groups. Each observation from the unknown group is placed in the group which gives the smallest generalized squared distance or the highest discriminant score.

4.5 Results and Discussion

The procedure and possible results of discriminant analysis can best be illustrated by an example. For example, some sheep born in 1982 were culled in 1986 after three lambings (1984, 1985 and 1986) with three NLB, one NF, and two OR records (six variables in the discriminant function). Within this group of sheep, four ewes were classified into an unknown-group (Table 4.1) . Correspindong to this unknown-group, an F+-group with 18 ewes and a ++-group with 8 ewes

were found (Table 4.2). Through the Discriminant Procedure in SAS the results of analysis are shown in Table 4.3.

Table 4.1 The reproduction records of the sheep in the unknown group

TAG	YC	L1	L2	L3	NF1	OR1	OR3
-41082	86	1	1	1	2	0	2
-41982	86	1	1	2	2	2	2
-40482	86	2	2	0	2	2	0
-42282	86	2	1	0	2	1	2

where: TAG = the tag number of the sheep,
YC = the year when the sheep was culled,
Li = number of lambs born at the ith lambing,
NF1 = number of foetus at the 1st lambing, and
OR1 and OR2 = ovulation rate at the 1st and 3rd lambings.

Table 4.2 The reproduction records of the sheep in the known groups

GROUP	TY	YC	L1	L2	L3		NF1				OR1	OR3	
	f41482	87	1	2	2	2	2	.	2	0	1	3	2
	f43082	87	2	1	1	2	3	.	1	2	1	2	2
	f43582	87	2	2	0	3	3	.	0	2	4	4	3
	f43782	87	2	1	2	1	0	.	2	0	2	3	1
	f44182	87	2	2	0	2	2	.	0	1	3	3	1
	f44482	87	2	1	1	2	2	.	1	2	0	3	2
F+	f44782	87	2	2	0	3	3	.	0	2	1	2	3
	f47182	87	2	0	2	3	3	.	2	3	2	0	2
	f48482	87	2	2	2	0	3	.	1	0	2	3	1
	f49182	87	1	1	0	1	1	.	0	1	1	3	1
	f50582	87	2	1	3	1	3	.	0	1	1	2	1
	f51982	87	1	2	0	1	2	.	0	1	2	3	1
	f52282	87	1	2	0	1	1	.	0	1	2	3	1
	f52382	87	2	2	1	1	2	.	1	1	1	3	1
	f52982	87	2	2	0	3	2	.	0	2	2	3	2
	f50382	86	2	3	0		2				3	3	
	f42682	87	1	2	3	3	2	3	0	2	1	4	3
	f49582	87	2	1	1	2	2	3	1	2	0	2	3
	+42082	87	1	1	1	2	1	.	0	2	1	2	2
	+45082	87	1	2	1	1	1	.	1	1	1	2	1
	+49982	87	1	2	1	1	1	.	1	1	1	2	1
++	+47382	87	1	0	2	1	1	0	1	1	2	0	1
	+48382	86	0	0	1		1				1	2	
	+43282	86	1	1	0		0				2	0	
	+43682	86	1	1	1		1				0	2	
	+42882	86	1	1	1		1				1	2	

Table 4.3 The results of discriminant analysis for classifying sheep from both known- and unknown-group into either F+- or ++-group

GROUP	TY	FROM GROUP	CLASSIFIED INTO GROUP		PROBABILITIES OF BEING ++	F+
	41482	F	F		0.1269	0.8731
	43082	F	F		0.0005	0.9995
	43582	F	F		0.0000	1.0000
	43782	F	F		0.0070	0.9930
	44182	F	F		0.0003	0.9997
	44482	F	F		0.0003	0.9997
	44782	F	F		0.0018	0.9982
	47182	F	F		0.0536	0.9464
	48482	F	F		0.0001	0.9999
F+	49182	F	F		0.2066	0.7934
	50582	F	F		0.0006	0.9994
	51982	F	F		0.0763	0.9237
	52282	F	F		0.3908	0.6092
	52382	F	F		0.0006	0.9994
	52982	F	F		0.0004	0.9996
	50382	F	F		0.0009	0.9991
	42682	F	F		0.0064	0.9936
	49582	F	F		0.0061	0.9939
	42082	+	+		0.8710	0.1290
	45082	+	+		0.9620	0.0380
	49982	+	+		0.9620	0.0380
	47382	+	+		0.9986	0.0014
++	48382	+	+		0.9974	0.0026
	43282	+	+		0.9999	0.0001
	43682	+	+		0.9114	0.0886
	42882	+	+		0.8710	0.1290
	41082	?	+	*	0.5698	0.4302
??	41982	?	F	*	0.3803	0.6197
	40482	?	+	*	0.8428	0.1572
	42282	?	F	*	0.0037	0.9963

where: TY is defined in Table 4.1
+ = the ++-group
F = the F+-group

From Table 4.3, it can be seen that within the four ewes in the unknown group, each was assigned into one of the groups with a known probability. The discriminant analysis also reclassified the animals in the known groups into either the F+- or the ++-group. With respect to this analysis, no misclassification occurred, i.e., the classification for the known-genotype individuals by the discriminant analysis is totally consistent with that based on the segregation

criteria of Piper & Bindon (1982a, b) and Davis et al (1982b). This close agreement between the two methods suggests that the discriminant analysis is a appropriate method to assign a genotype to a ewe which cannot be decided via the criteria of Davis et al (1982b) due to insufficient lambings. Another advantage of this method (the discriminant analysis) is that the analysis gives the posterior probabilities of individuals being of the F+- and the ++-group, respectively. For sheep with less than three lambings, it is very difficult to accurately assign sheep to a genotype, furthermore, it would be unsatisfactory to assign ewes into either the F+- or the ++-group based on the segregation criterion of Piper & Bindon (1982a, b) and Davis et al (1982b). The discriminant analysis procedure would be more appropriate, since the analysis classifies a ewe into a group with a known probability.

Discriminant analysis classifies the individuals in the unknown group based on the corresponding data of known groups. Therefore, it is very important that the definition of known groups is correct. In the present study, some errors are likely to exist:

(1) The definition of ++-group is very arbitrary, and some errors are likely to exist. Additionally, the prolific value of the ++-group might be biased upwards, since classification of groups were mainly based on the NLT which had more records than NF and OR, since only NLT was recorded every year. Among the three reproductive traits (NLT, NF and OR, respectively) the value of NLT is likely to be the smallest due to embyro loss before birth. However, the same segregation criteria of Davis et al

(1982b) were applied to the three traits when defining F+- and ++ -group. Consequently, some sheep which might had 3 or more NF and/or OR, but actually showed less than 3 lambs were classified into the ++-group. This biasedness can also be seen from comparison of the present NLW value of ++-group (1.13, Appendix) with the corresponding value (1.0) of Leyva (1986) who had a similar crossbreds composition to the present flock.

(2) The definition of F+-group was based on the criteria of Piper & Bindon (1982a,b) and Davis et al (1982b) which were appropriate only for a prolificacy level of around 1.4-1.5 (Piper et al, 1985). The prolificacy level of the Massey Booroola- cross flock is unknown, but the estimated mean NLT value for the ++-group was 1.23. This value is lower than the corresponding values (1.36 and 1.48, respectively) of Davis et al (1982b) and Piper & Bindon (1988). However, even this value (1.23) might be biased upwards as discussed in the previous paragraph. Therefore, the segregation criteria of Piper & Bindon (1982a, b) and Davis et al (1982b) might not be appropriate in the present flock. The low percent of FF individuals identified by the segregation criteia of Davis et al (1982b) in the present study reflects this problem.

(3) The reproductive records cannot be expected to be entirely accurate due to mismothering (for NLB), technical difficulties of measuring NF and OR accurately. This problem involves records of all ewes (including ewes in the unknown group).

Another possible problem in this analysis is that year effect was not taken into account. The data in the unknown-group came from the

same age but not necessarily the same years as the F+- and ++-group, because there were only a few individuals in the known groups coming from the same year with the sheep in the unknown group. Consequently sheep from different years had to be divided into the same known group. It was reported that under New Zealand conditions the proportion of F-gene carriers identified at any single ovulation record was not significantly affected by year of birth (Davis et al, 1982b). However, this proportion was highly significantly affected by the year of measurement under Australian condition (Piper & Bindon,1982a). In such cases, the effects of year have to be taken into account.

C H A P T E R F I V E

SELECTION OBJECTIVE AND INDEX

5.1 Introduction

Recently, animal breeders have recognised the importance of having a clear definition of breeding objectives for any breeding programme. James (1982) defined the breeding objective as what breeders seek to maximise in their populations in order to improve the efficiency of animal production. Typically, it is a combination of traits which are to be improved, since income is normally made up of several components. Dickerson (1970) listed the possible sources of costs and returns for general animal production, and Ponzoni (1982) catalogued items of returns and costs, and their corresponding biological traits in sheep. Ponzoni (1986) detailed a systematic approach for the definition of a breeding objective.

The aggregate genotype of an animal (H) (or, equally a linear selection objective) was defined by Hazel (1943) as the sum of its several genotypes (assuming a distinct genotype for each economic trait), each genotype being weighted according to the economic value of that trait. Mathematically, it can be expressed as:

$$H = \sum a_i G_i$$

where: a_i = the economic weight of the ith triat in the objective (i= 1, 2, ..., m), and

G_i = the genotype (additive breeding) value of the ith trait in the objective.

Since genetic values cannot normally be directly observed, selection of animals for improved genetic merit is often implemented by using correlated characters as selection criteria (James, 1982; 1986; Ponzoni, 1986). Selection criteria are often not formally defined, but are chosen as being the traits: expressed early in life, and capable of being measured with minimum cost and technical difficulty (Ponzoni, 1979). Some of the traits in the selection objective may not be used as selection criteria, especially for an objective of lifetime production.

Several methods of selection are available to implement multivariate selection objectives. However, under most conditions the use of a selection index is likely to result in the greatest genetic gain (Hazel & Lush, 1942; Young, 1961; Abplanalp, 1972). Index selection has also been shown as the most efficient method to utilize major genes in a breeding programme (Smith, 1967). Possible methods for incorporating a major gene into a selection index have been suggested by Soller (1978) and Smith & Simpson (1986).

The selection index can be mathematically defined (Hazel, 1943) as:

$$I = \sum b_i X_i \ ,$$

where: b_i = the weighting factor of the ith trait in the index, which is derived by maximising the correlation between the aggregate genetic value and the selection index, and

X_i = the record of the animal for the ith trait in the index, expressed as a deviation from its mean.

A method was developed by Cunningham (1975) to combine an index into another index. He first combined r variables (out of n) into an index I_1, then incorporated I_1 with the remaining (n-r) traits into the second index I_2. Mathematically, it could be expressed as:

$$I_1 = b_1 * \underline{X}'_1 \qquad [\ \underline{X}_1 = (x_1, x_2, \ldots, x_r)\ ], \text{ and}$$

$$I_2 = b_{21} * I_1 + \underline{b}_{22} * \underline{X}'_2 \qquad [\ \underline{X}_2 = (x_{r+1}, x_{r+2}, \ldots, x_n)\ ].$$

where: b_1 = a vector of the index cofficients in the first selection index I_1,

b_{21} = the index coefficient of variate I_1 in the second in index I_2, and

$\underline{b}_{22}$ = a vector of the index coefficients, corresponding to the vector of variates $\underline{X}_2$ in the second index.

I_1 was treated as a variate in the index I_2, and selection was applied on I_2.

5.2 Setting of Selection Objectives for Booroola Sheep

Sheep can be divided into three categories based on fibre diameter, i.e., apparel-wool type, general-purpose wool type, and speciality carpet wool type. In apparel wool production, clean fleece weight and average fibre diameter are the most important traits while in general-purpose wool, fleece weight, colour, and possibly bulk are important (Rae,1982; Ponzoni,1982).

Rae (1982) stated that reproductive rate was always a most important trait whenever the farming system involved sale of lambs. Returns from sale of lambs depend mainly on number of lambs produced and weaning weight of the lambs.

The Massey Booroola flock is derived from 1/2 (Merino x Romney) and 1/2 Perendale sheep. The fibre diameter is usually within the range of 25-35um (G. A. Wickham, pers. comm.). It is considered to belong to the dual-purpose category. Consequently, both wool and meat production have to be considered when defining the selection objective. But only those traits which have the most impact on net returns for farmers and will respond to genetic selection or are correlated with other important traits will be considered. The traits to be included in the objective are:

(1) NLW. As suggested by Rae (1982), the number of lambs produced each year in a breeding flock is usually of major importance in controlling the financial returns from the flock. Increasing NLW will consequently increase the number of lambs available for sale and replacement, as a result, increase future selection differentials and genetic gains.

(2) WW. This trait is a measure of the potential growth rate of a lamb to weaning. It is a possible indicator of the lambs value as a meat animal.

(3) CFW (i.e. clean fleece weight). This trait is the major determinant of wool returns provided the fleece do not have any specific faults, e.g., coloured fibres (Turner,1976).

(4) MFD and SL (i.e. mean fibre diameter, and mean staple length, respectively). These two traits are usually not major price determinants in wool other than that produced by the Merino breed, or crosses with it. Recently, MFD has shown

some effect on wool selling price for wools up to 35 micron in diameter. The relationship between SL and wool selling price was confirmed by McPherson (1982) to be non-linear, with SL having a greater effect on price of shorter wools.

(5) SCG (i.e. scoured colour grade). Good colour is desirable, and McPherson (1982) showed that colour has a significant effect on selling price.

The breeding objective (H) for Massey Booroola sheep will be defined as:

$$H = a_1xNLW + a_2xWW + a_3xCFW + a_4xMFD + a_5xMSL + a_6xSCG$$

Where: a_1, a_2, etc. are the relative economic weights of the traits in the breeding objective, respectively.

The relative economic weights of the traits in the objective are estimated on the basis of the extra profit made over the lifetime of an animal that would acrue from each extra unit of production. The economic weights of wool quality traits (MFD, MSL and SCG) are derived from the regression of selling price on the levels of wool traits while the estimate of the economic weights of other traits follows the technique used by Morris et al (1982).

Details of assumptions and calculations for estimating the economic weights of the traits in objective are given in Appendix 1, and the final results are listed in Table 5.1.

Table 5.1 Lifetime economic weights[1] of the traits in the selection objective

TRAIT	CALCULATION	ECONOMIC WEIGHT
		$
NLW	4.76 matings * $11.30	53.79
WW	5.17lambs*47%*$0.983/kg	2.39
CFW	8.33shearings*$5.146/kg	42.87
MFD	8.33shearings*3.5kg*$-0.30/um	-8.75
MSL	8.33shearings*3.5kg*$0.01/mm	0.29
SCG	8.33shearings*3.5kg*$0.108/G	3.15

(1) NLW ($/lifetime/lamb weaned)
WW and CFW ($/lifetime/kg)
MFD ($/lifetime/um)
MSL ($/lifetime/mm)
SCG ($/lifetime/grade)

Thus, the selection objective for the Massey Booroola flock can be defined as the linear function:

$$H = 53.79NLW + 2.39WW + 42.87CFW - 8.75MFD + 0.29MSL + 3.15SCG,$$

where: H = economic return (in dollars) per ewe lifetime.

The selection objective defined here is similar to that of Leyva (1986) and the clean wool objective of McPherson (1982). The relative weights given to each trait in the objectives can be seen from Table 5.2.

From Table 5.2, it can be seen that the relative values given to each trait in the current study are also very similar with those of Leyva (1986), and are generally in consistent with those of McPherson (1982). The emphasis in all studies were on NLW, CFW and MFD [MFD was not significant in the study of McPherson (1982) due to the coarser wool he studied, and consequently, MFD was not included in the objective of his study]. The reduced weight for NLW in the present

and Leyva's (1986) study, compared with that of McPherson (1982), is primarily due to the negative trend of meat price relative to wool over recent years. Furthermore, McPherson (1982) assumed a lower value per kg of wool because he was studying coarser wool (33-40um).

Table 5.2 Comparison of economic weight estimates relative to WW from the present study with 2 others

Source of Estimate	WW	NLW	CFW	SCG	MFD	MSL
McPherson (1982)	1	45.73	16.49	-1.67		0.84
Leyva (1987)	1	26.85	25.29	0.37	-3.77	
Present estimates (1988)	1	22.51	17.94	1.32	-3.66	0.12

The different sign for SCG in the current study and Leyva (1986) from that of McPherson (1982) was due to the different systems used. The Scoured Colour Grade system was used here. The higher value for SCG in the present study than that of Leyva (1986) was because the weight in his study was halved. The MFD in the present study was similar to that of Leyva (1986) and Elliott & Johnson (1976), i.e., about 30um. The economic weights assigned to MFD in these studies were also very similar [Elliott & Johnson (1976) assigned a value of -2.00 for MFD realtive to a value of 15.00 for GFW]. There is recently a trend of increased price for finer wool than 35um. The weight of MSL here was small due to the range of variation the Booroola-cross wool fall (90-110mm). The value of 0.84 for MSL in the study of McPherson (1982) was derived from a much wider variation of length (25-175mm).

5.3 Selection Index

5.3.1 Selection criteria

As mentioned previously, the components of tbe breeding objective can not always be measured directly. Therefore, it is necessary to establish a corresponding selection index which contains traits referred to as the selection criteria. In the present study, the traits chosen to act as selection criteria are hogget live weight (HLW), greasy fleece weight (GFW), quality number (QN) and greasy colour grade (GCG) as well as the traits in the objective.

Reproductive rate needs special consideration given that this trait in Booroola sheep is largely controlled by a major locus, i.e., the F-locus. As a result, it is reasonable to suppose that the reproductive rate of Booroola sheep is totally controlled by the F-locus, and consequently, the estimated genotype for the individual at the F-locus (later referred as the F-locus due to the problem mentioned later) is chosen as the selection criteria for NLW.

Following the method of Cunningham (1975), the selection criteria can be partitioned into two components:

(1) the first part ($\underline{X}_1$) contains only one trait; that is the F-locus, and

(2) the second part ($\underline{X}_2$) consists of the remaining traits.

5.3.2 The major gene selection index (I_F)

With a major gene such as that found at the F-locus, the breeding value can be directly estimated from the knowledge of gene frequency and phenotypic performance of the various genotypes. Assuming the genotypic values of FF, F+ and ++ on the number of lambs born to be a, d and -a, respectively, and the frequency of F and + in the population concerned to be p and q, respectively, then the breeding values of the three genotypes at the F-locus can be estimated using the approach of Falconer (1981) as:

breeding value for FF (BV_{FF}) = $2q[a+d(q-p)] = 2q\alpha$,

breeding value for F+ (BV_{F+}) = $(q-p)[a+d(q-p)] = (q-p)\alpha$,

and

breeding value for ++ (BV_{++}) = $-2p[a+d(q-p)] = -2p\alpha$.

where: $\alpha = a+d(q-p)$.

Estimates of a and d were found to be 0.30 and 0.10, respectively, in the Massey Booroola flock (Appendix 2). The population gene frequency of F and + (p and q, respectively) cannot be estimated until at least one of the individual genotypes can be clearly identified. The technique of identifying the genotype of any individual was described in Chapter 4 of 'Discriminant Analysis'. In fact, most sheep in the Massey flock cannot be accurately assigned to any of the three genotypes. Therefore, the breeding value of any individal for the F-locus will be:

$$BV_F = p_{FF}BV_{FF} + p_{F+}BV_{F+} + p_{++}BV_{++},$$

where: p_{FF}, p_{F+} and p_{++} = the probabilities of an individual belonging to FF, F+ and ++ genotypes, respectively.

Once the reproductive performance of sheep are known, P_{FF}, P_{F+} and P_{++} can be found by discriminant analysis.

Multiplying the breeding value for the F-locus (BV_F) by the economic weight will express the breeding value (BV) in economic units. Due to the lack of genotypic effects at the F-locus on other economic important traits, the relative eonomic value for the F-locus in the present study cannot be estimated through the way suggested in Section 2.4.1. On the basis that the major change of genotypes at the F-locus in the present study is from ++ to F+ genotype, and according to previous reports (Piper & Bindon, 1982a, b; Davis et al, 1982b), the difference between the ++ and F+ sheep was about a lamb born, therefore, the economic weight for the F-locus (a_F) is set to be equal to the economic weight of NLB. The economic weight of NLB is the economic weight of NLW (53.79), adjustfied by the survivig rate of the lamb from NLB to NLW (0.92).

To allow for the estimation of BV from a dam, the BV_F has to be halved to transfer the BV_F of the dam to the individual being considered.

Then the major gene selection index (I_F) can be finally given as:

$$I_F = \frac{1}{2} \times a_F \times BV_F \times \text{surviving rate}$$

$$= 0.5 \times 53.79 \times 0.92 \times BV_F$$

$$= 24.74BV_F \ ,$$

where: BV_F = the breeding value of the dam of the individual

being considered for the F-locus, estimated from data of number of lambs born (NLB).

5.3.3 The quantitative selection index (I_Q)

The second set of the selection criteria ($\underline{X}_2$) can be dealt with by the ordinary quantitative method of Hazel (1943) as:

$$I_Q = \underline{b}'\underline{X}_2,$$

where: $\underline{b}'$ = the vector of regression coefficients in the index, and

$\underline{X}2$ = the vector of performance in the selection criteria relevant to I_Q.

The parameters required for the construction of an index are the estimates of: heritability ,genetic and phenotypic correlations, phenotypic standard deviations, and the economic weights. The economic weights are given in Table 5.1. Other parameters are largely based on the values used by Leyva (1986), since the composition of the flock in his study (Merper) is very similar with that of present study. In the absence of estimates from Leyva (1986), representative values from related breeds were included. The estimates used are set out in Table 5.3.

Based on the estimates in Table 5.3, index solutions were obtained using a modified version of the genetic selection index computer program, SELIND (Cunningham & Mahon, 1977). Six index solutions were shown in Table 5.4. Index.1, which inludes all traits in the selection objective, was set to be the base level to evaluate the efficiency of other indices. Index.2, including all selection

Table 5.3 Estimates of parameters required for the calculation of a selection index

Traits	ai	Phenotypic sd[1]	Heritabillities and correlations[2]									
			WW	HLW	CFW	GFW	SCG	GCG	MFD	MSL	Y	QN
WW	2.39	3.00(Kg)	0.16	0.70	0.20	0.20	0.00	0.00	0.00	0.00	0.00	0.00
HLW	0.00	3.78(kg)	0.50	0.30	0.30	0.30	-0.25	-0.08	-0.07	0.20	0.00	-0.20
CFW	42.87	0.30(Kg)	0.30	0.30	0.30	0.87	0.00	0.00	0.25	0.55	0.40	-0.34
GFW	0.00	0.40(Kg)	0.30	0.40	0.94	0.28	0.00	0.04	0.25	0.55	0.00	-0.40
SCG	3.15	0.89(grade)	0.00	-0.06	-0.13	-0.05	0.09	0.70	-0.40	0.00	0.10	0.40
GCG	0.00	0.84(Grade)	0.00	-0.02	0.02	0.04	0.38	0.38	-0.40	0.00	0.70	0.40
MFD	-8.75	2.17(um)	0.10	0.13	0.25	0.25	-0.33	-0.30	0.30	0.40	0.16	-0.30
MSL	0.29	1.66(mm)	0.10	0.13	0.54	0.50	0.00	0.00	0.40	0.40	0.42	-0.40
Y	0.00	4.00%	0.00	0.00	0.40	-0.10	0.10	0.00	0.30	0.25	0.35	-0.40
QN	0.00	2.24(Grade)	0.01	-0.14	-0.38	-0.34	0.04	0.04	-0.30	-0.55	-0.40	0.39

[1] sd = phenotypic standard deviation.

[2] heritabilities on the diagonal, genetic correlations above the diagonal and phenotypic correlations below the diagonal.

criteria defined previously, was taken as a full index, from which gradualy deletion of traits was undertaken, resulting in reduced indices (index.3, index.4 and index.5, respectively). Deletion of traits was on the basis of:

(1) value of the trait in the index, and

(2) cost of measurement of the trait.

The sixth index was called the restricted index, which will be described later in a seperately section (Section 5.3.8).

The relative efficiencies of various indices can be represented by several methods:

1. the ratio of the standard deviations of the two indices (Cunningham, 1969; Falconer, 1981),
2. by comparing means of the coefficient of determination (r_{GI}^2) (Gjedrem, 1967),
3. by comparing the correlation r_{GI} (Falconer, 1981) between the aggregate genetic value (H) and the index (I), and
4. examining the loss in overall genetic gain, after removing the trait from the index.

The third method (r_{GI}) would be used here.

Index solutions in Table 5.4 show that addition of extra selecion criteria to the basic index (from index.1 to index.2) increased both overall genetic gain and index efficiency (from 6.49 to 7.18 and 0.54 to 0.60, respectively).

Table 5.4 Full and reduced selection indices

Variates in objective Overall		WW	CFW		SCG		MFD	MSL			
Variates in indices	HLW	WW	CFW	GFW	SCG	GCG	MFD	MSL	QN	r_{IG}	genetic gain[a] ($)
Index.1											
B-value[b]		0.37	13.01		0.03		-2.77	0.12			
Value of variate[c]		1.35	12.11		0.00		34.48	0.03		0.54	6.49
% overall gain[d]		5.96	24.60		2.64		66.81	-0.01			
Genetic gain[e]		0.16	0.04		-0.05		-0.50	-0.00			
Index.2											
B-value	0.89	-0.14	32.86	-16.91	0.39	1.53	-2.47	0.24	0.47		
Value of variate	6.79	0.11	8.65	4.09	0.08	1.30	20.83	0.08	0.71	0.60	7.18
% overall gain	0.00	8.28	27.12	0.00	2.67	0.00	61.82	0.11	0.00		
Genetic gain	0.67	0.25	0.05	0.02	0.06	0.15	-0.51	0.03	0.20		
Index.3											
B-value	0.60	---	11.84	---	1.43	---	-2.61	---	---		
Value of variate	5.10	---	12.26	---	1.39	---	34.97	---	---	0.57	6.85
% overall gain	0.00	7.69	23.14	0.00	2.60	0.00	66.52	0.05	0.00		
Genetic gain	0.60	0.22	0.04	0.04	0.06	0.14	-0.52	0.01	0.06		
Index.4											
B-value	0.56	---	---	4.41	---	3.39	---	---	0.61		
Value of variate	10.7	---	---	6.54	---	24.70	---	---	4.55	0.36	4.31
% overall gain	0.00	15.42	32.99	0.00	5.80	0.00	45.13	0.66	0.00		
Genetic gain	0.54	0.28	0.03	0.05	0.08	0.25	-0.22	0.10	0.31		

Table 5.4 (continued)

Index.5											
B-value	---	0.57	---	---	---	---	---	---	---		
Value of variate	---	99.98	---	---	---	---	---	---	---	0.22	1.71
% overall gain	0.00	67.06	32.94	0.00	0.00	0.00	0.00	0.00	0.00		
Genetic gain	0.58	0.48	0.01	0.02	0.00	0.00	0.00	0.00	0.00		
Index.6											
B-value		0.20	13.29	---	0.62	---	-0.55	0.21			
Value of variate		0.92	35.36	---	0.81	---	18.02	0.24		0.36	4.22
% overall gain		10.89	86.66	---	0.47	---	0.00	1.98			
Genetic gain =		0.19	0.09	---	0.01	---	0.00	0.29			

[a] 'VALUE OF OVERALL GAIN': or equivalently the standard deviation of the index, gives the value, in economic units, of the genetic gain in aggregate genotype achieved by one standard deviation of selection on the index.

[b] 'B-VALUE' is the weight that the record of each trait is multiplied by in calculating the selection index. The set of B-values is calculated to maximize the overall genetic gain.

[c] 'VALUE OF VARIATE', i.e., value of each variate in the index, is the percent reduction in the rate of overall genetic gain that would result, if that trait was not included as a selection criterion.

[d] 'PERCENTAGE OVERALL GAIN' is the percentage of overall gain accounted for by the gain in each trait.

[e] 'GENETIC GAIN' is the gain made per generation, from using the selection index assuming a selection differential of one standard deviation.

The relative importance of the traits in the index is generally consistent with the index solutions of Leyva (1986). From index.2, it can be seen that MFD, CFW, HLW and GFW are most important selection criteria in that order. MFD shows great importance in the index due to its relative high economic weight in the objective and standard deviation. Although both GFW and HLW were not included in the selection objective, they showed importance in the index since they were moderately heritable and moderately to highly correlated with CFW and WW (Table 5.3). The negative weight assigned to GFW in the index.2 is because the selection objective is for clean fleece weight and CFW is also included as a selection criterion. Both McPherson (1982) and Leyva (1986) also found negative values of GFW when the objective was to improve CFW.

From index.2, it can also be seen that some traits (e. g., MSL nad SCG), have very limited usefulness in the index. Deletion of MSL, SCG, WW and QN from index.2 resulted in a reduction of $0.05 in the overall genetic gain and almost no effect on index efficiency (r_{GI} changes from 0.60 to 0.59). Further removal of GFW reduced the overall genetic gain from $7.13 to $6.85 (a reduction of $0.28) and r_{GI} from 0.60 to 0.58.

Based on costs of measurement, CFW and SCG were removed from index.2, resulting in reductions of $0.65 in the overall genetic gain and 0.06 in r_{GI}, respectively. Further deletion of MFD reduced the overall genetic gain by $2.19 whereas additional removal of MSL and WW resulted in index.4, with an additional decrease of $0.03 in the overall gain.

Deleting all criteria except the lamb trait (WW) from index.2 resulted in index.5. Both values of the genetic overall gain and index efficiency were reduced by more than half.

5.3.4 The final selection index (I) combining the quantitative and qualitative traits

Due to inadequate information (only three FF individuals were identified for the whole flock), the correlations between the F-locus and other traits in the index could not be estimated. However, from published estimates (McPherson, 1982; Leyva, 1986), it appeared that the genetic and phenotypic correlations between NLW (F-locus) and most other traits in the selection index (I_Q) were close to zero. The only exceptions were the correlations between NLW and WW, and NLW with HLW, which were about 0.10-0.20. Thus, for simplicity, it was assumed that there was no relationship between I_F and I_Q. Following the method of Soller (1978), the final selection index was calculated as:

$$I = I_F + I_Q.$$

Applying this equation to the Booroola two-tooths available for selection in 1988, I can be calculated by first estimating I_F and I_Q.

Sheep born in 1986 have individual records of WW, HLW and GFW available. Based on these traits, I_Q was calculated (index.4 in Table 5.4) as:

$$I_Q = 0.13WW + 0.48HLW + 3.55GFW.$$

There were no reproductive records available for the hoggets. From their dams' reproductive records (with lambings from 1 to 5), the gene frequencies of F and + (p and q, respectively) in the dam population were estimated to be 0.35 and 0.64. Then, the breeding values for the three genotypes were estimated to be:

$$BV_{FF} = 2q[a+d(q-p)] = 0.42,$$

$$BV_{F+} = (q-p)[a+d(q-p)] = 0.10, \text{ and}$$

$$BV_{++} = -2p[a+d(q-p)] = -0.23.$$

Accordingly, the major gene selection index for the 1988 hoggets is:

$$I_F = 24.74*BV_F = 24.74(P_{FF}BV_{FF} + P_{F+}BV_{F+} + P_{++}BV_{++})$$
$$= 10.39P_{FF} + 2.47P_{F+} - 5.69P_{++}.$$

The results of IF, IQ and I were listed in Table 5.5. The distributions of both I_F and I_Q are non-normal with IF having relatively smaller range of variation (-5.75 to 6.43) in the present population than I_Q (-11.64 to 12.76). Smith (1985) mentioned that major genes affecting important traits might dominate the index. It seems in the current selection stage, this problem will not occur.

Table 5.5 Selection index values for tag 1986 Booroola-cross sheep

TAG	SEX#	Ig	If	I
15786	1	-2.1215	2.3347	0.2130
4486	1	0.1210	0.2274	0.3484
7786	1	-1.8285	2.3371	0.5086
23886	1	-0.9250	1.5412	0.6162
8586	1	2.2810	-1.6132	0.6678
8786	1	-1.5180	2.2204	0.7024
16486	1	-1.3880	2.3079	0.9200
20286	1	-1.3825	2.3185	0.9360
27486	1	-1.3790	2.3363	0.9573
10986	1	2.6625	-1.6132	1.0493
4686	1	-1.1845	2.3233	1.1388
12286	1	-1.0575	2.3363	1.2790
4886	1	-0.7045	2.2528	1.5483
7586	1	-0.6750	2.2674	1.5924
9386	1	-0.7190	2.3371	1.6181
9986	1	2.9445	-1.1609	1.7836
20386	1	-0.5160	2.3185	1.8020
15486	1	4.0690	-2.1797	1.8890
8686	1	7.4360	-5.4265	2.0095
586	1	3.7550	-1.6132	2.1418
26886	1	0.1850	2.0948	2.2803
28186	1	0.3380	2.3379	2.6764
11986	1	0.8220	2.0283	2.8503
23786	1	1.3490	1.5412	2.8902
8886	1	0.6885	2.2204	2.9089
18386	1	0.7380	2.2107	2.9490
15186	1	1.2775	2.0283	3.3060
9186	1	1.0475	2.3371	3.3846
22586	1	1.0945	2.3347	3.4290
24886	1	1.3880	2.0948	3.4833
16986	1	1.4715	2.2107	3.6820
6686	1	1.8900	2.0948	3.9848
8986	1	2.8935	1.2041	4.0976
7386	1	2.0145	2.2569	4.2714
2686	1	5.9660	-1.6132	4.3528
17886	1	2.6590	2.2107	4.8700
2286	1	3.0290	2.0948	5.1238
16786	1	3.0290	2.2204	5.2490
6486	1	3.0025	2.3242	5.3266
19886	1	3.1845	2.3371	5.5220
8386	1	3.2050	2.3339	5.5389
186	1	7.3770	-1.1188	6.2582
6086	1	7.9730	-1.6132	6.3598
4086	1	2.1400	-2.1797	-0.0397
8286	1	-2.3755	2.3339	-0.0416
21786	1	-2.4845	2.2366	-0.2480
25686	1	-2.6490	2.0948	-0.5537
10886	1	-2.6530	2.0948	-0.5582
14686	1	-1.5015	0.6529	-0.8490
27186	1	-3.1690	2.2569	-0.9116
28386	1	-3.3670	2.3193	-1.0477
22086	1	-2.4500	1.2041	-1.2460

Table 5.5 (continued)

9086	1	-2.5630	1.2041	-1.3589
23186	1	-3.7930	2.3193	-1.4740
25986	1	-2.2360	0.6529	-1.5826
386	1	3.1160	-4.8405	-1.7245
7086	1	-3.9310	2.1783	-1.7527
5986	1	-4.1385	2.3233	-1.8152
28586	1	-4.1620	2.3379	-1.8241
16386	1	1.2940	-3.1490	-1.8550
12386	1	-4.2905	2.2520	-2.0380
14886	1	-0.0300	-2.1359	-2.1660
13986	1	-0.0350	-2.1359	-2.1710
29086	1	-4.6570	2.2601	-2.3969
18886	1	-4.6310	2.0948	-2.5360
286	1	-0.9750	-1.6132	-2.5882
25486	1	-1.4420	-1.1609	-2.6024
4586	1	3.0155	-5.7547	-2.7392
8186	1	-5.1215	2.3169	-2.8047
1686	1	-1.1855	-1.6602	-2.8457
686	1	-5.2910	1.9335	-3.3575
18786	1	-5.6370	2.0948	-3.5420
15686	1	1.2440	-4.8405	-3.5970
10486	1	-5.8730	2.2601	-3.6129
12186	1	-0.4770	-3.1685	-3.6450
17386	1	-5.7470	2.0948	-3.6520
15386	1	-1.5190	-2.1797	-3.6990
23086	1	-6.2345	2.3193	-3.9150
25186	1	-6.3330	2.0948	-4.2377
24186	1	-0.0120	-4.2788	-4.2909
7486	1	1.3655	-5.6583	-4.2928
21486	1	-2.1385	-2.1797	-4.3180
24486	1	-1.1120	-3.2179	-4.3294
26586	1	-6.8080	2.0948	-4.7132
1886	1	-4.9680	0.2274	-4.7406
17786	1	-7.3895	2.3079	-5.0820
22786	1	0.1885	-5.4176	-5.2290
3286	1	-3.6575	-1.6132	-5.2707
14186	1	-1.0845	-4.2788	-5.3630
10086	1	-0.1260	-5.4176	-5.5436
19986	1	-1.8735	-3.6710	-5.5440
5686	1	-3.4615	-2.1797	-5.6412
13186	1	-0.6265	-5.4265	-6.0530
20086	1	-3.0410	-3.6710	-6.7120
10186	1	-1.3050	-5.4176	-6.7226
3686	1	-1.2230	-5.5521	-6.7751
5286	1	-3.2205	-3.6710	-6.8915
17586	1	-1.1890	-5.7288	-6.9180
28486	1	-2.6650	-4.2788	-6.9434
17486	1	-1.2770	-5.7288	-7.0060
22386	1	-7.6170	0.2274	-7.3900
12086	1	-4.3390	-3.1685	-7.5070
23386	1	-2.0225	-5.7288	-7.7510
19386	1	-2.3095	-5.7288	-8.0380
13786	1	-3.0235	-5.5562	-8.5800

Table 5.5 (continued)

1386	1	-7.2580	-1.6132	-8.8712
1786	1	-7.4650	-1.6602	-9.1252
27586	1	-12.228	2.3363	-9.8912
19086	1	-5.5760	-4.8891	-10.4650
18586	1	-6.2150	-5.4265	-11.6420
16286	2	4.6980	-3.1490	1.5490
22986	2	0.3895	2.3193	2.7090
9886	2	0.7340	2.3047	3.0387
10386	2	1.0320	2.2674	3.2994
25086	2	1.7410	2.0948	3.8363
21586	2	4.4155	2.2569	6.6720
2386	2	4.6275	2.0948	6.7223
11686	2	5.6680	2.0948	7.7628
12486	2	5.6760	2.2520	7.9280
13386	2	6.8925	2.3379	9.2300
26786	2	7.9230	1.8589	9.7824
21886	2	8.8260	1.2041	10.0300
27686	2	7.8840	2.3096	10.1941
4986	2	7.9980	2.3023	10.3003
15886	2	8.0485	2.3331	10.3820
26686	2	8.6170	1.8589	10.4764
18686	2	8.3920	2.0948	10.4870
17686	2	8.4780	2.3079	10.7860
11586	2	10.2530	2.0948	12.3478
10586	2	10.4235	2.3331	12.7566
23486	2	6.9780	6.4300	13.4080
28786	2	3.2950	-4.2788	-0.9839
21686	2	-3.6650	2.2569	-1.4080

VARIABLE	N	MEAN	STANDARD DEVIATION	MINIMUM VALUE	MAXIMUM VALUE
Iq	133	-0.00	4.31	-12.23	10.42
If	133	0.04	2.94	-5.75	6.43
I	133	0.04	5.41	-11.64	13.41

# 1 = ewe
2 = ram

The smaller values of I_F than the I_Q in this population resulted from genotypes of ewes classified (++ or F+). The dam of sheep 23486 had reproduction records of 1, 1; 2, 1, 1; 6, 2 (2 NLT records, 3 NF records and 2 OR records, respectively). According to the segregation criteria of Davis et al (1982b), this dam should be identified as FF. However, all values of records except one (6) of this dam are no bigger than 2. From the dam's parent information, this dam could not be clearly identified as being homozygous FF since its dam was culled after just two lambings. Consequently, the BV_F of the dam of sheep 23486 was derived by giving $P_{FF}=0.5$, $P_{F+}=0.5$ and $P_{++}=0.0$. No other dam in this population was identified as being homozygous FF.

5.3.7 The recommended selection indices for lambs, ram and ewe hoggets

5.3.7.1 Lamb selection index

Early disposal of surplus lambs offers considerable advantages to breeders (Young, 1964). Although it may reduce the rate of genetic gain compared with that which could be achieved if selection was at 14-18 months of age, Ponzoni (1981) pointed out that an appropriate choice of selection criteria at an early age could result in an important reduction of the cost of measurement with little loss of genetic gain. Therefore, an index based on traits which can be assessed early in life (i.e., NLW from the dam and WW on the individual) is given for the selection of lambs (index.5), with I_F being derived from the dam's reproductive data:

$$I_L = 0.57WW + 24.74BV_F$$

Comparing index.5 with index.1, the relative efficiency of the former is only 40.7% of the latter. Both Ponzoni (1981) and Leyva (1986) had also found that selection on dam's NLW and WW were about half as effective as selection based on the complete set of criteria. In the present study, the recommended lamb selection index (with the F-locus) could be more efficient.

5.3.7.2 Ram selection index

The traits MSL, SCG, WW and QN were excluded from the ram selection index due their small contribution to the overall genetic gain. GFW was also deleted from the ram selection index despite its relative importance in the index (a reduction of $0.28 with the deletion of GFW), since when both CFW and GFW were included in the index a negative weight was always given to GFW, i. e., selection for high yield. Over-high yield is undesirable. Removal of GCG from index.3 resulted in a reduction of $0.10 in the overall genetic gain, consequently, GCG was retained in the ram selection index. Furthermore, SCG was already deleted from the index. GCG could be included in the index as a representative of SCG. Although measurement of CFW is expensive (about $4.00 for yield), CFW is retained in the ram index due to its high value in index.2 (12.26%) and the great importance of ram selection in a breeding programme. As stated by McPherson (1982), the costs incurred in assessing rams could often be recouped due to the greater number of progeny that each ram produces compared with individual ewes. MFD is also retained in the ram selection index due to its great importance in the index.

Therefore, index.3 is recommended as the ram hogget quantitative selection index, and the final selection index for rams will be:

$$I_R = 0.60HLW+11.84CFW+1.43GCG-2.61MFD+24.74BV_F$$

Leyva (1986) suggested a ram index with GFW in place of CFW seen here. The efficiency of his ram index was as high as that of his basic index which included all traits in the objective in his study. From Table 5.4, it can be seen that index.3 is more efficient than the basic index (index.1). If CFW was replaced by GFW here, the overall genetic gain would be decreased by $0.40. Therefore, CFW is worthwhile to be included in the ram selection index.

5.3.7.3 Ewe hogget selection index

For ewe selection, the costs of measurements are considered to be more important than for rams because each ewe has only a small impact on the rate of genetic gain. The importance of the various traits are then considered. As mentioned by McPherson (1982), in the case of ewe selection, costs of assessment could seldom be recovered, hence, accuracy must be compromised by consideration of economy and efficient time utilisation.

Due to the high costs of meausurements, CFW, SCG were MFD first omitted from the ewe selection index, followed by the exclusion of MSL, SCG and WW due to their small contribution to the rate of overall genetic gain.

Deletion of QN from index.4 resulted in a reduction of \$0.20 in the overall genetic gain, consequently, QN was retained in the ewe selection index. Furthermore, including QN in the index was considered to avoid the wool becoming coarse when MFD was not available.

Consequently, index.4 was suggested as the ewe quantitative selection index, and the final ewe hogget selection index is:

$$I_E = 0.56HLW + 4.41GFW + 3.39GCG + 0.61QN + 24.74BV_F.$$

Leyva (1986) recommended a similar index for ewe selection with an extra criterion of WW despite the unimportance of WW in the index. The efficiency of the ewe index in Leyva (1986) was 74.4% of that of the basic index, whereas in the present study, the efficiency of index.4 is 66.7% of that of the basic index. However, consideration of the F-locus in the ewe selection index would increase the index efficiency. Therefore, the index with only five traits (HLW, GFW, GCG, QN and the F-locus) is efficient enough for the ewe hoggets.

5.3.8 Restricted index

A restricted selection index (Cunningham et al, 1970) was derived by imposing a zero genetic change in MFD. The resulting index (index.6 in Table 5.4) showed a decrease in the overall genetic gain but an increment in the genetic gain in CFW. Similar results were found by Leyva (1986) when MFD was maintained constant. McPherson (1982) also found a decrease in the overall genetic gain when restriction was on EBW (ewe body weight). Therefore, it seems not

whorthwhile to restrict the change in MFD to zero in the Massey Booroola.

5.3.9 Sensitivity analyses

5.3.9.1 Sensitivity to change of genetic and phenotypic parameters

Genetic and phenotypic parameters will change with space and time. In addition, it was assumed in previous sections that there were no genetic and phenotypic correlations between the F-locus and other selection criteria. It is therefore pertinment to investigate the effects of varying genetic and phenotypic parameters on the efficiency of the various selection indices.

The only parameters investigated were the genetic and phenotypic correlations between WW and CFW and W and GFW. Both genetic correlations were changed from 0.2 to -0.1 and both phenotypic correlations were modified from 0.3 to 0.5.

The index solutions derived after altering the genetic and phenotypic correlations were shown in Table 5.6. Generally only small changes occurred provide CFW was included in the index. The overall genetic gain and efficiency of index.2 following modification of the correlations increased about $0.10, whereas in index.1, index.3 and index.4 decreased up to $0.30, compared with the original values. When CFW was excluded from the index (index.5), considerable reduction resulted in the overall rate of gain.

Table 5.6 The effect of changes in the genetic and phenotypic correlations on various selection indices

Variates in objective		WW	CFW		SCG		MFD	MSL		r_{IG}	Overall genetic gain
Variates in indices	HLW	WW	CFW	GFW	SCG	GCG	MFD	MSL	QN		
Index.1											
B-value	---	-0.19	13.30	---	0.09	---	-2.70	0.16	---		
Value of variate	---	0.30	10.97	---	0.01	---	42.09	0.05	---	0.53	6.13
Index.2											
B-value	1.20	-0.92	37.84	-19.13	0.70	1.48	-2.38	0.17	0.67		
Value of variate	12.7	3.95	10.71	5.20	0.26	1.19	18.64	0.04	1.35	0.63	7.27
Index.3											
B-value	0.64	---	10.01	---	---	1.49	-2.55	---	---		
Value of variate	6.24	---	9.22	---	---	1.63	35.87	---	---	0.57	6.62
Index.4											
B-value	0.62	---	---	2.90	---	3.43	---	---	0.53		
Value of variate	14.3	---	---	2.99	---	27.76	---	---	3.71	0.36	4.15
Index.5											
B-value	---	0.29	---	---	---	---	---	---	---		
Value of variate	---	99.96	---	---	---	---	---	---	---	0.08	0.87

Similar conclusions were given by Ponzoni (1982), who stated that the loss in total economic gain resulting from the use of alternative correlations would often be small, but under some circumstances it would become a matter of concern (e.g., from r=0.0 to r=-0.5). However, the genetic gain in individual traits could be affected to an extent that the accuracy of the predictions could be seriously undermined.

Considerable changes were found by Leyva (1986), where the genetic correlations between GFW x MFD and CFW x MFD were changed from negative to positive.

5.3.9.2 Sensitivity to change in economic weight of CFW

As prices of wool and meat change with time, it is worthwhile to study the sensitivity of indices to changes in the economic weights.

One of the most important traits in the selection objective is CFW. It is also very sensitive to market price fluctuation. Therefore, a sensitivity analysis was conducted for a change in the relative economic weight for CFW. The new economic weight assigned to CFW was:

CFW = $55.73/lifetime (+30%).

For other traits in the objective, the economic weights remained the same.

The corresponding index solutions after increasing the economic weight of CFW by 30% are shown in Table 5.7. In all indices except index.5, little change occurred except the genetic gain in economic units was increased (up to $0.70), even when CFW was not included as a selection criterion. This resulted from the increased economic weight for CFW.

Similar results were shown by Vandepitte & Hazel (1977), McPherson (1982), Ponzoni (1982), Smith (1983) and Leyva (1986). Vandepitte & Hazel (1977) stated that errors in single economic weightings of $\pm$50% reduced the relative efficiency of the index by < 1% for all traits considered. Smith (1983) concluded that large losses in efficiency of index occured only when either:

(1) important traits were omitted or unimportant traits were given importance, or

(2) when the direction of selection was reversed for an important trait.

Table 5.7 The effect of increasing the relative economic value of CFW by 30% on various indices

Variates in objective		WW	CFW		SCG		MFD	MSL			Overall
Variates in indices	HLW	WW	CFW	GFW	SCG	GCG	MFD	MSL	QN	r_{IG}	genetic gain
Index.1											
B-value	---	0.31	16.91	---	0.21	---	-2.76	0.19	---		
Value of variate	---	0.77	17.86	---	0.03	---	30.87	0.06	---	0.54	7.06
Index.2											
B-value	0.99	-0.26	41.57	-20.75	0.77	1.42	-2.43	0.32	0.55		
Value of variate	7.02	0.34	11.78	5.18	0.27	0.93	16.46	0.12	0.80	0.60	7.85
Index.3											
B-value	0.60	---	15.71	---	---	1.40	-2.62	---	---		
Value of variate	4.35	---	19.18	---	---	1.14	28.99	---	---	0.57	7.40
Index.4											
B-value	0.55	---	---	6.79	---	3.35	---	---	0.55		
Value of variate	8.03	---	---	12.79	---	18.65	---	---	2.95	0.37	4.82
Index.5											
B-value	---	0.63	---	---	---	---	---	---	---		
Value of variate	---	99.98	---	---	---	---	---	---	---	0.14	1.88

5.3.5 An alternative approach to incorporate a major gene into the selection index

It is also possible to incorporate the F-locus into an index by the traditional quantitative selection index approach as proposed by Hazel (1943). This method requires the estimation of parameters relevant to the F-locus to enable its inclusion in the index. The formula to estimate the heritability of a major locus was shown in Section 2.3 to be:

$$\frac{2pq\alpha^2}{2pq\alpha^2+(2pqd)^2}.$$

The phenotypic standard deviation (sd) of a major locus is the square root of the genetic variance of the major locus, where the genetic variance of the major locus is $[2pq\alpha^2+(2pqd)^2]$. Substituting a, d and the population gene frequencies, the heritability (h^2) and sd of F-gene can be calculated. For example, the h^2 and sd of the 1988 hogget population were found to be 0.95 and 0.21, respectively. The genetic and phenotypic correlations between F-locus and other traits, in the present stage, are assumed to be zero for the same reason as mentioned in the previous section. The economic weight of the F-locus in the present study is the economic weight of NLB. Then, based on these data together with the parameters in Table 5.3, the final selection index can be calculated.

This approach is especially usefull when the correlations between the F-locus and other selection criteria can be estimated and significant.

CHAPTER SIX

GENERAL DISCUSSION

There is no doubt that the F-gene exists in the Massey Booroola-cross sheep since the sires used in the first two generations were F-gene carriers, and the reproductive records from later generations further supported the presence of a major locus in the current flock. However, it seems that the segregation criteria of Piper & Bindon (1982a, b) and Davis et al (1982b) have to be modified before they can be applied to the Massey Booroola flock. The basic prolificacy level of the sheep in the current flock is much lower than those of Piper & Bindon (1982a, b) and Davis et al (1982b). Furthermore, the genotypic values of a and d (FF and F+, respectively) estimated here were also much smaller. The limitation of the application of the segregation criteria suggested by Piper & Bindon (1982a, b) and Davis et al (1982b) has already commented upon by previous reporters (Owens et al, 1985; Piper et al, 1985; Elsen et al, 1988). Possibly, other statistical methods (e.g. cluster analysis) will be more appropriate in distinguishing between the various genotypes, however, until extensive studies are undertaken, the suggested segregation criteria still have to be used.

With the situation that culling occurs at young ages and early selection is required in an animal breeding programme such as in the present study, the use of discriminant analysis was found to be satisfactory. However, the dependence of discriminant analysis on accurate classification of animals into groups of known genotypes requires that the means of distinguishing between the various

genotypes is well established for this method to be of use. Unfortunately, biases in the classifying of animals into the known groups are likely to exist in the present Massey Booroola flock, as discussed in Chapter 4.

Selection objectives are defined for the future, consequently the relative economic importance of traits should reflect the economic situation that will apply in coming years. However, the task of forecasting future economic conditions is formidable. Relative economic values are typically derived from historical information. However, the sensitivity analysis in Section 3.5.7.2. showed that the efficiency of index selection was not very sensitive to changes of economic weights. Ponzoni (1982) concluded that if breeders choose the economic values well, commmonly experienced price fluctuations should have negligible consequences on the overall effectiveness of their breeding programmes. Although the economic weights only define a particular economic environment from which they are estimated, they can give an idea of the relative importance of the traits in the selection objective.

The incorporation of measurement costs into the economic weight estimation of each trait has been suggested, but generally not recommended (Miller & Pearson, 1979). It is argued that such costs are a function of the entire farming enterprise, rather than an attribute of individual animals and hence should be accounted for by a systems analysis approach.

Some problems are likely to exist in the definition of the production system and hence the breeding objective. For example, which level of the production system (on the basis of animal, farmer, industry or national) is the profitability maximisation for (Miller & Pearson, 1979)? The way of combining the costs and returns may affect the relative economic values of traits in the objective (James, 1982). Morris et al (1982) suggested that a selection objective designed to maximise profit in a ram breeding flock may not be the best for improving the profitability of the commercial farms which use the rams. They stated the problems exist in the traditional system of ram purchasing. Ponzoni (1982) reviewed these problems in the practical definition of breeding objective.

Ponzoni (1986) indicated that the definition of a breeding objective consisted of four main phases:

(1) specifiation of the production and marketing system,
(2) identification of sources of income and expense in commercial populations,
(3) determination of biological traits influencing income and expense, and
(4) calculation of economic value for each trait.

In the current study, five traits (WW, CFW, MFD, MSL and SCG) were included in the selection objective. The relative economic values of these traits calculated here are generally in agreement with the previous reports (Elliott & Johnson, 1976; McPherson, 1982; Leyva, 1986). The low value (0.29) for MSL was due to the variation in staple length in the Massey Boorooola sheep falling into a non-

critical range for price premuims. The impact of MSL in the selection indices also showed its lack of importance as an indicator trait. Therefore, MSL may be excluded from the selection objective without any appreciable loss in the efficiency.

There are actually more traits which affect profitability of an animal. However, traits such as feed consumption and disease resistance, are precluded due to difficulties of measuring of them. For other traits such as mature liveweight (EBW), previous reporters (Clarke & Rae, 1976, 1977; Morris et al, 1982) have estimated zero economic weights, resulting in their exclusion from the objective. Ponzoni (1982) discussed the problems involved with these traits in the definition of animal breeding programmes.

Corresponding to the objective defined here, ten traits were chosen as selection criteria. As outlined previously, the major requirement of a selection criterion is that it is readily and cheaply measured while contributing towards the prediction of the selection objective. However, it seems that some traits, e.g., MSL and SCG, were of limited value in the index. Consequently, they could be excluded from the selection index.

The use of WW as a selection criterion is of limited value. Absence of WW from the index did not influence either the overall genetic gain or the efficiency of the index. This result was also shown by McPherson (1982) and Leyva (1986). However, commercial farmers often prefer to use WW as a selection criterion on the grounds that it is available at a young age and the only trait not biased by prior

selection (McPherson, 1982). Furthermore, collection of WW records will not incur great cost since the animals are already being handled. In the case of high prolific Booroola sheep, including WW as a selection criterion is expected to improve maternal ability of the dam rather than the lamb's genes for growth rate.

MFD showed great importance in the present study. However, it was excluded from the ewe selection index. Possibly, with MFD finer than 35um it is worthwhile to be included in the ewe selection index, especially in a stud flock.

Consideration was given to replace CFW in the ram quantitative selection index (index.3 in Table 5.4) with GFW and yield (Y). A reduction of $0.42 in the overall genetic gain was resulted from the replacement. Therefore, it seems the original index is more efficient.

The existence of a major locus, the F-locus, led to the inclusion of F genotype in the selection criteria, and consequently the incorporation of the F gene in the index. With a major gene in the selection index, the breeding value of the trait affected by the major gene can be directly estimated (Falconer, 1981). In this report, the breeding value of the dam for the F-locus was used to predict the breeding value for individuals without reproductive records, because identification of genotypes at the F-locus are still based on individual performance for ewes and progeny tests for rams. Once an alternative technique is available to classify individuals earlier than their own lambing, the individuals own breeding value

could be estimated. As a result, selection should be more accurate and response to selection greater. Furthermore, the problem of fecundity being a sex-limited trait could be averted if an effective indirect indicator trait could be found to identify the genotypes of sires. These are the main advantages of using the F-locus rather than NLW in the selection. However, some of the advantages cannot be realized as yet in the Booroola sheep.

Index selection is never less efficient than any other methods, even with the involvment of a major gene (Smith, 1967). The method used here is mathematically simple. However, the assumption was made that the two parts, I_F and I_Q, were independent from eachother, while there may in fact be some relationship between them. However, serious errors may not result if this assumption is wrong, since sensitivity analysis showed that a change of 0.30 in the correlation would not markedly alter the overall genetic gain or the relative importance of the traits in the index. However, it would be interesting, and selection would be more accurate, if the effects of the F-gene on traits other than reproductive rate could be estimated, especially the traits normally having relatively high correlations with reproductive rate. If the correlations between them are high in the Booroola-cross, the alternative method of selection index (Section 5.3.5) would be more appropriate. With the method of Cunningham (1975), the parameters for the first index (I_F) will be required, which will be more complicated than the parameters just for a major locus. However, with any of the above approaches, the index has to be regularly modified with the involvment of a major locus, since genes frequencies change with selection. In the present study, the F-gene

frequency is less than 0.5, therefore, relatively large responses to selection at the F-locus can be expected. Once the F-gene frequency passes the mid-point, the gene frequencies will change more slowly. Furthermore, with the present management and economic conditions it is not desirable to have the Massey Booroola flock entirely homozygous FF due to the high mortality of lambs of FF dams. The selection index approach will be inefficient in attempting to obtain a homozygous FF population.

The methods proposed here to combine the information on the F-locus into an index is useful in the Booroola sheep. It may also be applied to other major loci or various markers such as the halothane gene in pigs and the double-muscled gene in cattle for multi-trait selection. However, the problem that the effect of the gene in the homozygous form is too large to manage still exists with these major genes. Smith (1985) mentioned the very high incidence of calving difficulty with the double-muscled gene would rule out its use even in selection with an index, which included calving ease. It seems that the method of index is more valuable with the major genes with moderate effect.

In the past years, many studies have been undertaken to investigate the possible effects on wool and body traits by crossing the Booroola Merino with other breeds. However, it seems that the effects of the three genotypes at the F-locus on these traits have not been studied. To utilize a major gene effectively, it is essential to estimate all effects of the gene on all economic important traits and have these effects balanced (see Section

2.4.1.). It was reported (in Section 2.5.4.) that the F-gene had some effect on lamb WW and HLW and CFW when the Booroola was crossed with strong-wool breeds or Romney. If the genotypic values of FF, F+ and ++ on all economically important traits can be estimated in the Massey Booroola flock, the economic values of various genotypes at the F-locus will be more accurately assessed. Consequently, the accuracy of the selection index can be improved.

The high prolificacy of the Booroola sheep and the presence of a major locus in the Booroola sheep offer special value in terms of both research purposes and commercial utilization. They would be useful in embryo transfer or transgenic experiments. They also have the potential to produce more lambs and finer wool than Romney under North Island conditions. However, no genetic parameters have yet been reported for the Booroola sheep. Therefore, some studies should be undertaken before the Booroola sheep is widely used commercially.

CHAPTER SEVEN

CONCLUSION

Although the segregation criteria proposed by Piper & Bindon (1982) and Davis et al (9182b) to distinguish FF, F+ and ++ genotypes at the F-locus were used in the current study, modification of the criteria was required for its application to the Massey Booroola-cross sheep. Discriminant analysis was used to classify sheep into one of the three genotypes at the F-locus and was found to be useful in the situation where sheep did not have lifetime reproductive records, and consequently, the genotypes could not be accurately recognized using the segregation criteria.

The selection objective defined for the Massey Booroola-cross flock was:

$$H=53.79NLW+2.39WW+42.87CFW-8.75MFD+0.29MSL+3.15SCG.$$

NLW, CFW and MFD were clearly the most important traits in controlling financial gains for this flock, while other traits were of limited importance.

Among the ten selection criteria chosen to predict the objective, MFD, CFW and HLW were found to be the traits of major importance. The traits MSL, SCG and WW were of very limited value in the index, and omitting them from the index had little effect on the rate of genetic gain in the objective.

The method proposed to incorporate the F-locus into the selection index is statistically simple, and seems appropriate, provided I_F and I_Q were independent of each other. I_F can be calculated provided the genotypes of individuals can be defined. In the present study, a combination of segregation and discriminant analysis was used. I_Q was derived from traditional quantitative selection index method. If the correlation between I_F and I_Q is subsequently found to be significant in the Booroola sheep, an alternative method incorporating the information on the F-locus directly in the index has to be used. This mehtod requires the estimation of parameters for the F-locus to enable construction of the index.

Sensitivity analysis showed that moderate changes in genetic and phenotypic parameters, or economic values would not markedly affect the efficiency of selection or the overall genetic gain to selection.

It is concluded that the methodology explored here is of benefit when trying to select for a combination of major genes and quantitative traits.

APPENDIX.1

Underlying Productivity Assumptions and Calculations for Estimation of Economic Weights

(1)For NLW.

Assuming there are five age groups in the flock and a mortality rate of 3%, the proportion of two-tooth in the flock is:

$$\frac{1}{1 + 0.97 + 0.94 + 0.91 + 0.88} = 0.21$$

Hence, the number of matings per lifetime is:

$$\frac{1}{0.21} = 4.76$$

Booroola lamb carcasses will typically fall into the carcass grades of YL, PL, YM and PM. Therefore, the net value per lamb is \$11.30/lamb[a].

Hence the economic weight for NLW is:

a1 = 4.76 x \$11.30 = \$53.79/lamb.

(2)For WW.

Lambing% = 1.414[b]

Lamb mortality rate to meaning = 8.37%[b]

Therefore, Weaning% = 1.414 x (1-8.37%) = 129.56%,

and total lambs weaned per ewe lifetime is:

4.76 x 129.56% = 6.17lambs

One lamb has to remained to replace its dam, therefore, the number of lambs on which higher returns from higher weaning weights are based is 5.17 (6.17-1) lambs.

Lamb carcass value per kg = $ 0.983[a].

Dressing% = 47%.

Therefore, the economic weight of WW is:

a2 = 5.17 x $0.983 x 47% = $2.39/kg.

(3) For CFW.

From above, the number of matings per lifetime is 4.76. Therefore, the number of years of fleece production per lifetime (up to the final lambing) is:

4.76 + 1 = 5.76.

Assuming ewes are culled 6 months after lambing, then add another 0.5 year:

$$5.76 + 0.5 = 6.26$$

Credit from culled ewe hoggets is:

$$\frac{(1/2) \times 1.29 - 0.21}{0.21} = 2.07,$$

where: 1.29 is the weaning%, and

0.21 is the proportion of two tooth in the flock.

Therefore, the total annual expressions of fleece production per ewe lifetime is:

$$= 6.26 + 2.07 = 8.33.$$

The net value of CFW for wool of 25-35um is \$5.15 per kg.[c]

Hence the economic weight of CFW is:

$$a3 = \$5.15 \times 8.33 = \$42.87/kg.$$

(4) For MFD.

The diameter of Massey Booroola-cross sheep is usually within 25-35um. Using partial regression analysis, the value of per micron increase in fibre diameter for this fineness is -0.30/um[d], and the anumal clean fleece weight is about 3.5kg.[e]

Hence the economic weight for MFD is:

a4 = $-0.30 x 3.5 x 8.33 = $-8.75/um.

(5) For MSL.

The MSL of Massey Booroola-cross sheep is between 90 to 110mm. In terms of this range, the value per mm increase in length for one kg CFW is $0.01/mm[d].

Thus the economic weight for MSL is;

a5 = $0.01 x 3.5 x 8.33 = $0.29/mm.

(6) For SCG.

The SCG of Booroola wool is within the range of 2 to 7. Within this range, the value of per grade increase per kg CFW is $0.108/grade.[d]

Therefore, the economic weight for SCG is:

a6 = $0.108 x 3.5 x 8.33 = $3.15/grade

In the above:

(a) The value was calculated from the New Zealand Farmer magazine of years from 1987 to 1988. The prices of

lamb values being adjusted back to farm gate.

(b) This value was calculated from the flock in the present study flock, composed of sheep born from 1980 to 1987.

(c) This value was the average calculated from

a: the N.Z.M.W.B.E.S. (1983 to 1987)

b: The N.Z. Wool Market Review (1987/1988)

(d) The values were the partial regression coefficients of selling price on these traits. The Data from Wool News (1984/1985) and the N.Z. Wool Market Review (1987/1988).

(e) The value of 3.5kg clean fleece weight per sheep per year was suggested by G. A. Wickham (pers. comm.).

APPENDIX 2

ESTIMATION OF BREEDING VALUES OF THE GENOTYPES AT THE F-LOCUS

Breeding values of the genotypes at the F-locus can be derived following the approach of Falconer (1981). Assuming that the genotypic values of FF, F+ and ++ are a, d and -a, respectively, with the frequencies of F and + alleles being p and q, respectively, then, the breeding values of the three genotypes will be (Falconer, 1981):

$$\text{breeding value for FF (BVFF)} = 2q[a+d(q-p)] = 2q\alpha,$$

$$\text{breeding value for F+ (BVF+)} = (q-p)[a+d(q-p)] = (q-p)\alpha,$$

and

$$\text{breeding value for ++ (BV++)} = -2p[a+d(q-p)] = -2p\alpha.$$

where: $\alpha = a+d(q-p)$.

To estimate a and d in the breeding value, records of three genotypes FF, F+ and ++ are required. The mean litter size of F+ and ++ sheep over 3-6 observations in the Massey Booroola flock was calculated as being 1.63 and 1.23, respectively. However, only three FF individuals were identified in the Massey flock. As a substitute, the results of Davis et al (1982b) have been used to derive the possible mean litter size of the FF genotype in the Massey Booroola

flock. The mean litter sizes recorded by Davis *et al* (1982b) are shown in the following Table 1.

Table A.1 Mean litter size of FF, F+ and ++ individuals

	Massey Booroola	Davis *et al* (1982)	Derived Massey Booroola
FF		2.69	1.83
F+	1.63	2.25	1.63
++	1.23	1.36	1.23

From the values of Davis *et al* (1982b), the mean litter size of FF genotypes for the Massey Booroola flock can be calculated as:

$$1.23 + \frac{1.63-1.23}{2.25-1.36} \times (2.69-1.36)$$

$$= 1.83$$

Then the genotypic values of FF, F+ and ++ (a, d and -a) will be:

$a = (1.83+1.23)/2 - 1.23 = 0.30,$

$d = 1.63 - (1.83+1.23)/2 = 0.10,$ and

$-a = -0.30.$

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