INBREEDING AND POPULATION STRUCTURE STUDIES IN THE NEW ZEALAND ANGUS BREED

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To my Mother and Father

ABSTRACT

The breed structure and genetic history of the New Zealand pedigree Angus breed were analysed by Robertson and Asker's (1951) modification of the Wright-McPhee (1925) pedigree sampling method.

The pattern of the breed structure obtained is generally similar to that found in other studies, but it is both diffuse and dynamic owing to the present rapid expansion of the breed. There are changes taking place in the herd composition of the major breeders' herds and many new herds have yet to find their level in the structure.

Considerable emphasis has been placed on the use of imported animals in the development of the breed. Of all herds registering in Volume 61 of the herd book, 20.5% used imported sires, and the percentage of genes in the breed in 1966/67 derived from animals imported since 1863 was 85.4.

The most important herd in 1969 has a genetic contribution to the breed of 21.9 per cent, while the contributions of the four next most important herds were 8.72, 8.7, 4.7 and 3.7 per cent. In the four-generation pedigrees from which these figures were derived, the contribution of imported animals was 42.4%. The relationship between herd size and importance of the herd was considered. Herd duration was also discussed, in so far as it relates to improvement of the breed.

The animal with the highest relationship to the breed was Blackleg (11.65% in the 1900 pedigree sample). But overall, the most important animal over the period 1900-1966/67 was Lancer of Advie. Of the 33 sires and 9 dams whose direct relationships are 3.0% or more in any of the 8 sample years, 19 sires and 3 dams were imported.

The total inbreeding in 1966/67 (base year 1863) was 1.80%. This comprised 0.09% current inbreeding, 0.95% long-term inbreeding, and 0.76% strain inbreeding. The index of subdivision calculated from the non-current and long-term inbreeding is 1.79, indicating that there is only a slight tendency towards family formation in the breed.

The effective generation length is approximately 5.6 years. About 50-56% of the animals in the 1966/67 sample were sired by bulls 4 years old or younger, while about 38% are from dams 4 years or younger.

It is unlikely that there is much genetic variation between herds. This is because bulls from major breeders' herds are used widely throughout the breed while about 80 percent of sires and 37 per cent of dams are bred in herds other than the one in which they were used.

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"Lewontin confessed that each year he lectures on inbreeding, and each year he realises that he does not yet completely understand it."

Bruce Wallace, 1968.

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CHAPTER 1

INTRODUCTION

In the absence of native breeds of cattle, New Zealand has relied entirely on importations in establishing its present cattle population. Where beef cattle are concerned, the Aberdeen Angus has played a significant role in this respect. Angus cattle were first brought to New Zealand in 1863. That shipment, by the New Zealand and Australian Land Company, comprised 3 bulls and 4 cows, and with the exception of one bull, the other 6 animals were all bred by William McCombie (1805-1880) of Tillyfour, Scotland, regarded by many breeders as the leading pioneer in the development of this breed.

The object of the Company was to improve their ordinary grade stock. This proved to be very successful and led to subsequent importations. During those early days the cattle numbers rose slowly even though importations were numerous (by existing standards of that era). There was no move towards the formation of a breed society until some 50 years later when the New Zealand Aberdeen Angus Association was established in 1917.

While the dependence of the more popular breeders on importations during the past century has been generally recognized, no attempt has been made to assess the influence of these imported stock on the breed as a whole. If the imported animals differ in their genotype from New Zealand-bred stock, then a general preference for the former or their descendants should gradually change the average genotype of the breed. For example, in various studies (Robertson and Asker, 1951; Stewart, 1952 and 1955; Barker, 1957; Barker and Davey, 1960; Davey and Barker, 1963) it was found that the various cattle breeds were divided into strata and that the herds using imported sires were in the upper and most important strata. There is no way, however, of assessing whether imported or New Zealand-bred animals do differ genetically. Nevertheless, estimates of the proportion of the genes in the breed as a whole, for which imported animals are ultimately responsible, are of more than academic interest. For instance, such estimates would indicate the approximate rate at which actual genetic changes within the breed could take place. Moreover, in general, imported animals have been held to be superior in type to the average New Zealand Angus and the disproportionate importance of imported animals or their progeny would, in the absence of performance details, suggest an emphasis on type among the selection criteria of past breeders. Furthermore, there is no information concerning the role of different mating systems in the development of the New Zealand Angus breed. It is generally thought that many pedigree breeders practise mild line breeding with the occasional outcross and that many believe in the existence of certain well-defined families within the breed. The Duchess family of Shorthorns, as bred by Thomas Bates is a case in point.

In view of a lack of information on pedigree breeding in the Angus breed in New Zealand, the main objective of the present study is to trace the development of the breed, with particular emphasis on the role that inbreeding has had in the past. Apart from assessing the influence of prominent animals, a further objective is to obtain some measure of tendencies, if any, of the breed to split into families or strains. The latter part of the study will be devoted to some consideration of the breed structure and registration practices.

CHAPTER 2

BREED EXPANSION

Data for this aspect of the present study were abstracted from the New Zealand Angus Herd Books. An indication of the growth of the breed is given by Figure 2.1 which shows the numbers of males and females registered in each volume of the herd book since its establishment in 1917. There was a steady increase in the annual number of heifer registrations to 1948 (corresponding to volume 40 of the herd book) followed by a lapse in the number registered. From 1954 (volume 46) onwards, the rate of increase has been more rapid, although there have been marked fluctuations in the number of annual registrations. On the other hand, the annual number of full registrations was practically stationary to 1934 (volume 26). A gradual increase followed and since 1940 (volume 32) the annual bull registrations have been more or less static. Up to and including volume 68 of the herd book (i.e. July 31st 1976) 32,166 bulls and 163,076 cows had been registered, while 587 bulls and 8,370 cows were registered in 1976.

On the basis of Figure 2.1, eight points were selected for a more detailed analysis of breed expansion. Annual heifer registrations for 10-year intervals were recorded, as were the increase in number of herds. The results are summarized in Table 2.1.

The rate of growth in number of herds and in number of females registered per annum (as shown by the proportionate increase during each period) has varied from period to period. Table 2.1 also shows that the average proportionate increase for number of females registered was greatest from 1910 to 1920 whereas the period from 1950 to 1960 saw a notable increase in the growth in number of herds. The figure for the

Fig. 2.1—Growth of the Angus breed in New Zealand: number of male and female registrations in each volume of the New Zealand Angus Herd Book since 1917. (See Appendix I)

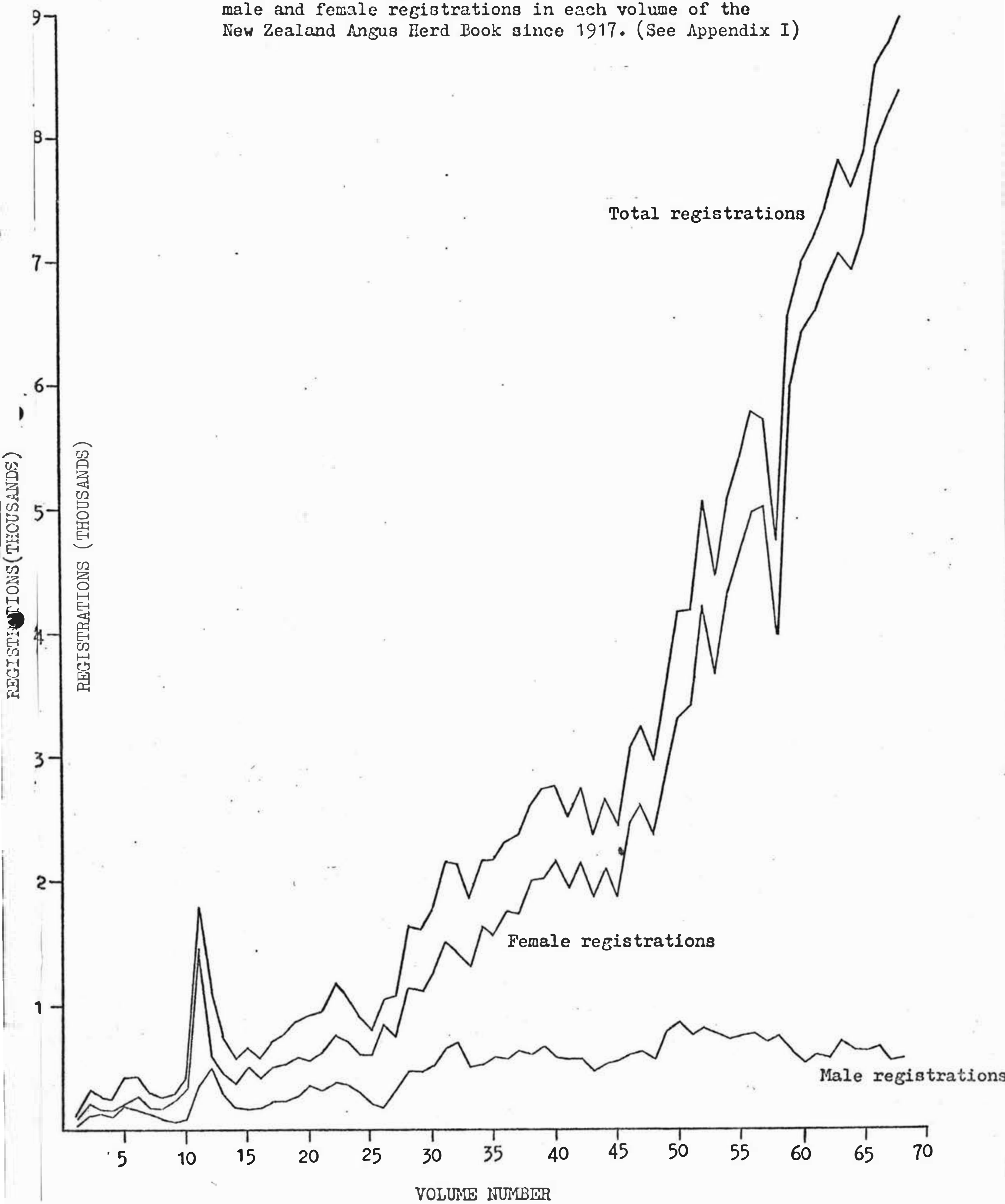


TABLE 2.1

Proportionate increases in number of females Registered Per Annum and Number of Herds during Seven Periods of Time

Increase	1900-1910	1910-1920	1920-1930	1930-1940	1940-1950	1950-1960	1960-1970
Number of females registered per annum	3.2*	3.4	1.5	2.3	1.2	2.2	1.7
Number of Herds	2.0	2.6	1.4	2.1	1.5	2.6	1.2

* The proportionate increase is the ratio of the number in 1910 to the number in 1900. This equals 139/44. See Appendix II for details of corresponding data for subsequent time periods.

1960-1970 period may suggest a doubling of the number of female registrations within the next 10 years. Nevertheless, it is not possible to extrapolate to predict future increases in the annual number of registrations. Sooner or later forces must come into operation to check the rate of expansion and, eventually, to limit the size of the population. This stage apparently had not been reached by 1970.

CHAPTER 3

REVIEW OF LITERATURE

I. THE MEASUREMENT OF INBREEDING: SOME THEORETICAL CONSIDERATIONS

Inbreeding may be broadly defined as the mating of animals more closely related to each other than the average relationship within the population concerned. That inbreeding has been practised in the breeding of all domestic animals is well appreciated. For example, Lush (1943) wrote:

> "All animals that can be mated at all are related, at least slightly. Each individual has two parents, four grandparents, eight grandparents, and so on, the number of ancestors doubling each generation. In the tenth generation of its pedigree an animal will have more than a thousand ancestors if there has been no inbreeding. If two animals are unrelated in the nearest ten generations of their pedigrees, the thousand ancestors of the one cannot include any of the nearly contemporary thousand ancestors of the other. If there has been no inbreeding, each animal has more than a million ancestors in the twentieth generation of its pedigree. If the pedigree is followed much further, these numbers become greater than the number of animals alive at that time could have been."

In attempting any analysis of the problem of inbreeding from a theoretical standpoint, one is faced with the necessity for an appropriate and valid method of pedigree analysis which should satisfy two conditions. First the method has to be unique in the sense that the values obtained in any particular instance can only be affected by the degree or amount of inbreeding which has been practiced in the line of descent under consideration. Secondly, it has to be general, in the sense that it can give comparable results when applied to two (or more) different pedigrees and to all degrees and types of inbreeding.

An early proposal for measuring inbreeding in livestock pedigrees was that of Pearl (1913). He devised a coefficient based on the smaller number of ancestors in each generation back of an inbred individual, as compared with the maximum possible number. A separate coefficient is obtained for each generation by the formula

$$Z_n = 100\left(1 - \frac{q_{n+1}}{p_{n+1}}\right) = 100\left(1 - \frac{q_{n+1}}{2^{n+1}}\right) \quad \ldots (1)$$

where $q_{n+1}/2^{n+1}$ is the ratio of actual to <u>maximum</u> possible ancestors in the n+1st generation. By finding the ratio of a summation of these coefficients to a similar summation for the maximum possible inbreeding in higher animals, viz, brother-sister mating, he obtained a single coefficient for the whole pedigree.

This coefficient has the defect, as Pearl himself pointed out, that it may come out the same for systems of breeding which are known to have radically different effects. For example, in the continuous mating of double first cousins, an individual has two parents, four grandparents, four great grandparents and four in every generation, back to the beginning of the system. Exactly the same is true of an individual produced by crossing different lines, in each of which brother-sister mating has been followed. Yet, in the first the individual will be homozygous in all factors if the system has been in progress sufficiently long; in the second it will be heterozygous at a maximum number of loci.

In order to overcome this defect, Pearl (1917) devised a partial inbreeding index to modify his initial concept which was, in turn, updated by Ellinger (1920) who suggested certain alterations and extensions. Despite this, the problem of devising a more suitable means of computing the inbreeding coefficient was left unresolved until a subsequent development by Wright (1922). His method was essentially based on path coefficients (standardized partial regression coefficients) and is now in universal use for describing breeding plans where inbreeding is involved.

Wright proposed the use of the coefficient of correlation (F) between the genic content of uniting egg and sperm to measure the intensity of inbreeding. The use of this coefficient is logical since it measures the probable increase in homozygosity which is the primary effect that inbreeding has. Since the genic content of the gametes cannot be measured directly, the correlation between them is computed from the relationship between the mates. The formula is as follows

$$F_X = \Sigma[(\tfrac{1}{2})^{n_S + n_D + 1}(1 + F_A)] \qquad \ldots (2)$$

where F_X is the inbreeding coefficient of the individual X; n_S is the number of generations from the sire to the common ancestor and n_D from the dam. F_A is the inbreeding coefficient of the common ancestor (A) through which the sire and dam are related. The summation is carried out over every line by which the parents are related. (See Appendix III for an example of the use of this formula.)

The inbreeding coefficient so obtained has the following features: The coefficient starts at zero for random mating relative to the population and increases towards 100% as the probable proportions of heterozygosity approaches zero. An inbreeding coefficient of, say, 25% may be interpreted in the following way: If the non-inbred population contained on the average 100 pairs of heterozygous genes, then the individuals produced by a breeding plan which results in an inbreeding coefficient of 25% will have on average only 75 gene pairs which are heterozygous. It is necessary to note that

(a) The inbreeding coefficient expresses only the most probable result. The percentage of heterozygous gene pairs in a particular individual produced by the mating plan may deviate from this most probable result because of the sampling variations inherent in the Mendelian mechanism.

(b) The inbreeding coefficient does not (and cannot) measure the actual number of heterozygous gene pairs in the individual. It is defined only in relation to the average condition of the population chosen for a base. The most convenient population in animal breeding is the breed at the date to which the pedigrees are traced. It is then assumed that those foundation animals are a random sample of the breed at that date. The inbreeding coefficient then measures the proportion of the gene pairs which were heterozygous in the base population that have become homozygous as a result of the inbreeding, but does not specify how many of the gene pairs in the base population were in fact homozygous.

(c) The inbreeding coefficient measures the increase in homozygosity resulting only from the inbreeding. It does not include any additional increase which may occur as a result of selection or mutation.

The coefficient of inbreeding has a number of uses. One is in the analysis of the methods used in building up breeds. Others are in making an estimate of the results, good or bad, or a mating, when the worth of the common ancestor of the sire and dam is reasonably known, and in assessing, before an animal has actually been used for breeding, the possibility of it being prepotent.

Inbreeding has a number of practical applications in relation to selection. For example, when a superior individual has been found, inbreeding is the only method of keeping stock closely related to it, whether the desired characteristics are highly inherited or not. Genetic relationship cannot be more than 50% unless some inbreeding takes place. This situation can arise in the formative period of a breed, when animals with the desired combination of traits are relatively rare; for instance, the Colling brothers mated Favourite to his own daughters for four generations. Unfortunately, inbreeding is sometimes made to only ordinary animals, as in small herds or flocks where it is cheaper to put a sire to some of his descendants rather than replace him; in many cases, this can lead to bad results. Inbreeding is also useful as a means to reveal any comparatively rare recessives so that they can be culled from the stock, but culling may be an expensive process if the number of undesirable recessive genes is great, and in any event the selection should also be made against the heterozygous parents of the recessives. If no undesirable characteristics emerge, there is evidence of the absence of causal genes, so that in this sense inbreeding can also be considered a test of genetic worth.

II. ALTERNATIVE APPROACHES TO INBREEDING

Another method, particularly suitable for computing inbreeding coefficients in small populations, is based on the coefficient of coancestry (coefficient de parenté as proposed by Malécot (1948)). From earlier discussion it is agreed that inbreeding results when two individuals which are related are mated together, i.e. they are related because they have a common ancestor or ancestors.

The essential point raised by the fact that the mated individuals have a common ancestor is that they may both be carrying replicates of one of the genes present in the ancestor and they may pass on these replicates to an offspring. Hence, inbred individuals (resulting from the mating) may carry two genes at a locus that are replicates of one and the same gene in an earlier generation.

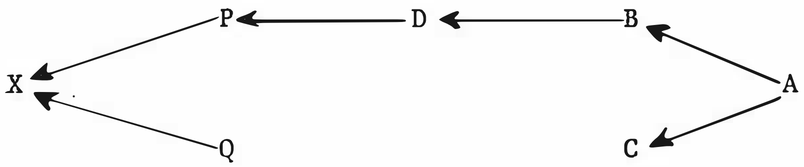
Thus, we need to distinguish identity between genes of two sorts:

(a) Genes can be the same in the sense that they are both A, or a, or A', alike in state or function.

(b) Genes can be the same in the sense that they both arose through the replication of a gene in an earlier generation.

Malécot then defined the coefficient of inbreeding to be the probability that the two genes at any locus in an individual are identical by descent.

Consider the following pedigree:



It is required to find the probability that X receives identical alleles through P and Q from A. For B and C, the probability that they receive identical genes from A (i.e. replicates of the same gene) is ½ and the probability of different genes is ½. But, if they receive different genes, then these could be identical because of previous inbreeding (prob.F_A). Thus, the total probability of identity is

$$\tfrac{1}{2} + \tfrac{1}{2} F_A = \tfrac{1}{2} (1 + F_A)$$

Now, the probability that B passes the gene it received from A to D is ½, and the probability of D passing it to P is ½ and from P to X is ½. Similarly for C.

$P(C \longrightarrow Q) = \tfrac{1}{2}$ $\qquad$ $P\ (Q \longrightarrow X) = \tfrac{1}{2}$

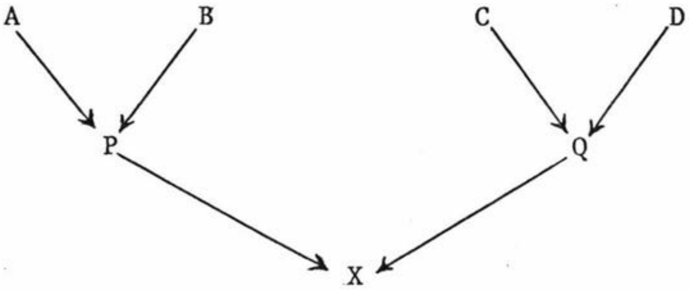
Putting all these together gives

$$\tfrac{1}{2}\ (1 + F_A)\ (\tfrac{1}{2})^{3+2}$$

or $\quad (\tfrac{1}{2})^{n_1 + n_2 + 1}\ (1 + F_A)$

This expression has to be summed over each common ancestor.

Another approach is suggested - working from the past forward to the present, computing the inbreeding which will result from the matings about to take place. As pointed out previously, the inbreeding coefficient of an individual depends on the parents having a common ancestry, i.e. the relationship between the two parents. Malécot (as noted earlier) calls this coefficient de parenté, Falconer coancestry, and Kempthorne (1969) coefficient of parentage. It is the probability that two gametes (or genes), one from each individual are identical by descent. Consider,



Consider coancestry of P and Q. Let P have genes a, b and Q c, d. Then,

f_{PQ} (i.e. coefficient of coancestry between P and Q)

$$= \frac{1}{4}\,[P(a+c) + P(a=d) + P(b=c) + P(b=d)]$$

but P(a=c) is really the coancestry of A and C. So,

$$f_{PQ} = \frac{1}{4}\,[f_{AC}+f_{AD}+f_{BC}+f_{BD}] \qquad . \; . \; . \; (3)$$

Note that this f_{PQ} is equal to F_X (i.e. $f_{PQ} = F_X$) for the possible offspring are $\frac{1}{4}(ac) + \frac{1}{4}(ad) + \frac{1}{4}(bc) + \frac{1}{4}(bd)$ and the probability of identity of these are

$\frac{1}{4}P(a=c) + \frac{1}{4}P(a=d) + \frac{1}{4}P(b=c) + \frac{1}{4}P(b=d)$,

which is the same as f_{PQ}.

In addition to this, consider the coancestry between individuals belonging to different generations, e.g. P and C, P and D.

Consider f_{PC}

Let A have genes a, a'
B " " b, b'
C " " c, c'
P " " a, b

Then, $f_{PC} = \frac{1}{4}[P(a=c)+P(a=c')+P(b=c)+P(b=c')]$

$= \frac{1}{4}[f_{AC} + f_{AC} + f_{BC} + f_{BC}]$

$= \frac{1}{2}[f_{AC} + f_{BC}]$ . . . (4)

Similarly, $f_{PD} = \frac{1}{2}(f_{AD} + f_{BD})$ . . . (5)

now, $f_{PC} + f_{PD} = \frac{1}{2}[f_{AC} + f_{BC} + f_{AD} + f_{BD}]$

$= 2f_{PQ}$

or, $f_{PQ} = \frac{1}{2}(f_{PC} + f_{PD})$ . . . (6)

Note also f_{AA}

Let A have genes a, b

Now, $f_{AA} = \frac{1}{4}[P(a=a) + P(a=b) + P(b=a) + P(b=b)]$

Remembering that $P(a=a) = P(b=b) = 1$

and $P(a=b) = P(b=a) = F_A$, by definition

So $f_{AA} = \frac{1}{4}(2 + 2F_A)$

$= \frac{1}{2}(1 + F_A)$ as shown before, i.e. the probability that 2 gametes taken at random from A will contain identical alleles.

As an example of the use of coancestry for computing inbreeding coefficients, see Appendix IV . The method shown can be used to keep a current chart of relationship and inbreeding, generation by generation.

At this juncture, it is appropriate to mention briefly the various procedures that have been devised to facilitate the computation of inbreeding coefficients. Such procedures are necessary, especially when complicated pedigree networks extending over many generations are involved. These methods are basically alike and have been reported by Cruden (1949); Emik and Terrill (1949); Plum (1954); Kudo (1962) and Willis (1968). The method described by Dorothy Cruden is of particular interest. The reasoning is along similar lines described earlier, as it entails the construction of covariance charts involving all the animals in a closed population and makes it unnecessary to trace any paths once the covariances among the foundation animals have been computed.

Where sex-linked genes are concerned, some modification is necessary for calculating the inbreeding coefficients. A solution to this problem has been suggested by Kudo and Sakaguchi (1963).

In randomly-bred closed populations, Lush's (1943) formula of $\frac{1}{8M} + \frac{1}{8F}$, where M and F are the effective numbers of sires and dams respectively, is a satisfactory measure of the loss of heterozygosity per generation. Where the construction of complete pedigrees is inconvenient, Robertson and Asker's (1951) modification of the sampling technique devised by Wright and McPhee (1925) can be used. This will be examined in detail later.

A. Relationship coefficients between collateral relatives

Methods of calculating relationships are very similar to those used for calculating inbreeding coefficients, and arrow diagrams are again of value in this respect. The formula is as follows:

$$R_{xy} = \frac{\Sigma[(\tfrac{1}{2})^n \ (1+F_A)]}{\sqrt{(1+F_x)\ (1+F_y)}} \qquad \ldots (7)$$

where R_{xy} is the relationship coefficient between animals X and Y.

n is the number of arrows connecting individual X with Y through the common ancestor for each path.

F_x is the inbreeding coefficient of animal X.

F_y is the inbreeding coefficient of animal Y.

and F_A is the inbreeding coefficient of the common ancestor.

If individuals X and Y and their common ancestor are not inbred, the formula reduces to:

$$R_{xy} = \Sigma[(\tfrac{1}{2})^n] \qquad \ldots (8)$$

B. Direct Relationships

It is sometimes of interest to know something about the relationship between an individual and some outstanding ancestor in the pedigree. This is of particular value when linebreeding has been practised, although the same procedure may be used for calculating the degree of relationship to any particular ancestor. The formula used is

$$R_{XA} = \Sigma(\tfrac{1}{2})^n \sqrt{\frac{1+F_A}{1+F_X}} \qquad \ldots (9)$$

This formula is correct only when the relationship is direct. Where there is a conbination of direct and collateral relationships, the general formula must be used.

IV. THE MEASUREMENT OF INBREEDING IN COMPLEX PEDIGREES

In the analysis of pedigrees going back one or two generations, the computation of inbreeding coefficients is relatively straight forward, using Wright's (1922) method. However, when pedigrees are long and complicated, going, say, 6 or 7 or more generations, the amount of work entailed becomes prohibitive. As a solution to this problem, a sampling technique was reported by Wright and McPhee (1925). In this procedure, also know as Wright's Short or Approximate Method, two lines of the pedigree are drawn back one from the sire's side and the other from the dam, of every animal in the sample. The choice of whether in any particular case to draw a line through a male or female is decided by consulting a table of random numbers. The pedigrees are then traced back either to imported or foundation animals.

It is necessary that the sample lines be chosen at random, for common ancestors are more likely to be males than females in livestock breeding. Thus, straight male or female lines are unsatisfactory, as also is a system of alternating male and female ancestors in any one line. If the same ancestor appears in the lines on both the sire's and dam's side, then the animal is obviously inbred. This is usually referred to as a 'tie'.

As pointed out earlier, the inbreeding due to a common ancestor A removed n_S generations from the sire and n_D generations from the dam is $(\frac{1}{2})^{n_s+n_D+1}$ $(1+F_A)$, where F_A is the inbreeding coefficient of the common ancestor. The sire has 2^{n_s} ancestors in the n^{th} generation and the dam 2^{n_D} ancestors in the $n_D{}^{th}$ generation. The sample pair of lines is thus only one among $2^{n_s+n_D}$ possible pairs going back as far as the common ancestor. If the single pair of lines is a random sample of the total, its contribution must be multiplied by $2^{n_s+n_D}$ to obtain an estimate of the inbreeding of the whole pedigree. On carrying out this multiplication, n_s and n_D disappear, and the coefficient takes the simple form $\frac{1}{2}(1+F_A)$. Therefore, in calculating the inbreeding indicated by a two-column pedigree, it is unnecessary to count the number of generations to the closest common ancestor, but merely to note whether there is a tie and which animal is responsible for it.

By determining the proportion of all such ties in a sufficiently large random sample of a family or breed, a measure of the average degree of inbreeding for that family or breed can be obtained to as high a degree of accuracy as desired. If, for example, 60 two-column pedigrees show a tie and 40 do not, then the average inbreeding is 30% (=60x0.5), i.e., neglecting the term $(1+F_A)$. Wright and McPhee (1925) also recommended that where certain ancestors are responsible for a large number of ties, their inbreeding coefficients should be calculated accurately so that the values for the term $(1+F_A)$ can be included to obtain the total coefficient. For those which occur infrequently, it is usually sufficient to assume an average degree of inbreeding equal to that of the breed as a whole at that time.

Coefficients of relationship may also be calculated from these random samples of pedigrees so that estimates may be made of direct relationship between a large group of animals and a particular animal (A). In this case the general formula for the coefficient of relationship

$$R_{xy} = \frac{(\frac{1}{2})^n\ (1+F_A)}{\sqrt{(1+F_x)\ (1+F_y)}}$$

(where, as indicated on Page 18, F_x and F_y are the coefficients of inbreeding of two individuals X and Y; F_A is that of common ancestor and n refers to the total number of Mendelian segregations in the path of descent through which X and Y are related)

becomes $R_{AY} = \frac{(\frac{1}{2})^n\ (1+F_A)}{\sqrt{(1+F_A)\ (1+F_y)}}$

Since Y could have 2^n ancestors in the generation in which A appears, the contribution of a single random line must be multiplied by 2^n to obtain an estimate of relationship between A and Y.

Thus, R_{AY} is estimated by

$$\frac{(1+F_A)}{\sqrt{(1+F_A)\ (1+F_y)}}$$

if a tie is present between single random lines back of the two animals considered (A,Y). In the case of four-line pedigrees, R is estimated by

$$\frac{\frac{1}{4}(1+F_A)}{\sqrt{(1+F_A)\ (1+F_y)}}$$

and so on.

In so far as Y is a sample of the population, an estimate of the relationship between A and the population is provided by the above coefficient. By taking a large sample of Y's the sampling errors are reduced and a reliable estimate of the relationship between a particular individual and the population ($R_{A.POP}$) is obtained.

When assessing the relationship of a large group to a particular animal the inbreeding ceofficient (F_A) of that animal should be calculated accurately. Unless these inbreeding coefficients are of reasonable dimensions, however, little error is introduced if they are neglected. For example, if F_A = 10% and F_{POP} = 5% then the expression $\dfrac{1+F_A}{\sqrt{(1+F_A)\;(1+F_y)}}$ would reduce to

$$\frac{1+0.10}{\sqrt{(1+0.10)(1+0.05)}} = \frac{1.10}{\sqrt{1.15}} = 1.02$$

Clearly the error introduced by neglecting

$$\frac{1+F_A}{\sqrt{(1+F_A)(1+F_{POP})}}$$

will be small if inbreeding coefficients are low. As Wright and McPhee (1925) pointed out, the method can be extended to determine the relationship between random individuals of the population or within a specially chosen section of the breed, or between two sections of a breed.

The above method of Wright and McPhee was applied by Lush (1932) to a study of the Rambouillet breed of sheep. He concluded that the method is about as accurate as its theoretical standard errors indicate, if all sources of systematic errors which might prevent the lines from being truly random are carefully avoided. He further cautioned that one must be on guard against systematic errors which at first thought appear to be so trifling as not to be worthy of attention, but which under certain circumstances, may creep into the supposedly random tracing of the lines.

Fowler (1932), in a study of the Ayrshire breed, concluded that Wright's "Long Method", in comparison with his "Short Method", gave far more reliable results especially when applied to breeds of relatively recent origin.

V. THE EFFECTS OF INBREEDING

The primary genetic effect of inbreeding is to increase the proportion of the loci in the population which are homozygous. This results from the fact that related mates are more alike in their genetic constitution than are mates which are chosen at random. Consequently, the uniting gametes will be alike in more genes and the resulting offspring more homozygous than if the parents were unrelated. All the other effects of inbreeding, such as the uncovering of recessives and the formation of distinct families follow from this primary effect.

Some mention should be made at this juncture of the phenomenon commonly referred to as inbreeding depression. It is well known that close inbreeding is nearly always accompanied by lowered fertility, reduction of libido, an increase in gametic sterility and embryonic mortality, as well as a reduction in the viability of newborn animals. Production is also adversely affected.

Wright (1922) explained this decline in vigour on the premise that Mendelain factors unfavourable to vigour in any respect are more frequently recessive than dominant. This situation is a logical consequence of the two ideas that

(i) mutations are more likely to injure than improve the complex adjustments within an organism and that

(ii) harmful dominant mutations will be weeded out relatively quickly, leaving the recessive ones to accumulate, especially if they happen to be linked with favourable dominant factrs.

Knowledge of the effects of inbreeding on productivity is useful for two purposes. Firstly, the accuracy of selection can be improved by correcting for any differences between individuals which result from variation in their degree of inbreeding. Secondly, in comparing breeding plans, allowance needs to be made for any differences in the rate at which they increase inbreeding.

A. Evidence of inbreeding depression in farm animals

There is a considerable amount of information on this subject. Evidence presented here, mainly from American studies, will be confined to dairy cattle. In most cases, the aim has been to try a combination of relatively mild inbreeding and selection as a method of breeding in dairy cows rather than to produce inbred lines for crossing with each other.

One such study was that by Swett, Matthews and Fohrman (1949). Cows of mixed ancestry were used as foundation females and they were mated to a proven Holstein bull. Their experiment was designed to look into the possibilities of building up a high-producing herd by using a proven bull and his sons, on cows of average production. Daughters, and in some cases even granddaughters, were back-crossed to the same bull, so that the progeny obtained carried 75 and 87.5 percent, respectively, of the genic constitution of their paternal ancestor.

This intensive linebreeding was accompanied by rather pronounced inbreeding depression symptoms. The number of services required per conception increased from 2.0 for non-inbred cows to 3.6 when the inbreeding coefficient of the calves reached 0.5. The mortality of inbred calves less than one month old was 15 percent. However, when the same bull was mated with unrelated cows, there were no deaths among the 43 calves born; but, in the 'purebred' Holstein herd served at the same time, 29 calves died out of the 300 born (9.7 percent). The effect of inbreeding on body-weight and production is illustrated by the relative figures shown below:

TABLE 3.3

The Effect of inbreeding on Body-weight and Milk Yield (after Swett *et. al.* 1949)

Degree of inbreeding	Birth Weight of Calves	Weight of heifers at 18 months	Cows which completed at least one Lactation			
			No. of Cows	Weight of		Yield of Butterfat
				Pituitary	Udder*	
non-inbred	100	100	22	100	100	100
F: 0.10-0.29	100.1	92.5	15	96.7	95.1	101.5
0.30-0.49	95.9	89.6	27	92.2	83.8	93.0
0.50-0.69	83.7	87.3	7	80.2	54.1	82.6

* The relative figures for the udder weights refer to full udders of lactating cows which were slaughtered.

The inbred animals were smaller at birth and grew more slowly than the non-inbreds; they were also listless and had coarse coats, which is indicative of lowered condition. The pituitary glands were also smaller. Milk and butterfat yield declined with increased inbreeding; the butterfat content of the milk decreased during the first generations of inbreeding but the reason for this would appear to be that the original cow population had a relatively high butterfat content (4.43 percent) and the mating took place with Holstein bulls.

Other studies of a similar nature have been reported by other workers (Tyler *et. al*. 1949; Robertson, 1954;Von Krosigk and Lush, 1958; Hansson *et. al*. 1961 and Mi *et. al*. 1965). Therefore, from the evidence presented, there is hardly any doubt that inbreeding carries with it reduced fertility, lowered viability in the offspring, especially in the first few weeks after birth, as well as decreased production. It is reasonable to expect the results to vary from case to case, depending on the genetic constitution of the animals used for inbreeding. Various studies have also clearly shown that crosses between different inbred lines, within which degeneration symptoms have been evident, result in increased fertility and viability of the progeny. Indeed, such increases in vitality (heterosis) are often seen in crosses between different pedigree lines or between breeds, even if no inbreeding of importance has taken place previously.

B. Explanations of inbreeding depression and hybrid vigour

From studies on maize, it was believed that the increase in vigour, which always accompanied crosses between two inbred lines, was due to heterozygosity *per se*. So, in a locus with two alleles say A_1 and A_2, the heterozygous combination A_1A_2 is superior to either of the possible homozygotes, A_1A_1 or A_2A_2. It is thought that the alleles A_1 and A_2 have separate effects (which in this case, may be responsible for crucial steps in a biochemical pathway) and the sum of their different products, or some interaction product between them, is superior, in terms of their effects on heterosis than that produced by either allele in the homozygous state.

It has also been suggested that heterosis may be explained in terms of ordinary dominance of genes relatively favourable for vigour and the corresponding recessiveness of genes unfavourable for vigour. This implies that in crosses between highly homozygous inbred lines the dominant and recessive alleles were brought together and the latter could not then exert their effect. East and Jones (1919) have also stated that homozygosity for all advantageous genes constituted the most favourable conditions for growth and reproduction. On the contrary, Srb, Owen and Edgar (1965) pointed out that no one has succeeded in producing, even in maize, a homozygous line which exhibits the same viability as the heterozygous crossbreds. It was then thought that this might be due to linkage between favourable and unfavourable genes, whereby the union of entirely favourable genes was prevented; but this explanation may be somewhat simplistic.

Inbreeding depression and its mirror image 'hybrid vigour' (heterosis) probably have several causes. Reiterating comments made earlier, it is certain that the inbreeding tends to increase the homozygosity of the offspring, with the following consequences:

(1) Segregation of recessive genes which often have unfavourable effects in the homozygous condition.

(2) Reduced frequency of heterozygous gene pairs. In so far as favourable interaction of alleles at the same locus (over-dominance) occurs, reduced heterozygosity is associated with lowered viability.

(3) Alteration in the gene combinations which, in turn, alters the interaction between genes at different loci (epistatic effect).

All three of these changes probably contribute to the decline in fertility and general vigour which invariably follows intense inbreeding when it is practised for several generations. Breeding populations of farm animals are highly heterozygous and, as such, are balanced for a more favourable interaction between the majority of genotypes and their environment. Increased homozygosity would disturb this equilibrium. On the other hand, one may expect that in many cases, a favourable effect should result from further increasing the heterozygosity by crosses between populations which have been bred as separate units for many generations.

To sum up, inbreeding depression and hybrid vigour have, in the main, the same basic causes. The heterozygosity and gene interaction which was lost by inbreeding can be restored by suitable crosses. Indeed, even as early as 1868, when animal breeding may be regarded as still in its infancy, Charles Darwin pointed out that inbreeding operates gradually but with accumulated effect, whereas crossing usually exhibits full effect in the first generation. To this day, this still retains its validity.

VI STUDIES OF GENETIC CHANGES IN LIVESTOCK POPULATIONS

Studies concerned with the changes in the genetic makeup of particular breeds with time have been numerous. One must, however, be cautious about comparing results from various studies since the genetic situation in a particular set of circumstances may be quite different from another. This is true between and within breeds, at different times, and at different locations. A summary of these studies is shown in Table 3.4.

Inspection of Table 3.4 shows that the increase in inbreeding seems quite uniform in view of the diversity of species. Great variability exists, however, between studies for total inbreeding and this arises partly from pedigrees being traced to more remote dates in some breeds than in others.

These studies of breed histories may be viewed from the standpoint of how much they indicate gene frequency to change merely from chance in the Mendelian sampling which takes place when one generation replaces another. Most of the studies show that the pure breeds lose something of the order of 0.5% of their heterozygosity per generation from this

TABLE 3.4 : Inbreeding and subdivision of the pure breeds of livestock.

Breeds Studied	Author	Inbreeding found (percent)		"Effective number" of males in the population[b]	Index of Subdivision[c]
		Total	Per Generation[a] in recent years		
Cattle:					
Shorthorns (Gt. Britain)	McPhee and Wright (1925)	26.0	0.6	21	1.0[d]
Jerseys (Gt. Britain)	Smith (1928)	3.9	0.2	62	
Ayrshires (Gt. Britain)	Fowler (1932)	5.3	0.5	25	
Friesians (Gt. Britain)	Robertson and Asker (1951)	1.2	0.2	69	1.4
Shorthorns (Gt. Britain)	Clayton (1956)	2.6	0.2	52	
Holstein-Friesians (U.S.A.)	Lush, Holbert and Willham (1936)	4.0	0.4	31	2.3
Brown Swiss (U.S.A.)	Yoder and Lush (1937)	3.8	0.5	24	1.7
Herefords (U.S.A.)	Willham (1937)	8.1	0.6	20	1.8
Aberdeen-Angus (U.S.A.)	Stonaker (1943)	11.3	0.3	41	1.6
Brown Swiss (Switzerland)	Sciuchetti (1935)	1.0	0.2	75	0.6
Telemark (Norway)	Berge (1930)	7.0	0.5	25	
Red Danish (Denmark)	Robertson and Mason (1954)	11.2	1.6	8	
Jersey (Australia)	Barker (1957)	4.2	0.4	30	5.6
Polled Hereford (Australia)	Barker and Davey (1960)	1.8	0.4	31	1.7
Hereford (Australia)	Davey and Barker (1963)	2.6	0.2	54	1.5
Jersey (New Zealand)	Stewart (1954)	2.5	0.3	50	2.3
Swine:					
Polard-China (U.S.A.)	Lush and Anderson (1939)	9.8	0.6	20	1.3
Landrace (Denmark)	Rottensten (1937)	6.9	0.5	27	0.8
Sheep:					
Border Leicester (Gt. Brit)	Young and Purser (1962)	5.8	0.3	39	1.1
Rambouillet (U.S.A.)	Dickinson and Lush (1933)	5.5	0.7	18	3.9
Hampshire (U.S.A.)	Carter (1940)	2.9	0.9	14	11.6[e]
Horses:					
Clydesdale (Scotland)	Calder (1927)	6.2	1.2[f]	10[f]	
Thoroughbreds)(U.S.A.)	Steele (1944)	8.3	0.6	20	1.0
Standardbred)		4.0	0.6	20	0.6
Saddle horse)		3.2	1 1	11	1.0

a. This is approximate. Several of the studies did not state the average number of generations involved. In some the figure includes only the changes in recent years; in others it includes the foundation period where (generally) the inbreeding was more intense.

b. These are the figures in the preceding column, converted into the N of the $1/8N$ formula which describes the random sampling variance of gene frequency which would occur in a population mating at random, with the probability of becoming a parent uniform among the males and also uniform among the females but there being far more females than males in the breeding population. N is the number of males which, under those conditions would have caused the observed rate of increase per generation in inbreeding.

c. This is $\frac{\text{inbreeding found}}{\text{inbreeding expected}}$ where the inbreeding expected is $\frac{R}{2 - R}$ and R is the average relationship between random members of the breed.

d. In recent years. It was 1.3 at the two earliest dates studied.

e. But this is based on a very small *inter se* relationship which has a high sampling error.

f. Assuming that the average generation interval is 11 years, which might be considerably in error here. Steele found it to be nearer 12 years in light horses.

cause alone. Selection may either enlarge or reduce that loss while it is conceivable that mutation may make the nett loss a bit less. If the per generation figures (of Table 3.4) are multiplied by q(-q)/100, this gives the variance in gene frequency from chance in one generation of breeding. In terms of standard deviations this represents about 0.02 to 0.05 as the standard deviation of the chance changes in gene frequency from one generation to the next when q is about 0.5, but considerably less when it is near extinction or complete fixation.

Chance is therefore of considerable importance in determining the changes in the composition of a breed from one generation to the next. It is not entirely clear as to why the chance changes are so much larger than would be expected to result merely from the finite size of the breed. The reason may be that only a few contemporary animals are famous at any one time and a considerable number of breeders make some efforts to head their herds with close relatives of those currently famous animals.

A further feature of the Table is that in most cases the effective numbers of sires is small - very much smaller than the actual census number.

CHAPTER 4

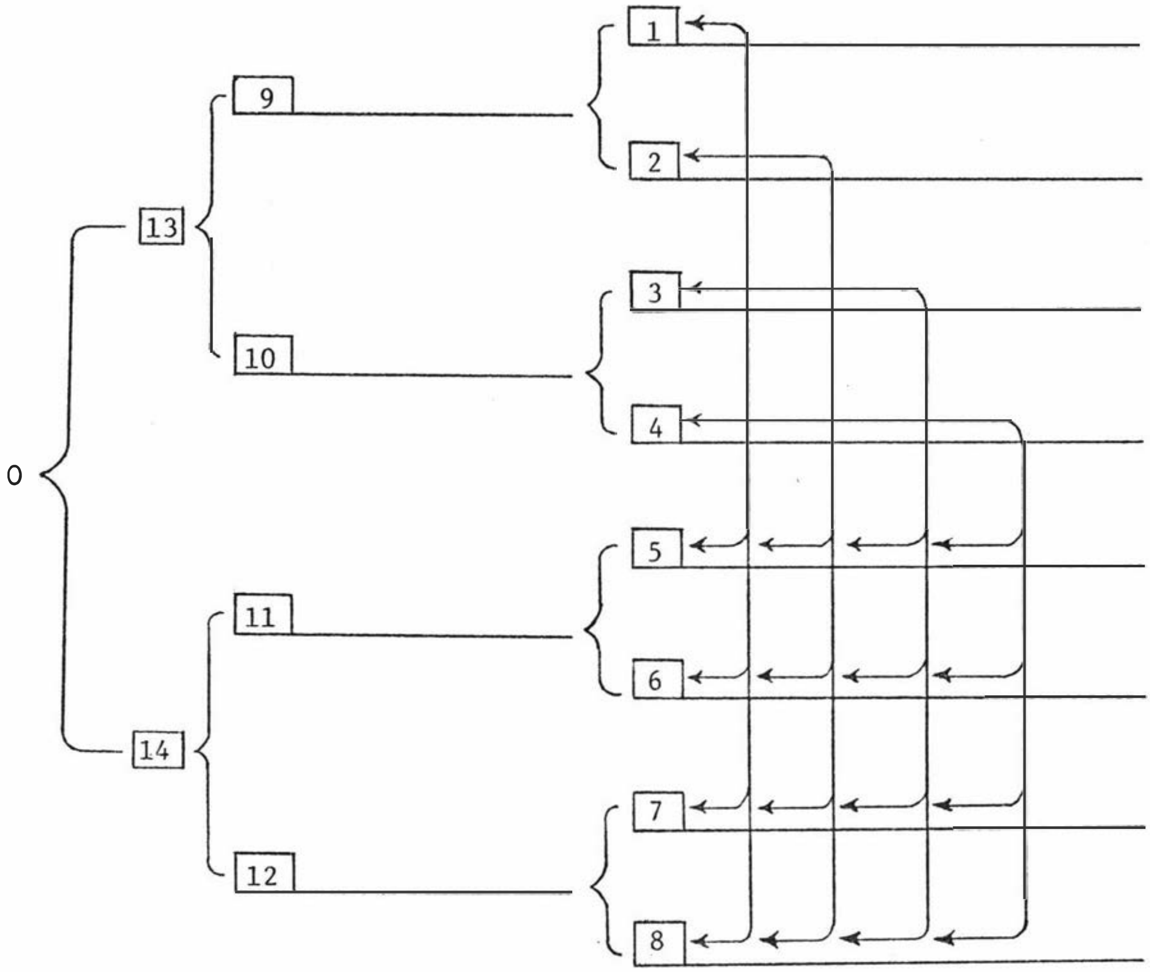
METHODS AND MATERIALS

I METHODS

In studies of the genetic history of various breeds of domestic animals, the complexity of the pedigree network, especially if traced to more remote ancestors, precludes the use of Wright's Long Method of analysis. As pointed out in Chapter 3, the sampling technique of Wright and McPhee (1925) is the method of choice under such circumstances. A broad outline of this technique has already been presented. In the present study, estimates of the levels of inbreeding were obtained by a modification of Wright's "Short Method" as described by Robertson and Asker (1951).

As the accuracy of estimates of the inbreeding coefficient depends on the total number of ties observed, it is apparent that any method of increasing the possible number of ties with the same amount of labour is advantageous. This can be done by drawing out more than two lines for each animal. Consider the situation where the pedigree is drawn completely to the eight great-grandparents. From each of them, a line is drawn at random until it terminates at an imported animal.

Fig. 4.1--The 16 possible ties in an eight-line pedigree.



As indicated in Figure 4.1, ties are possible between lines

1 and 5, 6, 7 and 8
2 " 5, 6, 7 and 8
3 " 5, 6, 7 and 8
4 " 5, 6, 7 and 8.

Therefore, there are 4x4=16 possible inbreeding ties (the same ancestor on both sire and dam's side) so that there are two possible ties per line drawn compared with half a tie per line in the 2-line method. The average inbreeding is then one half the actual ties divided by the possible ties.

Referring again to the diagram, it can be seen that half-sib matings would occur if the same animal appeared on the lines 9 and 11 and lines 10 and 12; paternal half sib in the former and maternal half-sib in the latter.

An actual pedigree drawn out completely to 8 great-grandparents, with a line drawn at random from each of them is shown in Figure 4.2 (see page 36).

In accordance with convention, the sire of each individual is placed at the top half of the pedigree, with the dam at the bottom half. For example, the sample female (registration number 42255) was sired by 13350, with 34313 as the dam; and so forth. Each registration number has a herd code denoted by a letter followed by a number, e.g. F12, F14, G9, etc. Where an animal is imported it is designated by an asterisk (*); its herd book number (which may be English, Canadian, Australian or American) is followed by its New Zealand Herd Book number (within brackets). In the fourth and subsequent generation the letter S or D preceding a number refers to the sex of the ancestor; S for sire and D for dam. The number after the decimal point refers to the year of birth. For example, an animal born in 1950 is denoted as .50; likewise, .43 refers to an animal born in 1943, and so on.

As indicated in the pedigree, there are four ties altogether, one of which is a Current inbreeding tie, as distinct from the other three which are Non-current inbreeding ties. Current inbreeding consists

Figure 4.2 : An actual pedigree drawn according to Robertson and Asker's (1951) modification of Wright's "Short Method".

In the pedigree below, the animals responsible for the 3 non-current inbreeding ties are bulls 5469, 8733* and 16891*. There is only one current inbreeding tie, the animal responsible being sire 11390.

Generation Number 1	2	3	4	5	6	7	8	9	10
F14 42255.50	F12 13350.46	G9 11390.43	M26 103095.38* (8733)						
			C22 114937.36* (16891)						
		F12 28497.43	H11 7596.36	H11 D10748.30	M4 D5133.21	M4 D2178.16	M4 S850.09	M2 D957.02	M2 D495.95	M5 D16750.90* (348)
			P2 15359.36	M14 S5469.31	M14 S4275.28	M28 S52317.22* (2677)				
	F14 34313.46	G9 11390.43	M26 103095.38* (8733)						
			C22 114937.36* (16891)						
		P2 17848.37	M14 5469.31	M14 D8002.26	B4 D4371.19	B4 S1061.15	R1 S23778.03* (536)			
			P2 9352.28	M4 S3885.24	M4 D4843.20	R2 D1926.14	M2 D958.03	M2 D710.03	E1 D507.95	T2 D19940.92* (358)

of matings involving close relatives such as parents and offspring, full or half-sibs; these matings lie completely with the parental or grandparental generations. Non-current inbreeding includes the inbreeding due to the repetition of more remote ancestors, part or all of which lie beyond the grandparental generation in both top and bottom halves of individual pedigrees.

The number of ties obtained is halved and divided by 16, this being the possible number of ties in an 8-line pedigree, to obtain an estimate of the inbreeding coefficient. As Wright and McPhee (1925) pointed out, the result so obtained means practically nothing as far as the individual is concerned, but by determining the proportion of ties in a sufficiently large random sample of a family or breed, a measure of the average degree of inbreeding of that family or breed can be obtained to as high a degree of accuracy as desired.

The methods of analysis for other aspects of this study will be outlined in the results. Those aspects may be regarded as incidental to the main topic of inbreeding and such an approach may help to maintain continuity from one topic to another.

II DATA

Data for the present study was obtained from the New Zealand Aberdeen Angus Herd Book, established in 1917. Since the study involves an analysis of a breed rather than of individuals, it is, of course, impossible to consider all the animals of the breed and the analysis must therefore be confined to random samples.

In the sampling process, it is necessary to decide whether the samples should include both male and female animals. In previous studies, as for example McPhee and Wright (1925); Dickinson and Lush (1933); Lush *et. al.* (1936); Willham (1937) and Stonaker (1943), pedigree samples from both sexes were included in the analyses. But for this present study, it was decided to consider only the pedigrees of registered females because in most cases, the number of bulls registered is always much less than that of females, and the selection of bull calves for registration is a potential source of bias. Furthermore, there is reason to believe that a large proportion of the heifers that live are registered. Therefore, the parents of registered heifers may be taken as representative of the breeding stock in use at that time.

The first step in obtaining the random sample has been to ascertain the number of pages in the herd book occupied by registrations in the year in question. A table of random numbers was then used to select the sample. In making the selection, the animal's name, breeder, or owner was not taken into consideration. There were altogether 8 samples, taken at 10-year intervals, starting with 1900 and extending to 1966/67. The modal birth dates of these samples were therefore 1900, 1910, 1920, 1930, 1940, 1950, and 1966/67. Having chosen the sample females, their pedigrees were traced according to the system as outlined at the beginning of this chapter.

The size of each sample relative to the population from which it was drawn is shown in Table 4.1.

TABLE 4.1

Proportions of the Registrations Included in each Sample

SAMPLE YEAR	Number of Heifers Registered	Sample Size	Percent of Heifers Registered
1900	44	44	100
1910	139	70	50.4 (1 in 2)
1920	473	82	17.3 (1 in 6)
1930	693	84	12.1 (1 in 8)
1940	1,603	79	4.9 (1 in 20)
1950	1,856	93	5.0 (1 in 20)
1960	4,344	102	2.3 (1 in 43)
1966/67	6,981	137	1.9 (1 in 51)

For each sample year, a further (larger) sample of pedigrees were traced back to the four grandparents and the extent of close matings obtained. This additional estimate of current inbreeding was added to that obtained from the pedigree samples (corresponding to the same year) and subjected to the 8-line method of analysis.

CHAPTER 5

GENETIC ANALYSIS

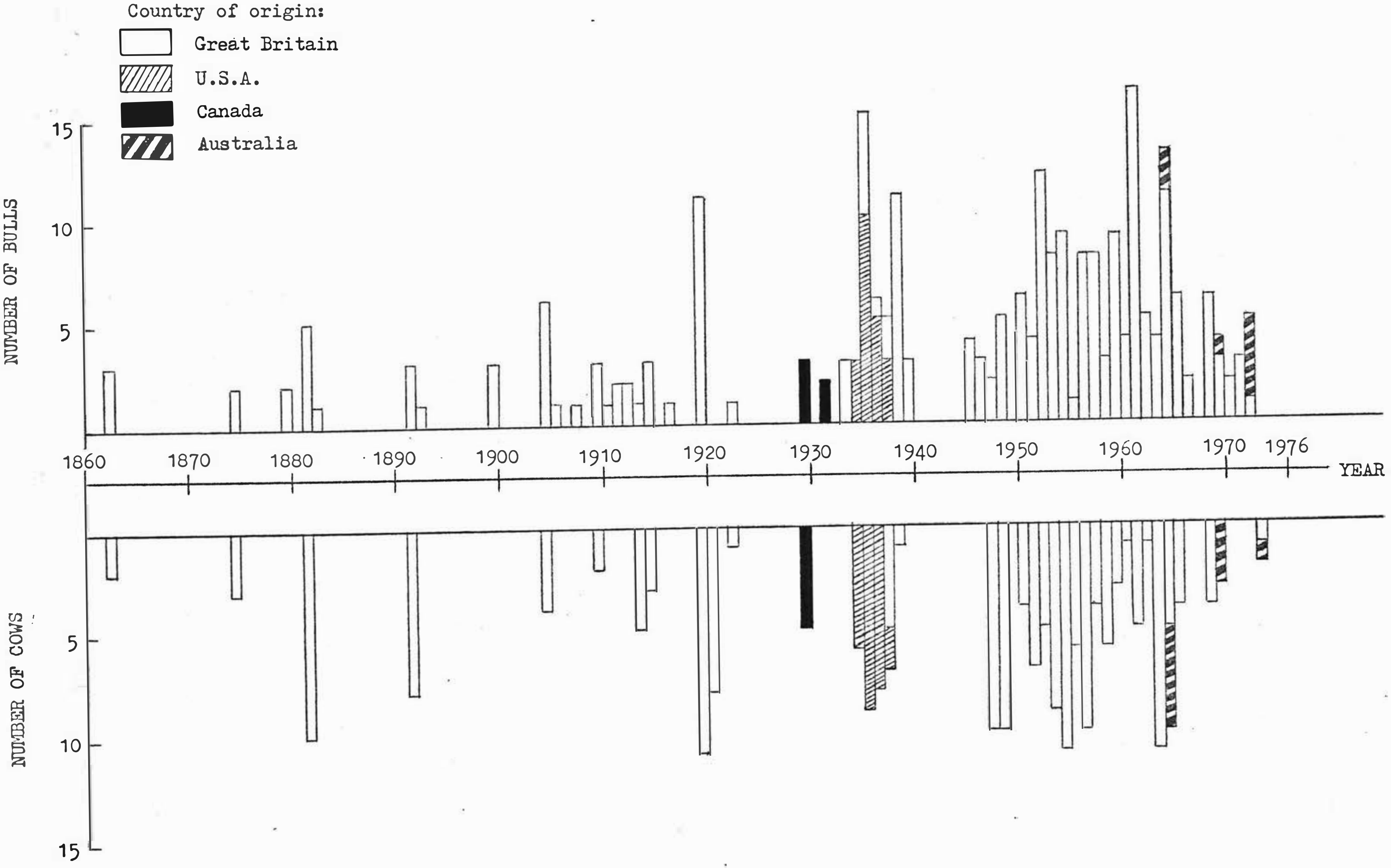
I INFLUENCE OF IMPORTATIONS

Imported cattle have always played a prominent role in the history of the New Zealand Angus breed. Subsequent to the initial importations in 1863 there was a steady, if not large entry of Angus cattle from overseas (Figure 5.1). The United Kingdom has been the main source of importations. But, as a result of the foot and mouth epidemic during the mid 1930's, quarantine regulations did not permit the direct entry of livestock from Britain. Consequently, a number of cattle were imported from Canada and the United States of America.

These imported stock appear to have generally been regarded by breeders as superior to New Zealand-bred stock, and as such have tended to elevate the herds in which they were used to something akin to a nucleus status. The actual importance of these imported animals as sources of genetic material in the breed as a whole may now be assessed.

The completed 8-line pedigrees for the 8 sample years (as indicated in Chapter 4) form the basis of this study. All the lines terminate at imported animals. A list of these animals was compiled and the dates of importation and country of origin were also noted (see Table 5.2 and Appendices V and VI). These animals fell into fairly well-defined groups

Fig. 5.1--Angus importations 1863-1976 (See Appendices V and VI).



and the importations were divided into 9 groups according to the ten-year period during which they entered New Zealand. Animals imported before 1896 were called Foundation Stock for convenience. The other categories, together with the number of bulls and cows comprising them are shown in Table 5.1.

In the eight sets of random eight-line pedigrees, the proportion of lines tracing back to foundation stock and to the groups of imported animals may be determined. This can be expressed as the percentage of genes derived from them and is shown in Table 5.3 and Figure 5.2.

TABLE 5.1

Numbers of Angus cattle imported into New Zealand during ten-year periods from 1863 to 1975

Group	Details	Bulls	Cows
Foundation (1st group)	Animals introduced before 1896	17	23
2nd group	Animals imported between 1896 - 1905	9	4
3rd group	Animals imported between 1906 - 1915	14	10
4th group	Animals imported between 1916 - 1925	13	20
5th group	Animals imported between 1926 - 1935	11	11
6th group	Animals imported between 1936 - 1945	40	25
7th group	Animals imported between 1946 - 1955	53	56
8th group	Animals imported between 1956 - 1965	71	57
9th group	Animals imported between 1966 - 1975	28	13
	TOTAL	256	219

TABLE 5.2 : Angus importations 1863-1976 distributed according to country of origin and year of entry into New Zealand

Date of Importation	Great Britain		U.S.A.		Canada		Australia		Totals	
	Bulls	Cows	Bulls	Cows	Bulls	Cows	Bulls	Cows	Bulls	Cows
1863 - 1899	17	23							17	23
1900 - 1909	11	4							11	4
1910 - 1919	13	10							13	10
1920 - 1929	12	20							12	20
1930 - 1939	22	6	21	25	5	5			43	36
1940 - 1949	17	20							17	20
1950 - 1959	59	62							59	62
1960 - 1969	63	34					2	5	65	39
1970 - 1976	9	1					5	4	14	5
TOTALS	223	180	21	25	5	5	7	9	256	219

TABLE 5.3 : The effect of the different importations on the breed at ten yearly intervals

Sample Year	Effect of Different Groups in Percentages							
	1st Foundation	2nd 1896-1905	3rd 1906-1915	4th 1916-1925	5th 1926-1935	6th 1936-1945	7th 1946-1955	8th 1956-1965
1900	81.8	-	-	-	-	-	-	-
1910	40.0	22.7	1.6	-	-	-	-	-
1920	24.5	31.1	18.9	0.2	-	-	-	-
1930	21.1	25.6	23.9	18.6	-	-	-	-
1940	14.9	20.1	21.5	23.1	3.8	3.0	-	-
1950	11.4	18.0	15.7	22.6	4.4	19.2	1.6	-
1960	9.8	9.9	10.2	15.9	2.9	20.8	17.5	0.4
1966/67	6.8	8.2	6.8	10.9	2.5	16.1	25.1	9.0

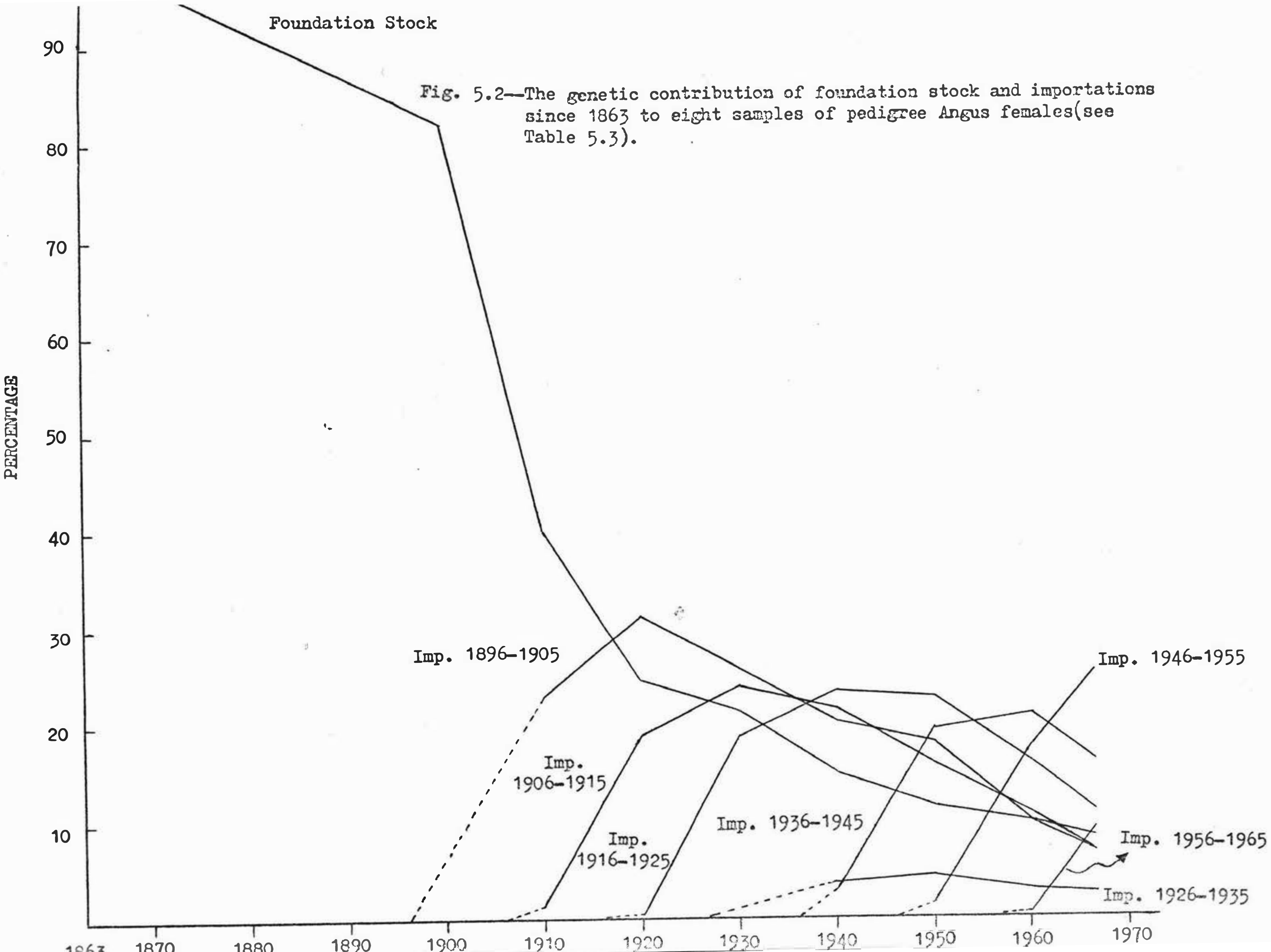


Fig. 5.2—The genetic contribution of foundation stock and importations since 1863 to eight samples of pedigree Angus females(see Table 5.3).

The contribution of the foundation animals has decreased from 100% in 1863 to 6.8% in 1966/67 and the relative effects of subsequent ten-year periods may be seen from Figure 5.2. Several features are worthy of note :

(a) The genetic contribution of animals imported in a 10-year period reaches a maximum in about 20 years and then declines.

(b) Early importations reach a maximum value more rapidly than later importations. This is due to the relatively few pedigree Angus cattle registered during the early years.

(c) As would be expected, the effects of large importations are greater than small importations.

(d) It is possible that certain individual animals in one period were more favoured than those in the other groups, thus accentuating the contribution of a particular period.

Clearly, the gene complex of a breed may be altered fairly rapidly even in the absence of artificial insemination. During a period of 87 years or approximately 17 cattle generations later (that is, in 1966/67) more than 93% of the original genes have been replaced. The replacement of the foundation genes for the other sample years are:

18.2% (1900)

60% (1910)

75.5% (1920)

78.9% (1930)

85.1% (1940)

88.6% (1950)

and 90.2% (1960)

The rapid rate of replacement of genes in the early years was probably the result of deliberate selection for "imported" genes. In the latter stages there was probably no deliberate selection against foundation genes as few, if any, published pedigrees traced back more than 30 years. The continued replacement of these foundation genes was probably the natural consequence of selection in favour of recently imported genes. The way in which these rapid changes have been effected may be appreciated if the structure of the breed is taken into consideration. As with other registered cattle breeds, the breed structure of the Angus is pyramidal, consisting of various strata (See Chapter 6). Each stratum obtains its sires from those above it. The top strata include those herds which use imported sires and these herds in turn supply other pedigree herds with sires which in turn supply bulls to other pedigree herds and so on. Thus, within 2 or 3 generations one imported sire may have hundreds of grandsons and great-grandsons.

Figure 5.2 suggests that the contribution of the foundation animals and the different importation groups may not alter greatly in the future. With the exception of 1946-1955 and 1956-1965 importations, the contribution from each period has remained relatively stable during the interval 1945-1966. This may be indicative of a lessening of the emphasis on imported animals as such and a tendency to select animals on performance rather than implied superiority due to "imported blood". Alternatively, it may indicate that certain imported animals may be held in high esteem and that in attempting to preserve their excellence, many breeders linebreed to them and thus preserve the relative importance of the period during which they were imported.

II AMOUNT OF INBREEDING

In breed studies an obvious problem arises from the relationship between animals both within and between the different importations which have taken place. For the inbreeding coefficients obtained to be meaningful, it is necessary to define the base population to which the present inbreeding is referred. An individual belonging to this base population will therefore be assumed to have an inbreeding coefficient of zero. In the present study it will be assumed that all imported animals were neither inbred nor related to each other. Consequently, the inbreeding estimates obtained are lower than their actual values.

The overall inbreeding averaged over the whole population may conveniently be divided into two categories:

(a) Current inbreeding, and

(b) Non-current inbreeding, the distinction between these two having been discussed in Chapter 4. The non-current inbreeding may be subdivided into two parts:

 (i) the long term inbreeding, due to the relationship of important animals to the whole breed; and

 (ii) deliberate non-current inbreeding, due to the separation of the breed into strains.

In the actual estimation of the total inbreeding, distinction was made only between current inbreeding, estimated on a large number of matings, and the non-current, estimated from the eight-line pedigrees (involving a smaller sample size) after omission of the current inbreeding in them. There were sixteen possible ties in each pedigree, so that the total number of ties divided by Nx16x2 (N being the sample size) gave the non-current inbreeding. Results obtained are indicated in Table 5.4.

TABLE 5.4

The extent of current inbreeding in eight sample years for the New Zealand pedigree Angus

Average birth year of sample females	Matings in sample *	Sire-dtr	Dam-son	Pat ½-sib	Mat ½-sib	Current inbreeding (%)
1900	44	-	-	3	-	0.21
1910	134	2	-	-	-	0.05
1920	245	-	1	6	-	0.089
1930	257	-	-	3	-	0.04
1940	319	1	1	12	2	0.16
1950	375	6	-	11	-	0.14
1960	410	1	-	9	-	0.08
1966/67	367	4	-	6	-	0.85

* The number sampled in each period was arbitrary.

There were marked fluctuations in the current inbreeding in the different periods (Figure 5.3). Of the total of 2,151 matings sampled, 14 were sire-daughter, 50 were paternal half-sibs, and there were two matings each of dam-son and maternal half-sibs. Over this period, therefore, about one mating in 150 was sire-daughter, one in 40 was between half-sibs and the remaining category represented about one

Fig. 5.3—Current inbreeding for each of the 8 sample years.

mating in 100. Corresponding figures for sire - daughter and half-sibs in other studies are indicated in Table 5.5.

TABLE 5.5

Extent of current inbreeding in other cattle breeds

Breed	Sire-daughter matings	Half-sib matings	Authors
British Friesians	1 in 200	1 in 30	Robertson and Asker, 1951
Jerseys	1 in 50	1 in 20	Stewart, 1954
Jerseys	1 in 40	1 in 30	Barker, 1957
Polled Hereford	1 in 200	1 in 20	Barker and Davey, 1960
Hereford	1 in 120	1 in 30	Davey and Barker, 1963

The non-current and total inbreeding are shown in Table 5.6 and Figure 5.4.

Fig. 5.4--Non-current inbreeding subdivided into long-term and strain inbreeding.

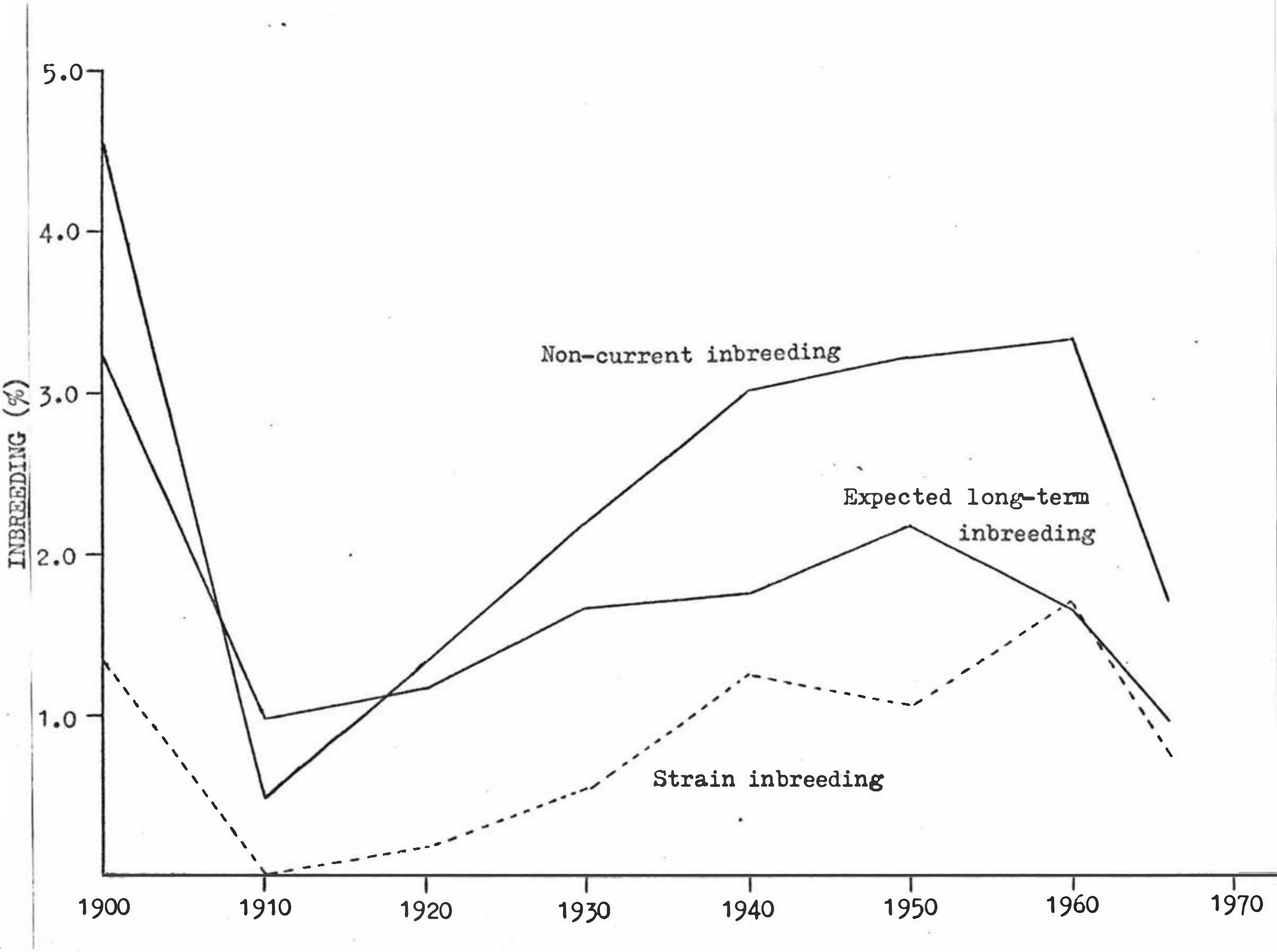


TABLE 5.6

Amount of total inbreeding in eight sample years
in the pedigree Angus in New Zealand

Birth year of sample females	Current inbreeding (%)	Non-current inbreeding		Total inbreeding
		No. of ties	Inbreeding (%)	%
1900	0.21	64	4.55	4.76
1910	0.047	11	0.49	0.54
1920	0.089	35	1.33	1.42
1930	0.036	59	2.19	2.23
1940	0.16	76	3.01	3.16
1950	0.14	96	3.23	3.37
1960	0.076	109	3.34	3.42
1966/67	0.085	75	1.71	1.80

The coefficient of inbreeding at 4.76% was highest in 1900 and this was followed by a marked decrease in 1910 to 0.54%, the lowest among the eight pedigree samples. This represents a decrease in the inbreeding coefficient of 88.7% during the intervening 10 year period. The expectation that a small number of foundation animals would lead to a fairly high degree of inbreeding during the formative years of the breed was borne out in this study. The level of inbreeding in the 1900 sample corresponds to a decrease in heterozygosity of about 0.87% per generation during the period 1863 to 1900, allowing for the fact that the earliest generation in cattle pedigrees cannot show any inbreeding. From 1910 onwards, there was a steady increase in the total inbreeding, reaching a second peak of 3.42% in 1960. This level of inbreeding is not unexpected, bearing in mind the low number of importations during the 1930's to early 1940's and the fact that it takes some 15-20 years before an imported animal exerts its maximum impact on the breed.

The rate of increase of inbreeding was highest (0.93) from 1930 to 1940 and could be related to the Depression years when importations were reduced considerably. No doubt the advent of the Second World War would have hindered matters somewhat. The embargo on importations from Britain on account of the foot and mouth epidemic there proved a further obstacle to importations. The drop in the inbreeding level to 1.80% in 1966/67 reflects the increased importations from the mid-1940's onwards. In terms of Wright's (1931) approximate formula of 1/8M for the fraction of the remaining heterozygosity lost per generation in a population of limited size, this inbreeding is about the same as if there were only about 125 bulls per generation in the whole breed actively and equally taking part in reporducing the breed, but mating at random with a much larger number of cows. Of course, these abstract conditions are not entirely realized. At all times many more than 125 bulls are actually in use in purebred herds, but they are by no means used equally. In practice, far less than 125 take so active a part that they have a distinct influence on the breed for more than a generation or two after their death. In fact, there is some slight tendency (to be discussed next) for breeding within family lines instead of entirely random mating with respect to pedigree relationship.

In many instances, far more than 125 are used only a little or have most of their descendants go to grade herds where their genes are lost to the pure breed. For example, showring successes may cause many breeders to seek sons or grandsons of the few currently famous sires to head their herds in each generation. Yet, the most famous sire next year or in the next generation will sometimes not be a son or a grandson or even a close relative of the most famous recent sire. Hence, this keeps shifting the emphasis of breeders' selections from one spot to another within the pedigree structure of the breed.

III THE HOMOGENEITY OF THE BREED

A very important question associated with a breed concerns its degree of homogeneity. For example, is mating more or less at random over the breed as a whole or does it comprise a collection of diverse families? The coefficient of inbreeding does not answer this question. A breed might become split up into several such families or strains each inbred within itself but having little relationship to each other. Indeed, such an assemblage might well show a high coefficient of inbreeding. To take an extreme example, a group of pedigrees picked at random from the herdbooks of various breeds of domestic animals might yield a high coefficient of inbreeding with no homogeneity whatsoever. Furthermore, even if prominent animals have high coefficients of relationship to the breed they belong to and thereby, providing some indication of breed homogeneity, the answer is far from complete.

This problem may be resolved by considering the *inter se* relationship (r) which gives an estimate of the average relationship existing at a particular period between any two animals chosen at random from the breed. The *inter se* relationship is obtained by matching the random lines from the sire's half of one pedigree against the dam's half from another pedigree to see how often ties are found in such comparisons. No random lines are used a second time in such matching.

Within each of the eight samples, the actual number of ties divided by the possible ties gave the *inter se* relationship. For example, in the 1900 sample (which consists of 44 pedigrees) the number of possible comparisons are 44x39 = 1,892. As there are 16 possible ties in each comparison, involving 4 random lines from the sire and 4 from the dam, the total possible ties are (44x43x16) = 30,272. The 1,889 ties in the 1900 sample, divided by (44x43x16) gave an *inter se* relationship of 0.063.

Having estimated this relationship the extent of the separation of the breed into strains (or alternatively, the degree of breed homogeneity) may be determined. The inbreeding (F) expected (that is, long-term inbreeding) is one-half the *inter se* relationship (r) or more exactly $r/(2-r)$. Subtracting the expected long-term inbreeding from the non-current inbreeding previously obtained gives the strain inbreeding.

Ideally, the sample size chosen for studying the *inter se* relationship should correspond to that used in the estimation of non-current inbreeding (See Table 4.1, section on 'Data'). However, that would involve a total of 63,988 possible comparisons. Because of the lack of a suitable computer programme to process this data, it was decided to reduce the sample size within each time period. As a result of this sub-sampling the number of comparisons over the 8 sample years amounts to 28,988. The results obtained by this proportionate sampling method would not deviate a great deal from that based on the original sample size (A. L. Rae, personal communication). The subdivision of the non-current inbreeding into long-term and strain inbreeding is shown in Table 5.7.

TABLE 5.7

Inter se Relationship and Non-current Inbreeding Subdivided into Long-term and Strain Inbreeding in Eight Sample Years for the New Zealand Pedigree Angus

Average birth year of sample females	No. of random matings	*Inter se* relationship %	Resultant expected long term inbreeding %	Non-Current inbreeding %	Strain inbreeding	Index of Sub-division
1900	1892	6.27	3.24	4.55	1.31	1.40
1910	4830	1.93	0.98	0.49	—	0.50
1920	6642	2.30	1.16	1.33	0.17	1.15
1930	3080	3.25	1.65	2.19	0.54	1.33
1940	2652	3.45	1.76	3.01	1.25	1.71
1950	3782	4.23	2.16	3.23	1.06	1.49
1960	2450	3.22	1.64	3.34	1.70	2.04
1966/67	3660	1.89	0.95	1.71	0.76	1.79

It is evident that the level of strain inbreeding waxes and wanes and this trend is more noticeable in Figure 5.4 (Page 52). With the exception of 1910, the observed coefficient of inbreeding was more than the expected in every other sample, the difference being most pronounced in 1960. The strain inbreeding (that is, the excess of the actual over the expected inbreeding) was 1.31% in 1900 and dropped to 0 in 1910. This was followed by a slight increase to 0.17% in 1920 and a further increment to 0.54% ten years later. A second peak of 1.25% was recorded in 1940. From a value of 1.06% in 1950, the level of strain inbreeding peaked again in 1960 (1.70%) and if the present level (that is, 0.76% in 1966/67) is any indication, the trend appears to be towards a further decrease in the level of strain inbreeding.

As mentioned previously, the non-current inbreeding consists of the long-term inbreeding and the inbreeding due to the separation of the breed into strains; the long-term inbreeding referred to here is derived from the relationship of important animals to the whole breed. Therefore, if the long-term inbreeding is low relative to the non-current inbreeding, it implies that the important animals have not spread their influence over the whole breed and consequently, the breed is to some extent subdivided into several strains. The results from the present study would suggest a tendency towards family formation in the breed. However, this tendency is rarely, if ever, carried so far that families are kept distinct for several generations. Presumably the more successful, or highly esteemed of these incipient families are used for top crossing.

on other families and are blended into the breed as a whole.

An alternative way of looking at the same problem was suggested by Lush (1946) who derived an index of subdivision which is calculated as:

$$\frac{\text{Actual non-current inbreeding}}{\text{Expected long-term inbreeding}}$$

In the idealized case, the ratio approaches unity implying that mating is entirely at random and there is no separation of the breed into families. Departure from this ratio provides some evidence of strain formation. This parameter, calculated for the eight sample years used in the present study, is presented in Table 5.7.

That there is little effective subdivision of the Angus breed into separate strains seems plausible as distance is certainly not a major hindrance towards stock movement within New Zealand. While some breeders tend to use sires bred near their own localities, many of them travel further afield for their sires. For example, a considerable number of stock transfers between herds, and also bailments (as recorded in the New Zealand Angus Herd Book) take place every year. Geographical isolation is therefore not a major contributing factor in family formation in the New Zealand context. This factor, however, assumes greater significance especially in countries like Australia, U.S.A. or Canada where distance alone may prevent mating from being entirely random within a breed, thereby leading to some partial isolation, even though there are no absolute barriers to the exchange of breeding stock.

An analysis of the animals contributing to the non-current inbreeding and *inter se* relationship ties provides a further indication of the emphasis placed on imported animals in the development of this breed (Table 5.8). In each sample, the most often appearing imported animal contributed more ties than all animals of the most important New Zealand herd (Table 5.9). As might be expected, the most often appearing New Zealand herds in each sample are the most important, as shown in Table 5.13, while the most often appearing imported animals are the important imported animals shown in Table 5.17.

TABLE 5.8

Contributions by Imported Animals to the Non-current Inbreeding and *Inter se* Relationship ties in the New Zealand Pedigree Angus

Sample Year	Non-Current Inbreeding Ties		*Inter se* Relationship ties	
	TOTAL	Number contributed by imported animals	TOTAL	Number contributed by imported animals
1900	57	34	1899	1165
1910	11	9	1494	1277
1920	31	25	2445	2063
1930	56	31	1603	917
1940	75	25	1465	752
1950	96	30	2563	1279
1960	102	44	1263	739
1966/67	75	39	1104	591

TABLE 5.9

Numbers of inter se relationship ties contributed by the seven most often appearing imported animals and the three most often appearing New Zealand herds in eight sample years for the New Zealand Pedigree Angus

	SAMPLE YEAR											
	1900			1910			1920			1930		
Imported animals	Blackleg		387	Lancer of Advie		255	Fashion's Prince		283	Ralph of Careston		162
	Waterside Eric		248	Baron Arradoul		252	Eblis of Ballindalloch		265	Mistral		118
	Bella 1st of Waimea		162	Fashion's Prince		205	Mistral		256	Lancer of Advie		62
	Megg Dodds		59	Mistral		194	B.B.B.		225	Heathen		59
	Solomon		57	Kathleen 2nd of Drummuir		62	Ralph of Carestin		181	The Quail		58
	Lancer of Advie		57	Quetta		51	Baron Arradoul		174	Fashion's Prince		56
	Robin Hood		37	Celandine of Drummuir		41	Lancer of Advie		158	Moose 2nd		41
New Zealand animals and herds*	Black Duke of Killara	a	203	Alberta	c	49	Alberta-Bred by John Elliot, Middlemarsh, Otago.		53	Baron of Ben Lomond		148
	McKinley		85	Amber		7	Engineer	Gladbrook	51	Dean of Ben Lomond		68
	Nelson		31	Grisette	Marainanga	22	Quetta 3rd		25	Duke of Argyle	Gladbrook	66
	Moss Rose		30	John Bull		20	Helen		19	Fame		41
	Solomon II	b	73	Sheila of Gwavas		14	Mason		19	Flower of Annadale		59
	Blair Athole		32				Dean of Ben Lomond		17			
	Oreti		32									
	Beatrice		28									
	Jamie of Killara		23									

* In the 1900 sample, only 2 herds can be listed; there are no contributions from other New Zealand herds.

[a] Bred by Matthew Holmes, Castlerock, Southland.

[b] New Zealand and Australian Land Company.

[c] Bred by John Elliot, Middlemarsh, Otago.

TABLE 5.9 (Cont'd.)

	SAMPLE YEAR							
	1940		1950		1960		1966/67	
Imported animals	Fashion's Prince	69	Hayston Elmore	360	Hayston Elmore	386	Hayston Elmore	219
	Hayston Bright Print	69	Eland of Bleaton	261	Emperor Elect of Douneside	56	Bruce of	79
	Eland of Bleaton	68	Hayston Bright Print	95	Eland of Bleaton	53	Greenyards	58
	Moose 2nd	64	B.B.B.	78	Eulijago of Kilham	41	Eland of Bleaton	23
	Lancer of Advie	64	Mulben Elbow	53	Etheridge of Tillyrie	21	Emperor Elect of	23
	Mistral	46	Fashion's Prince	45	The Quail	18	Douneside	
	Eblis of Ballindalloch	38	Mistral	34	Celandine of Drummuir	12	Lancer of Advie	23
							Etheridge of Tillyrie	23
							Eulijago of Kilham	22
New Zealand animals and herds	Roderick Dhu(Turihaua)	54	Ossian of Waiterenui	95	Roderick Dhu (Turihaua)	54	Roderick Dhu } Turihaua	45
	Sentry of Akitio	52	Baron of Ben Lomond	45	Embassy 5th of Mangatoro	54	Celia	22
	Acute of Akitio	26	Twig of Ben Lomond	39	Embassy 11th of Mangatoro	24	Ossian of Waiterenui	43
	Baron of Ben Lomond	32	Acute of Akitio	76	President of Mangatoro	22	Duke of Argyle } Gladbrook	26
					Ossian of Waiterenui	18	Quetta 3rd	15
					Nelson of Waiterenui	18		

IV GENERATION LENGTH

The average interval between one generation and the next is of considerable practical importance. For example, a breeder may wish to perpetuate the influence of a prominent animal by some system of linebreeding and a knowledge of the generation length will therefore enable him to estimate what he can accomplish. Also, it is useful in assessing what has been achieved in the past by the breeding systems actually followed. Furthermore, this information has an economic bearing as it allows a rough estimate of the probable replacement rate for breeding stock and the average number of offspring one may expect from animals actually retained for breeding purposes.

The data used were the birth dates of the sample animals and of the foundation animals in which the random ancestral lines terminated and a record of the number of intervening generations. The results are summarised in the table below.

TABLE 5.10

Average length of interval between generations

Year	Average generation interval (in years)	Number of Generation Intervals on Which This Average is Based
1900	5.16	962
1910	5.39	1104
1920	5.82	1755
1930	5.64	1767
1940	5.81	2054
1950	5.66	2831
1960	5.22	2331
1966/67	5.21	2821

Although the generation interval for the 1966/67 sample has only increased slightly compared to the estimate obtained in 1900, there were fluctuations during that intervening period. The generation intervals have tended to lengthen from 1900 onwards, reaching a maximum of 5.82 years in 1920. A slight decrease followed in 1930 and a decade later, the interval was estimated at 5.81 years. From then onwards, there has been a tendency towards shorter generation lengths.

Normally, in a breed which is approaching an equilibrium in numbers, the generation intervals would tend to lengthen. However, the data obtained for the period 1900-1940 cannot be explained on this premise. Given the economic climate during the Depression, and the advent of the Second World War, breed expansion was curtailed and consequently led to a lengthening of the generation length. The post-war years were followed by an upsurge in cattle numbers and this was paralleled by a gradual decrease in the generation interval, as borne out by the data.

The generation length, while of some use, is not as informative as its separate components; that is, the sire-son, sire-daughter, dam-son and dam-daughter intervals. Such intervals are calculated from the female samples in the eight sample years. As male samples were not used in this study, the four paths of the parent-offspring intervals could only be obtained by going back one generation in the pedigree samples. The birth dates of the sire and dam, along with their grandsires and granddams were tabulated. The mean of the four paths of the generation interval is the effective generation length, which is defined as the average age of the parents at the birth of their offspring. Distribution of parent-offspring intervals were obtained by taking the age of each parent, in years, at the birth of its offspring. The results are summarised in Table 5.11.

TABLE 5.11

Parent-offspring intervals and average generation length for pedigree Angus cattle in New Zealand

Parent-offspring Relationship	Interval (years)							
	1900 Sample	1910 Sample	1920 Sample	1930 Sample	1940 Sample	1950 Sample	1960 Sample	1966/67 Sample
Sire-son interval	5.05	3.81	6.03	4.42	5.30	3.91	4.05	4.26
Sire-daughter interval	5.06	5.08	5.01	5.40	5.04	4.79	4.66	5.62
Dam-son interval	4.51	8.31	6.70	5.62	7.37	7.08	6.14	5.85
Dam-daughter interval	5.85	6.32	7.63	6.15	6.26	6.54	6.43	6.73
Average Generation Length	5.12	5.88	6.34	5.39	5.99	5.58	5.32	5.62

The generation length has shown similar trends as that in Table 5.10 and has increased by 0.5 years over the intervening 66-year period. Except for the 1900 sample, the dams of the registered males and females are older than the sires of registered males and females. The dam-daughter interval for each of the eight samples is considerably longer than the average generation length.

The distributions of the parent-offspring intervals for each of the samples are shown in Figures 5.5 and 5.6. Differences between the various parent-offspring intervals are given in Table 5.12. In general, sires of both bull and heifer registrations are younger than their mates. The differences between the average ages of the parents of registered bull

Fig. 5.5--Distribution of the sire-son and sire-daughter intervals in the New Zealand pedigree Angus for the 8 sample years.

——— Sires of registered males

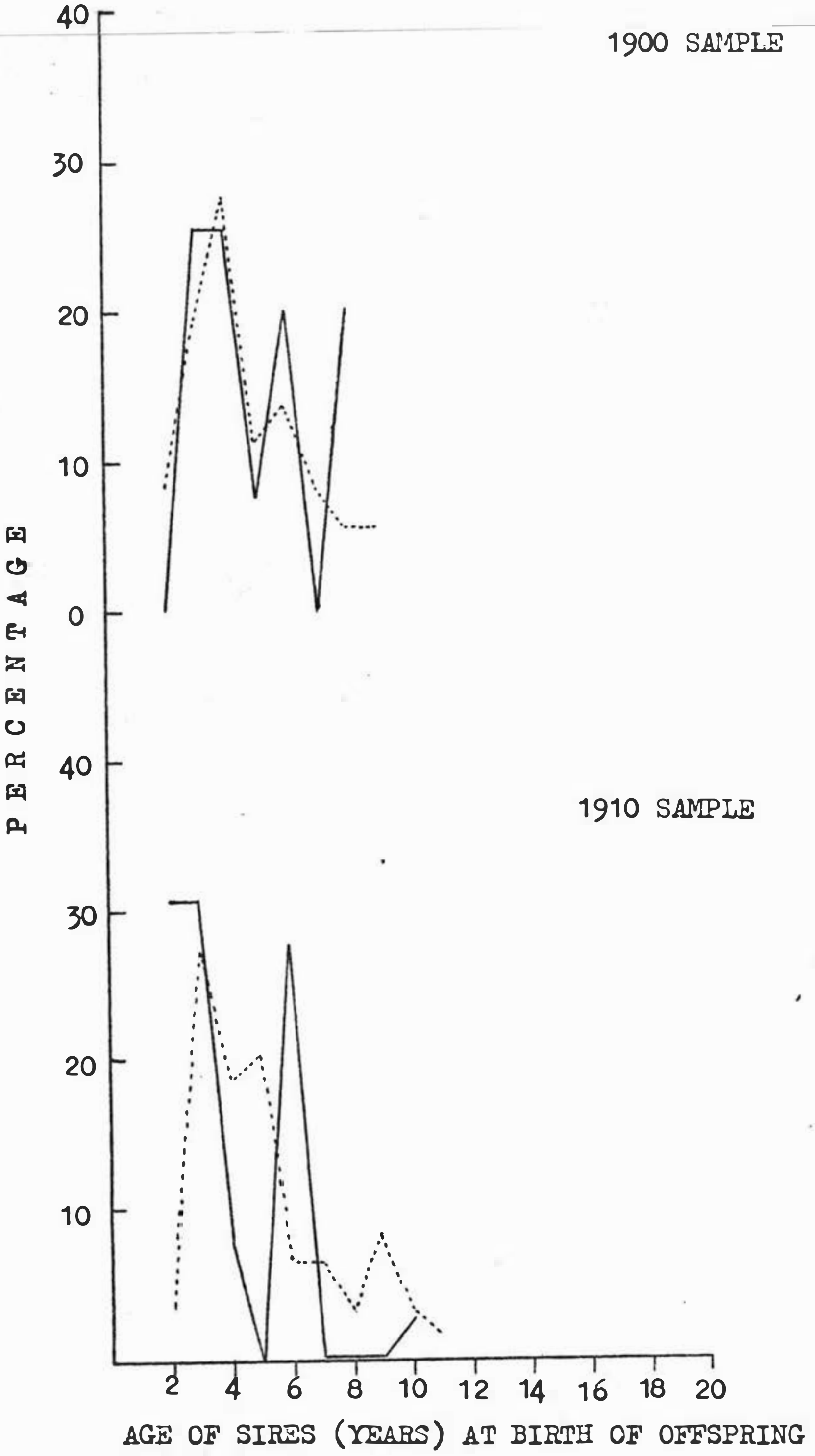
··········· Sires of registered females

Fig. 5.6--Distribution of the dam-son and dam-daughter intervals in the New Zealand pedigree Angus for the 8 sample years.

——— Dams of registered males

··········· Dams of registered females

(See Appendix VII)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1910 SAMPLE
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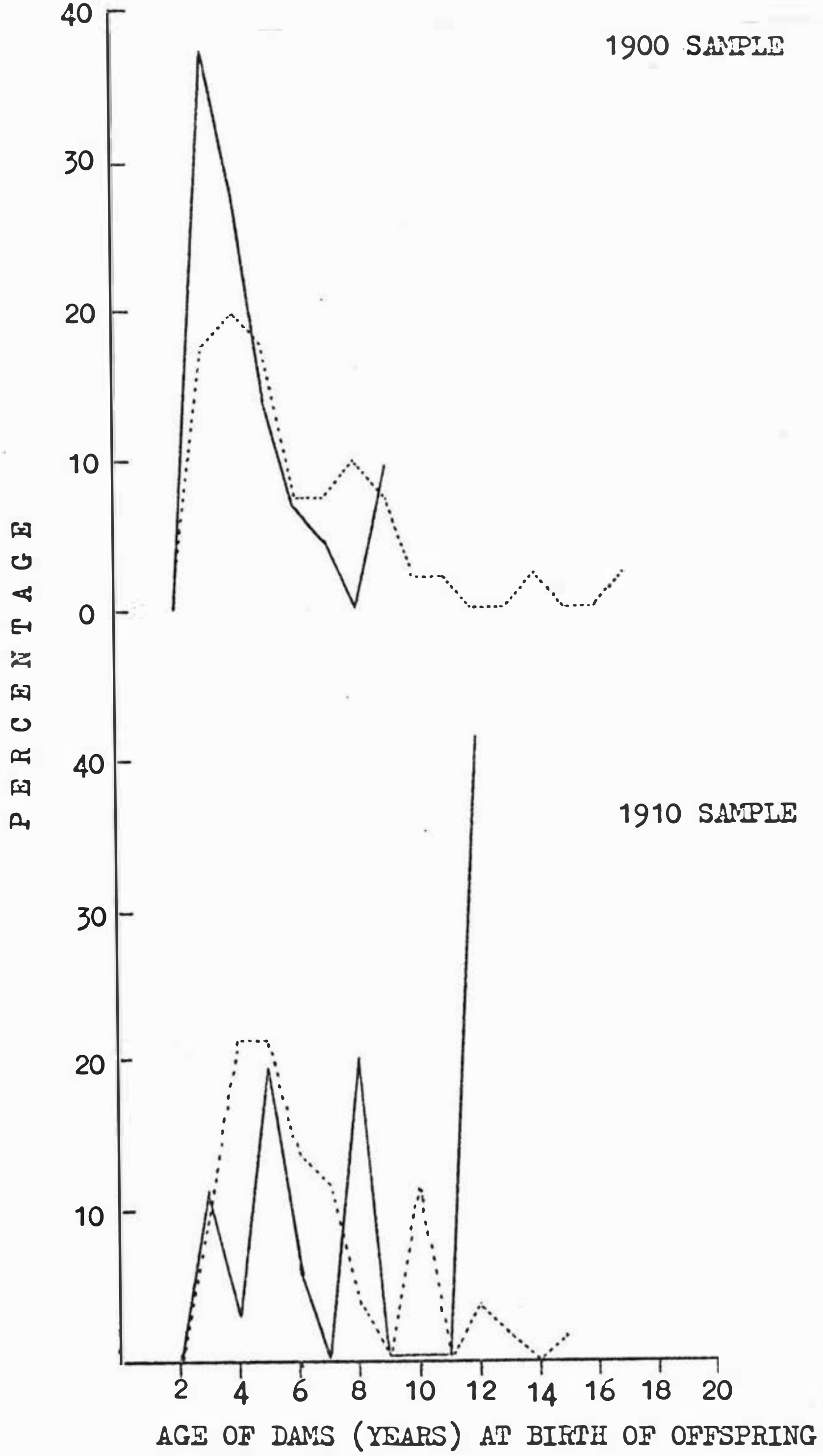
AGE OF SIRES (YEARS) AT BIRTH OF OFFSPRING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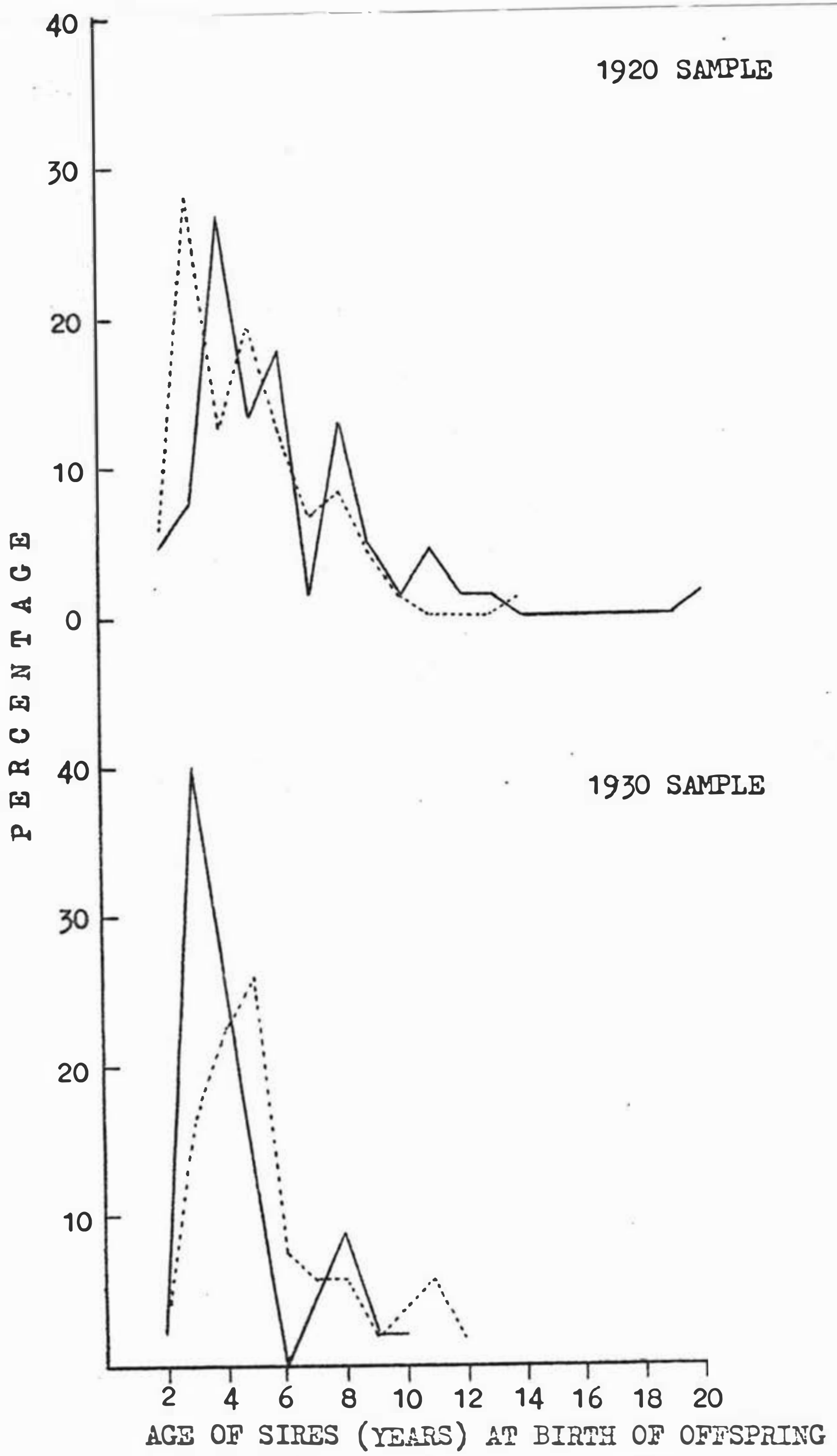
AGE OF DAMS (YEARS) AT BIRTH OF OFFSPRING



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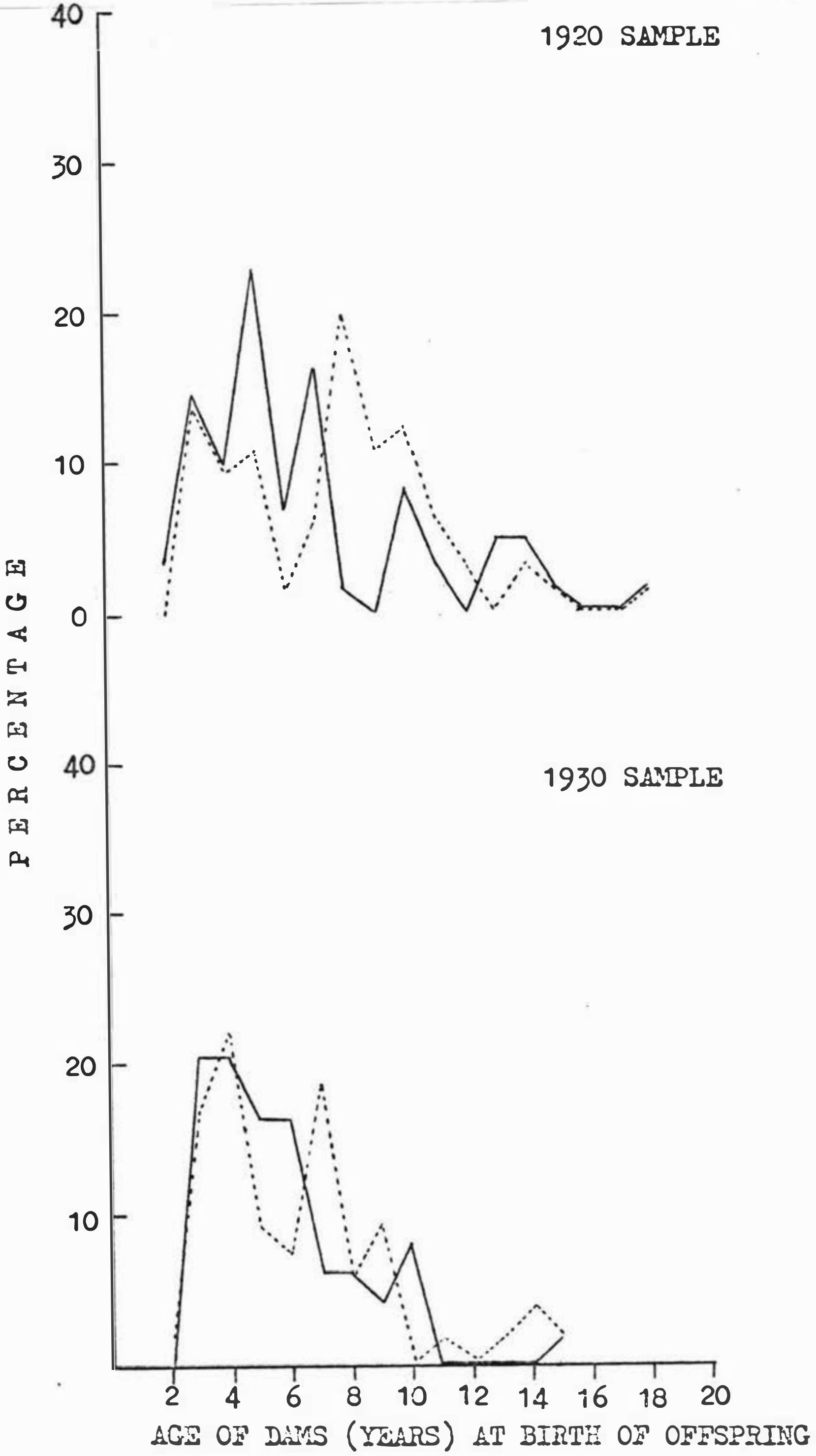
AGE OF SIRES (YEARS) AT BIRTH OF OFFSPRING



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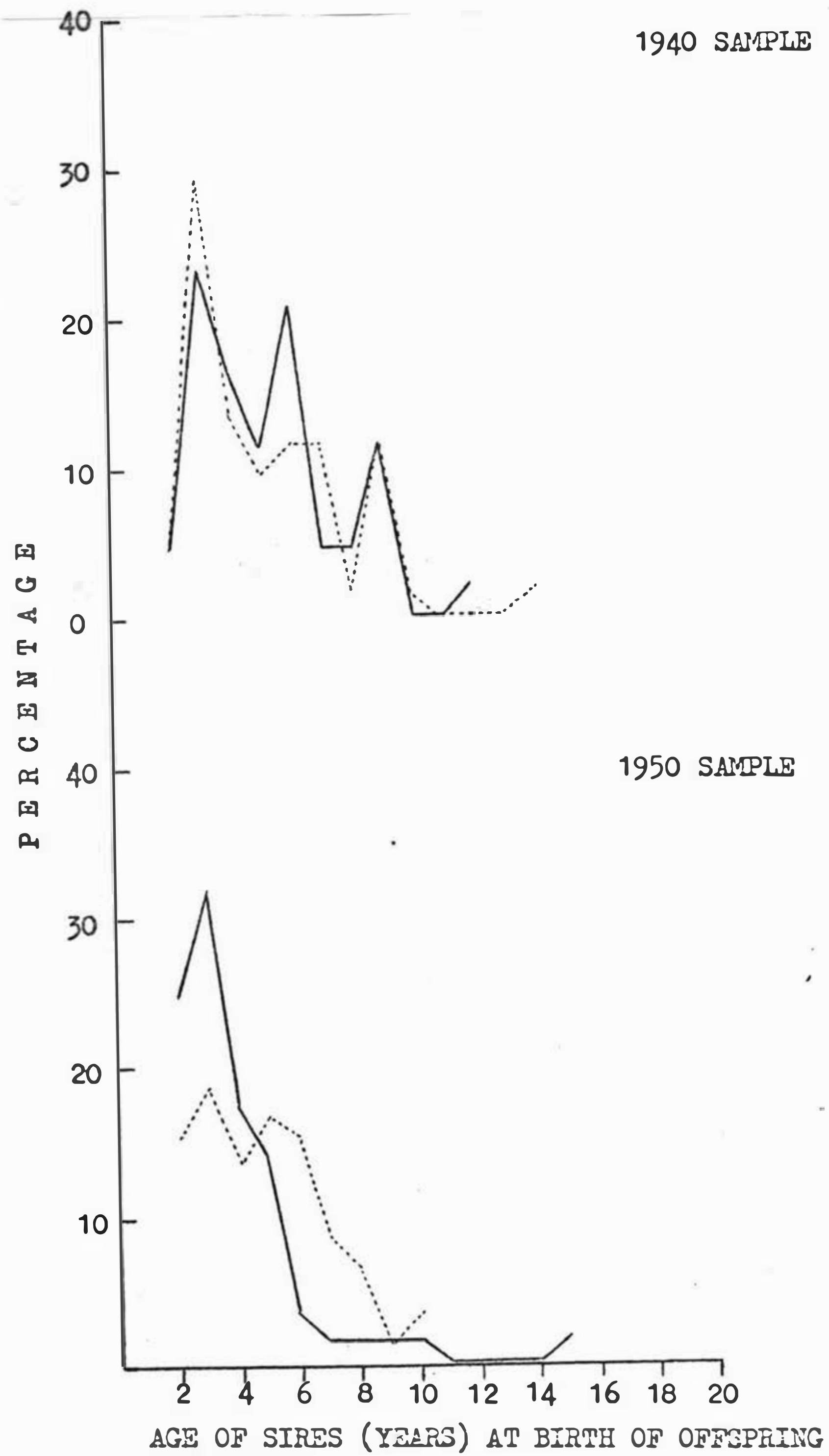
AGE OF DAMS (YEARS) AT BIRTH OF OFFSPRING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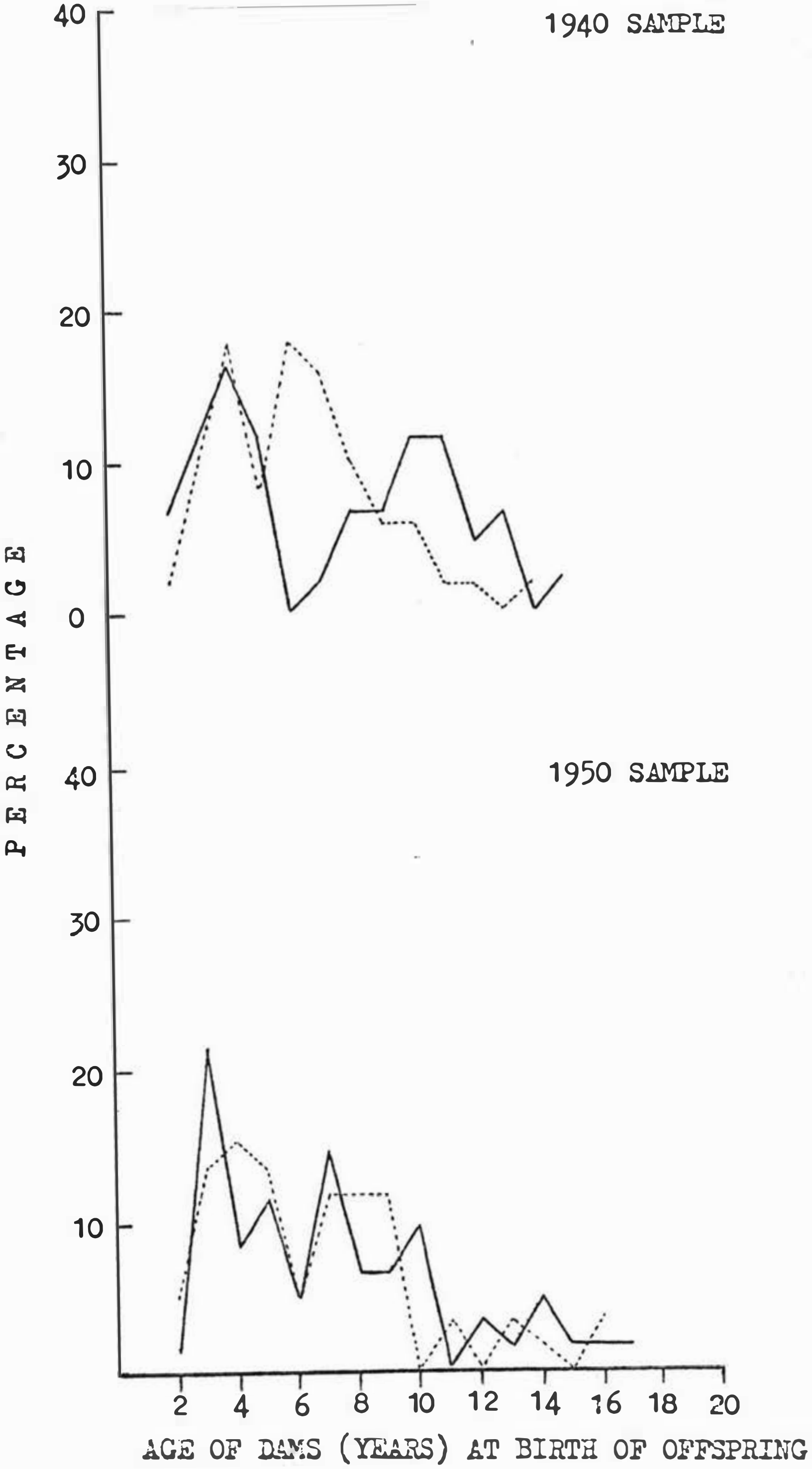
AGE OF SIRES (YEARS) AT BIRTH OF OFFSPRING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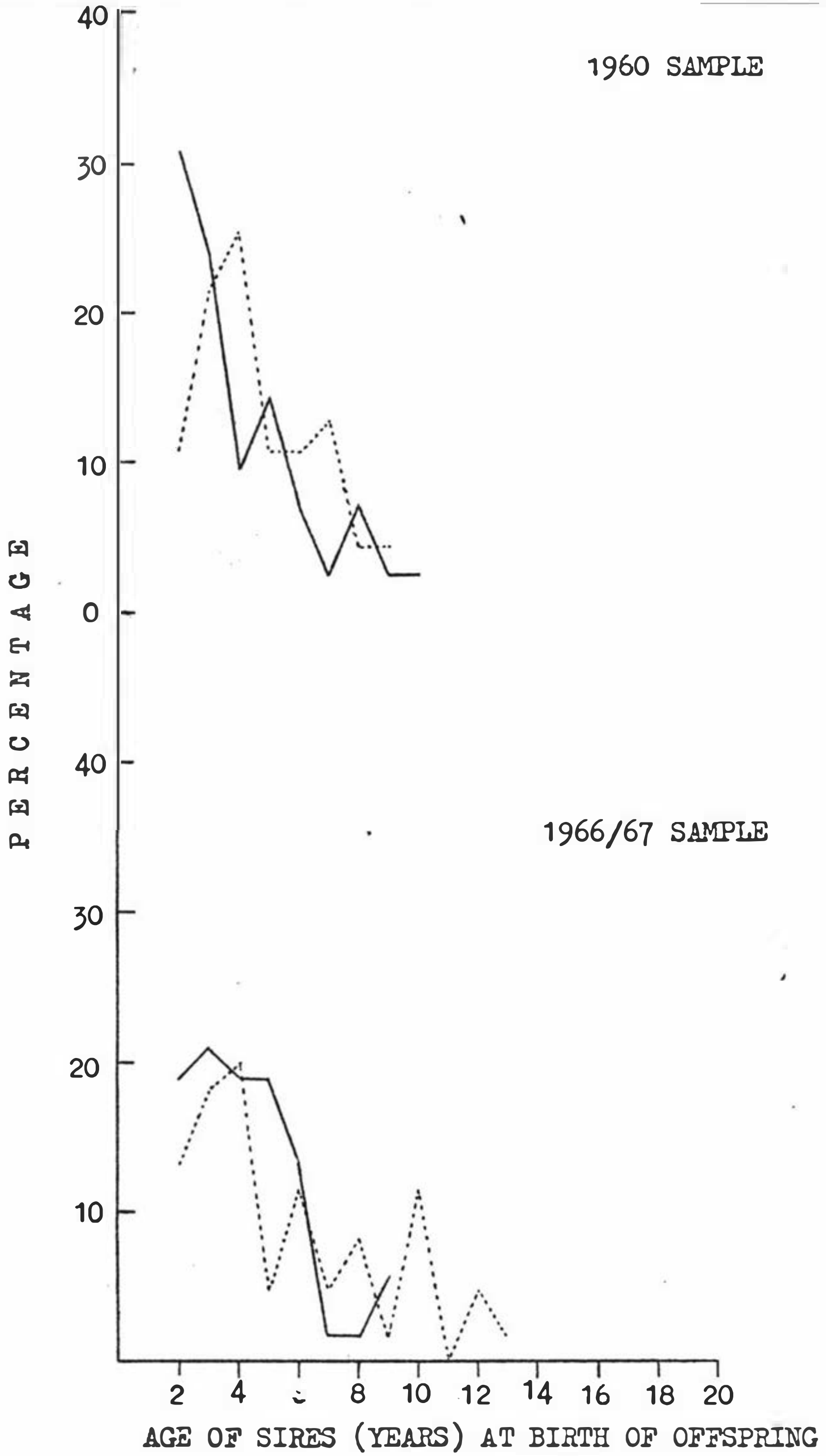
AGE OF DAMS (YEARS) AT BIRTH OF OFFSPRING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1966/67 SAMPLE
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AGE OF SIRES (YEARS) AT BIRTH OF OFFSPRING


1960 SAMPLE
1966/67 SAMPLE
PERCENTAGE
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AGE OF DAMS (YEARS) AT BIRTH OF OFFSPRING

TABLE 5.12

Differences between the various parent-offspring intervals (years) for pedigree Angus cattle in New Zealand

Parent-offspring Relationship	1900	1910	1920	1930	1940	1950	1960	1966/67
Sire-son and sire-daughter	0.01	1.27	1.02	0.98	0.26	0.88	0.61	1.36
Dam-son and dam-daughter	1.34	1.99	0.93	0.53	1.11	0.54	0.29	0.88
Sire-son and dam-son	0.54	4.50	0.67	1.20	2.07	3.17	2.09	1.59
Sire-daughter and dam-daughter	0.79	1.24	2.62	0.75	1.22	1.75	1.77	1.11

calves for the 8 samples are 0.54, 4.50, 0.67, 1.20, 2.07, 3.17, 2.09 and 1.59 years respectively(the difference of 0.54 years in the 1900 sample was caused by the longer sire-son interval). Between the parents of registered heifer calves, the corresponding differences are 0.79, 1.24, 2.62, 0.75, 1.22, 1.75, 1.77 and 1.11 years; these differences may be partly accounted for by the longer breeding life of female stock. There are also substantial differencea between the sire-son and sire-daughter intervals for all samples except that of 1900 and 1940; in two samples (1920 and 1940) the differences were contributed by a longer sire-son interval.

The differences between dam-son and dam-daughter intervals were small only for the 1960 sample. The big differences in the other samples would indicate a general policy of registering bull calves from dams with potentially more performance records than those from which registered heifer calves are saved.

The distributions of the parent-offspring intervals show that the sires were used as 2-to 6-year olds. Thus, in general, breeders are using bulls for about 4 years and then replacing them. Sires ranging from 8 to 20 years-old are also found in the distribution. Presumably, these animals were retained for longer periods in the herds because of their proven genetic merit. The same remark is equally applicable to the dams; they are used mainly from 2 to 8 years old and older.

About 50-56% of the 1966/67 sample animals were sired by bulls 4 years old and younger, while just over 75% were sired by bulls 5 years and younger. The equivalent figures for dams 4 years or 5 years old are approximately 38% and 50% respectively. Therefore, at least half the breeding animals are used before there could be even a subjective evaluation of their progeny and at the age when this information might be available, most of the animals are discarded.

V IMPORTANT HERDS

To determine the important herds, the procedure as outlined by Weiner (1953) was adopted, using pedigrees from the eight sample years, traced completely to four generations. Only the last four generations were considered because herds almost always have a limited duration and those herds that were of immediate importance to the breed in 1966/67 as bull-breeding herds were of relatively minor importance fifteen to twenty years previously. Because fewer herds breed bulls than breed cows only herds represented by males in these pedigrees were considered. Three methods were used:

(1) The total number of appearances of each herd in any of the 15 male positions.

(2) The total score of these male appearances. This score was calculated on the basis of an appearance in one generation being given twice the weight of an appearance in a preceding generation; an appearance in the parental generation (Generation 1) scored 8; an appearance in the grandparental generation (Generation 2) scored 4; and so on.

(3) The total number of appearances of each herd in the sires-of-sires line only.

In this study, only 3 sample years were considered, that is, 1900, 1930 and 1966/67. These three samples are spaced some 30 years apart and it was felt that such a choice of samples would enable some comparison to be made regarding the changes in the importance (with respect to ranking) of certain herds with time.

For convenience of comparison the appearances or scores may be converted to percentages of the total possible appearances or scores. For example, in the 1900 sample 198 Imported sires appeared in the 44 pedigrees.

As there are 15 males in each pedigree, the percentage of Imported sires appearing equals (198/660) X 100 = 30.0. The results calculated in this way are shown in Table 5.13.

In the 1900 sample, there is pretty close agreement, with respect to ranking of the herds, using three different approaches. However, in the other two samples, the correspondence is not as close, especially after the fourth or fifth most important herd. Davey and Barker (1963) have suggested that the importance of a herd is best demonstrated by the total score (that is, method 2) and so this will be the criterion adopted in this study.

In all three samples, Imported is consistently most important, but the importance of the New Zealand herds has changed considerably from one sample to another, with some herds gaining ascendancy while others have decreased in importance or dispersed. For example, in the 1900 sample, Gwavas was the seventh most important herd and by 1930 it was fourth in importance; however, it was dispersed in 1934. Opua (ranked fifth) and Tomoana (ranked sixth), both of which appeared in the 1900 sample were dispersed in 1920 and 1907 respectively. Of the three samples, only one herd (Gladbrook) has persisted, from 1900 through to 1966/67. However, it should be pointed out that this herd (established in 1884 and dispersed in 1918) differs from Gladbrook 2 as the latter herd was founded by the grandson of the original owner(Mr. John Roberts) in 1936, after a lapse of 18 years. Some idea of the duration of the more important herds may be obtained from Table 5.14.

In the 1930 sample, Ben Lomond was second in importance, followed by Turihaua. Since then, Ben Lomond had dispersed while Turihaua has lagged behind and ranks fifteenth in 1969.

TABLE 5.13 : Herds in order of importance for each of the three methods of analysis used to determine the important herds of the New Zealand pedigree Angus

Herd	Per cent of total number of males	Herd	Per cent of total score of males	Herd	Per cent of number of males in sires-of-sires line
1900 Sample:					
Imported	30	Imported	26.1	Imported	34.1
N.Z. & Australian Land Co.	13.8	Matthew Holmes	19.2	Matthew Holmes	29.5
Matthew Holmes	12.7	N.Z. & Australian Land Co.	16.8	N.Z. & Australian Land Co.	20.4
Gladbrook (1)	2.4	Gladbrook (1st)	8.8	Opua	5.7
Opua	1.5	Opua	4.3	Tomoana	2.3
Tomoana	0.9	Tomoana	2.0	Gwavas	
Gwavas	0.3	Gwavas (1)	0.6		
Marainanga	0.2	Marainanga	0.6		
1930 Sample:					
Imported	29.4	Imported	23.8	Imported	18.5
Ben Lomond	9.4	Ben Lomond	8.8	Ben Lomond	14.9
Gladbrook (1)	5.95	Turihaua	6.1	Turihaua	9.5
Turihaua	4.6	Gwavas (1)	5.6	Gwavas	8.3
Gwavas	3.7	Akitio	5.5	Mangatoro	7.7
Akitio	2.7	Gladbrook (1st)	5.1	Gladbrook	7.1
Gladbrook (2)	1.98	Waiterenui	3.2	Akitio	5.4
Marainanga	1.7	Mangatoro	2.7	Waiterenui	4.8
Mount Royal	1.5	Koiro	2.4	Koiro	3.6
Mangatoro	1.3	Springfield	1.6	Fairfield	1.8
Waiterenui	1.3	Tautane		Matapihi	
Woodlands	1.26	Omarunui	1.5	Manganui	
Fairfield	0.95	Woodlands	1.4	Symes	1.2
Koiro	0.8	Gladbrook (2nd)		Omarunui	
Tautane	0.5	Matapihi	1.3	Woodlands	0.6
Matapihi				Gladbrook (2nd)	
Springfield		Fairfield	0.89		
Omarunui		Mount Royal			
Bywell	0.3	Bywell	0.82		

TABLE 5.13 (continued)

Herd	Per cent of total number of males	Herd	Per cent of total score of males	Herd	Per cent of number of males in sires-of-sires line
1966/67 Sample:					
Imported	19.0	Imported	18.9	Imported	22.4
Mangatoro	11.8	Mangatoro	11.1	Mangatoro	12.5
Puketutu	5.5	Puketutu	6.1	Puketutu	6.98
Totaranui	3.3	Totaranui	4.8	Totaranui	5.5
Ngawaka (1st)	3.1	Waiterenui	2.3	Waiterenui	2.94
Waiterenui	1.9	Ngawaka (1st)	2.1	Brookfields	
Brooklands	1.4	Heathfield	1.9	Waiwhero	2.5
Heathfield	1.3	Brookfields	1.5	Gladbrook	2.2
Matapihi	1.2	Balfour	1.4	Balfour	
Balfour	1.0	Cricklewood	1.3	Brooklands	1.8
Cricklewood	1.0	Gladbrook (2nd)	1.26	Kahika	
Turihaua	0.98	Brooklands	1.2	Heathfield	1.47
Gladbrook	0.88	Waiwhero	1.03	Cricklewood	
Mangatu	0.83	Tautane	1.01	Ngawaka (1st)	1.1
Burford		**Turihaua**	0.98	**Turihaua**	
Akitio	0.78	Brackenfield	0.9	Brackenfield	0.73
Brackenfield	0.73	Kahika	0.87	Ribbonwood	
Ribbonwood	0.68	Matapihi		Mangamaire	0.37
Tautane		Ribbonwood	0.75	Matua	
Brookfields	0.63	Akitio	0.53		
Waiwhero		Matua	0.4		
Kahika	0.58	**Burford**			
Mangamaire	0.53	Mangamaire	0.36		
Matua		Mangatu	0.34		

TABLE 5.14 : Years of origin and dispersal of the most important pedigree Angus herds in New Zealand in 1900, 1930 and 1966/67

Herd	Year of Origin	Year of Dispersal
Important herds - 1900		
Gladbrook 1	1884	1918
Opua	1893	1920
Tomoana	1895	1907
Gwavas	1888	1034
Marainanga	1886	1908
Important herds - 1930		
Ben Lomond	1905	1925
Turihana	1906	-
Gwavas	1888	1934
Akitio	1908	-
Gladbrook 1	1884	1918
Waiterenui	1915	-
Mangatoro	1920	-
Important herds - 1966/67		
Mangatoro	1937	-
Puketutu	1927	-
Totaranui	1942	-
Waiterenui	1915	-
Ngawaka (2)	1960	-
Heathfield	1938	-
Brooklands	1919	-

In more recent years, Mangatoro has occupied a position second only to Imported. Indeed, many prize winners have been bred at Mangatoro, and also, many herds have been established and strengthened with Mangatoro females, both in New Zealand and Australia. Some of its stock have even been exported to America. Following behind Mangatoro are Puketutu, Totaranui and Waiterenui (Table 5.13). All four were apparently increasing in importance at this time, with the most significant increase being made by Totaranui and Mangatoro, who, in 1930 lagged behind Waiterenui in importance. In the breed structure analysis, Totaranui (established in 1942) was found to be B.H.(1b), but its bulls were used widely and it probably will become a B.H.(1a) herd.

It is interesting that over the three samples, there has been no concentration of imported males in the sires-of-sires line. However, over the period studied, the importance of Imported has been steadily decreasing. In the 1900 sample, the percentage of total score is less than the percentage of total number, implying that the usage of imported bulls declined over the generations prior to 1900. Since the percentage of total score, as a proportion of percentage of total number for Imported in 1930 (viz. 0.81) is less than this proportion for 1900 (viz. 0.87), the trend apparently increased over this period. Presumably, this was largely due to the reduced number of importations — the early 1920's were not entirely a happy time for the farming community.

A similar analysis for the period from 1930 to 1966/67 showed a reversal of the trend, that is, there was an increase in the use of imported bulls. There was also a tendency to register more sons of imported bulls as 22.4 per cent of males in the sires-of-sires line were Imported in

1966/67, compared with 18.5 per cent in 1930.

The distribution of herds supplying the sires in the four-generation pedigrees of the three samples are shown in Table 5.15. About 9.1% of the herds appearing in the 1900 sample supplied 27.5% of all the sires in the pedigrees. On the other hand, the same percentage of herds have appeared only once. From 1930 to 1966/67, the percentage of sires supplied by Imported decreased from 14.3 to 11.1; further decreases can be expected as a result of the recent decline in importations. Also, in the 1966/67 sample, 45.6% of all the herds supplied one bull each. This five-fold increase over the period sampled is indicative of the growth of the breed, especially in recent years, as this group supplying one bull per herd consists mainly of recently established herds.

The average number of times that Imported bulls were used in these pedigrees can be calculated from Table 5.15. For example, in the 1900 sample, Imported appeared 146 times, but only 14 bulls were used. That is, Imported bulls were used an average of 10.4 times each in the 1900 sample. The corresponding figures for the 1930 and 1966/67 samples are 7.7 and 4.5 respectively, which reflect the greater numbers and availability of imported bulls in more recent times.

TABLE 5.15

Distribution of herds supplying the sires in the four-generation pedigrees of samples of females born in 1900, 1930 and 1966/67

Total No. of Appearances per Herd	1900		1930		1966/67	
	Number of Herds	Number of Bulls	Number of Herds	Number of Bulls	Number of Herds	Number of Bulls
1	1	1	14	14	72	72
2-4	5	6	11	25	45	102
5-9			3	14	16	74
10-19	2	8	6	41	14	135
20-29			2	12	4	57
30-39			1	21	2	40
46			1	18		
62			1	17		
65					1	13
68					1	43
75	1	9				
77			1	22		
92	1	13				
114					1	54
119			1	31		
146	1	14 Imp.*				
232					1	107
277			1	36 Imp.*		
395					1	87 Imp.*
Total	11	51	42	251	158	784
Percentage of animals supplied by Imported		27.5		14.3		11.1

* Imp., imported

A. Genetic Contribution of important herds

As the appearance of a herd in the pedigree is frequently dependent on a previous appearance of that herd in the same pedigree, the total number of appearances is not necessarily a true indication of a herd's importance in the breed structure. For the same reason, a herd's genetic contribution to the breed cannot be estimated in this way. In order to calculate the contribution for the ten major herds to the 1966/67 sample, the method of Weiner (1953) was used. Animals appearing in the eight-line pedigrees described previously were coded to show the herds in which they were bred. At each of the 30 positions in the four-generation pedigrees, the number of appearances of a herd independent of an earlier appearance of that herd was counted. Thus, if a herd appeared in one position in generation 3, and in the same line in generation 4, the appearance in generation 3 would be counted while that in generation 4 would not. The contribution of each herd therefore depends on the number of independent occurrences in each pedigree and the generation in which each occurs. For example, in a sample of 100 heifers, one occurrence of a herd in the parental generation will mean that the herd has contributed 1/200 of the genes in the sample or one half of one per cent. Should one of this animal's parents be born in the same herd, the herd will also appear in the grandparental generation, but since its appearance is not independent of its occurrence in the parental generation, the herd makes no further contribution. Should the other grandparent in the same half of the pedigree be born in a second herd, this herd's contribution to the sample will be 1/400 or one quarter of one per cent, and so on. The genetic contribution of both sires and dams in each generation was then calculated and the results summed to give the total genetic contribution of the herd to the female sample, which is taken as the contribution to the breed in 1969.

The results obtained for the 10 major herds separately, and together with and without Imported, are given in Table 5.16. Only contributions made during the last four generations were considered because herds almost always have a limited duration and those herds that were of immediate importance to the breed in 1966/67 as bull-breeding herds were of relatively minor importance fifteen to twenty years previously. A further reason is that the contribution of herds that were important several generations previously becomes greater further back in the pedigrees. If the latter herds were included, as would be the case if many more than four generations were considered, the total genetic contribution made by all the selected herds could be considerably in excess of 100% of the genes existing in the 1966/67 sample. Therefore, the effect of taking many generations into consideration would be to give the relative importance of herds during the period for which authentic pedigree details were available, whereas interest is centred more on the absolute contributions of individual herds at a particular time.

From the table, the change in genetic contribution for successive generations is indicative of the gain or loss of importance by a herd. Thus, Imported has been steadily declining in importance. Mangatoro, which is second only to Imported, showed a very substantial drop in genetic contribution. Other herds showing a decline include Waiterenui

TABLE 5.16

Genetic contribution of Imported and the nine major herds to a sample of pedigree Angus females born 1966/67

HERD	Total Genetic Contribution %	Genetic contribution (%)							
		Generation 1		Generation 2		Generation 3		Generation 4	
		Males	Females	Males	Females	Males	Females	Males	Females
Imported	42.4	5.8	0.0	11.1	1.1	12.7	2.1	7.9	1.7
Mangatoro	21.9	4.4	0.0	6.4	0.9	4.6	0.3	5.1	0.4
Puketutu	8.72	3.3	1.5	2.0	0.6	0.6	0.6	0.09	0.05
Totaranui	8.70	3.7	0.7	1.8	0.6	1.0	0.4	0.5	0.1
Waiterenui	4.7	0.7	0.7	1.1	0.7	0.5	0.3	0.4	0.3
Ngawaka	3 69	0.0	0.0	0.6	0.4	1.5	0.1	1.1	0.1
Heathfield	3.97	1.5	0.0	0.7	0.6	0.6	0.3	0.3	0.1
Brookfields	4.6	1.5	1.8	1.1	0.2	0.1	0.0	0.0	0.0
Balfour	3.5	1.1	0.4	1.1	0.0	0.6	0.0	0.3	0.0
Cricklewood	2.1	0.7	0.0	0.6	0.2	0.4	0.0	0.3	0.1
Imported + nine herds	66.1	13.6	4.1	15.9	4.1	13.5	3.2	9.6	2.2
Nine herds	44.0	11.2	4.5	10.2	3.6	6.6	1.7	5.4	0.9

and Ngawaka while Cricklewood has remained stationary. The remaining herds listed have been increasing in importance, with Puketutu showing the most pronounced increase.

The 10 major herds had a total combined genetic contribution of 66.1 per cent to the breed in 1969, most of which was contributed by Imported, followed by Mangatoro. The contribution of Imported, independent of the other nine important herds, is only 22%, which implies that the majority of Imported genes in the sample have been introduced through these herds. The importance of Mangatoro to the breed is apparent from the fact that about 22 per cent of the genes in the sample have come through this herd in the last four generations. It will be appreciated that the genetic contribution of the 9 major herds plus Imported combined (66.1%) is not the same as the sum of their individual contributions (104.3%), since to some extent the bulls bred in these herds are used by one or more of the other eight herds.

B. Important Animals

The system of pedigree sampling adopted in this study provides an objective measure of the importance of various ancestors to the breed. This is determined by noting the proportion of lines which pass through or terminate at the animal in each sample. An ancestor which has an important influence on the breed would therefore be expected to appear in many of the random lines and consequently, has a good chance of scattering its genes throughout the breed.

The estimate obtained actually gives the direct relationship to the female sample, which is assumed to be representative of the breed at that time. If an animal with a high direct relationship also has sibs or other collateral relatives which contributed much to the inheritance of the breed, then the total relationship of such an animal to the whole breed would be higher than the results shown.

Table 5.17 shows those animals whose direct relationship to the breed was at least 3.0 per cent in two or more of the samples studied. As expected, the list is dominated by imported animals. The average time from year of birth to the year in which an animal has its highest relationship is about 22 years, but this varies from 10 years (Quetta) to 40 years (Megg Dodds).

The highest direct relationship of an individual animal to the breed at any one sampling date was that of Blackleg, imported from Britain in 1875. This bull was almost a great-grandsire to the breed in 1900; the heifer sample in that year derived about one ninth of their genes from this sire. With such a high direct relationship (11.65%) it would be expected to have a considerable influence in subsequent years. However,

TABLE 5.17

Percentage direct relationship for animals important to the breed in eight sample years

Registration Number	Name of Animal	Year of Birth	Herd	Percentage Direct Relationship							
				1900	1910	1920	1930	1940	1950	1960	1966/67
	SIRES										
95	Oreti	c.1872	Matthew Holmes	3.13	—	—	—	—	—	—	—
94	McKinley	c.1872	Matthew Holmes	5.97	0.36	—	—	—	—	—	—
946*	Robin Hood	c.1874	N.Z. & Australian Land Company	3.98	1.25	0.61	0.45	—	—	0.12	0.10
68*	Blackleg	1874	N.Z. & Australian Land Company	11.65	1.07	0.46	0.30	—	0.13	0.37	—
97*	Knight of the Thistle	1879	Matthew Holmes	3.41	0.36	—	—	0.16	—	—	—
7*	Waterside Eric	1881	N.Z. Agricultural Company	8.81	1.43	0.30	0.45	0.16	—	—	—
99	Nelson	1882	Matthew Holmes	4.26	0.89	—	—	—	—	—	—
2349*	Solomon	c.1883	N.Z. & Australian Land Company	5.68	1.61	1.07	0.45	—	0.13	0.12	0.36
71	Blair Athole	1884	N.Z. & Australian Land Company	3.41	0.18	0.15	0.45	—	—	—	—
21	Solomon II	1885	N.Z. & Australian Land Company	5.68	1.25	0.61	0.45	—	—	—	0.41
101	Black Duke of Killara	1887	Matthew Holmes	7.95	1.25	—	—	—	—	—	—
180*	Baron Arradoul	1890	Gladbrook	3.69	5.89	4.12	2.08	1.27	1.88	0.49	0.18
181*	Lancer of Advie	1892	Gladbrook	5.11	6.79	3.96	3.42	3.96	2.28	0.98	1.55
376*	Fashion's Prince	1899	Gladbrook	—	5.18	5.34	3.13	2.85	2.69	1.47	1.28
429*	Mistral	1899	Gladbrook	—	5.18	5.03	4.32	2.85	4.03	2.21	1.28

* Denotes imported stock

TABLE 5.17 (Continued)

Registration Number	Name of Animal	Year of Birth	Herd	Percentage Direct Relationship							
				1900	1910	1920	1930	1940	1950	1960	1966/67
	SIRES										
423*	Ralph of Careston	1899	Gladbrook	—	2.68	5.18	5.06	3.01	2.42	1.47	1.09
535*	B.B.B.	1903	Marainanga	—	2.50	4.73	2.98	2.53	3.63	2.21	1.73
526*	Eblis of Ballindalloch	1904	Gladbrook	—	2.86	5.03	3.13	4.43	1.21	0.86	0.82
525*	Heathen	1904	Gladbrook	—	1.07	2.29	3.87	2.37	2.15	0.98	1.09
675	Baron of Ben Lomond	1907	Ben Lomond	—	—	1.07	6.25	2.89	2.82	2.45	1.84
689	Duke of Argyle	1907	Gwavas	—	—	0.92	5.13	1.68	3.23	2.70	2.05
850	Dean of Ben Lomond	1909	Ben Lomond	—	—	1.37	4.91	1.44	1.41	1.72	1.03
955*	Moose 2nd	1914	Akitio	—	—	0.46	3.27	3.96	2.15	1.47	0.64
1060	Roderick Dhu	1914	Ben Lomond	—	—	0.30	3.35	3.61	4.84	4.17	2.87
2216*	Hayston Bright Print	1920	Akitio	—	—	—	3.13	3.48	3.36	2.33	1.46
2648	Sentry of Akitio	1922	Akitio	—	—	—	—	3.85	3.63	0.98	1.64
2677*	Eland of Bleaton	1922	Woodlands	—	—	—	0.45	3.80	6.59	4.78	4.20
4303	Acute of Akitio	1928	Akitio	—	—	—	—	2.89	3.63	—	1.64
4607	Ossian of Waiterenui	1929	Waiterenui	—	—	—	—	2.40	4.03	2.94	3.07
8733*	Hayston Elmore	1938	Akitio	—	—	—	—	—	9.27	9.31	7.94
9524	Embassy 5th of Mangatoro	1940	Mangatoro	—	—	—	—	—	1.21	3.92	1.03
14304*	Eulijago of Kilham	1947	Mangatoro	—	—	—	—	—	—	3.92	3.10
17108*	Bruce of Greenyards	1953	Mangatoro	—	—	—	—	—	—	1.35	3.47

TABLE 5.17 (Continued)

Registration Number	Name of Animal	Year of Birth	Herd	Percentage Direct Relationship							
				1900	1910	1920	1930	1940	1950	1960	1966/67
	DAMS										
1P*	Meg Dodds	c.1860	N.Z. & Australian Land Company	3.98	0.18	—	—	—	—	—	—
67	Beatrice	1879	N.Z. & Australian Land Company	3.13	1.07	—	0.45	—	—	—	—
209	Moss Rose	1879	Matthew Holmes	3.13	—	—	—	—	—	—	—
7563*	Bella 1st of Waimea	1882	N.Z. Agricultural Company	6.82	0.36	—	0.15	—	0.13	0.25	—
348*	Quetta	1890	Gladbrook	3.13	2.50	1.83	2.08	0.95	1.88	1.72	0.64
360	Alberta	1894	Middlemarsh	—	3.04	2.29	1.79	1.44	1.21	0.49	—
495	Quetta 3rd	1895	Gladbrook	2.27	0.54	1.68	3.80	1.92	2.42	1.23	1.64
727	Fame	1902	Gladbrook	—	—	0.46	3.13	1.68	1.01	1.96	0.82
957	Flower	1902	Gladbrook	—	0.18	1.22	4.24	2.89	3.43	2.21	1.84

its influence declined sharply in 1910. Further decreases followed and in 1940, not a single line could be traced to Blackleg. Its direct relationship to the breed increased slightly in 1950 (0.13%) and 1960 (0.37%) but thereafter, fell to zero in 1966/67.

Overall, the most important animal to the breed over the period 1900-1966/67 was Lancer of Advie which was imported from Britain in 1893. In fact, the relatively large contributions of importations during the period 1863-1896 is due mainly to the importance of Lancer of Advie. This bull has, however, declined steadily in importance after reaching a peak in 1910. In 1966/67 the direct relationship of this sire to the breed was established at 1.55%. In other words, about 1 in every 70 genes in the breed is probably derived from Lancer of Advie. Clearly, individual animals had more opportunity to become important in the breed during the early years when the breed was small in numbers. Relatively few of the later importations attain a direct relationship of 3% to the breed and these include Eulijago of Kilham and Bruce of Greenyards.

Owing to fewer offspring, cows do not have the same chance as bulls to attain high direct relationships. The most important cow was Bella 1st of Waimea (imported 1882) with a direct relationship to the breed of 6.82% in 1900. Other important cows include Quetta (imported 1892), Quetta 3rd, Flower and Alberta. It is significant that fewer cows appear in Table 5.17 despite the relatively large numbers of females imported during the early phase of the breed's development in this country. The list of important dams was dominated by animals imported or born between 1863 and 1902. The cows in subsequent importations did not have as much influence on the breed as did their predecessors.

A number of the dams listed owe their individual importance to popular descendants rather than their own popularity. For example, Fame is important because her son Baron of Ben Lomond was popular; a large proportion of the lines trace back to Fame through Baron of Ben Lomond. Similarly, Flower owes her importance to the popularity of her son, Dean of Ben Lomond. Indeed, many of the animals appearing in the upper part of Table 5.17 are ancestors of those in the lower half.

CHAPTER 6

BREED STRUCTURE

It may be surmised from what has been written (Lush, 1943, 1946) that some form of 'functional stratification' of pure-bred herds exists in most breeds of domestic livestock. The theoretical implications of this are summarized by Lush, who states that

> "the reduction in effective size of the population which such stratification causes, will largely increase the chance changes in gene frequency instead of the systematic changes caused by selection, although there will be some of the latter to the extent that stratification is based on the apparent merit of the animals in the herds."

The method of analysis adopted in the present study was that outlined by Wiener (1953) and later modified by Barker (1957). It involves following back the pedigrees of registered animals to find out in which herds ancestors have been bred. Data for this study were abstracted from Volume 61 (which includes all New Zealand herds registering from 30th July 1968 to 31st July 1969) of the New Zealand Aberdeen Angus Herd Book. All herds registering in this year were listed by their stud prefixes, together with the numbers of bulls and heifers registered by each, as well as the stud prefixes of the bulls used in each.

From these data were obtained the number of herds that registered

(i) females only

(ii) males and females and

(iii) the occasional male and no females; this last group is small and usually contains small herds or ones recently dispersed. A further classification is used which to some extent cuts across the division of herds made above. Here the fate of the animals bred is the criterion. The two major categories of herds which result are:

(a) Breeders' Herds - herds which have bred bulls appearing as sires in other pedigree herds in the data analysed.

(b) Multipliers' Herds - herds whose bulls have not appeared as sires in other pedigree herds in the data analysed. Bulls bred by these herds may have been used in the herd in which they were bred and have been used, presumably, in grade herds.

The only real difference among the categories (to be discussed shortly) forming the latter group is that the multiplication process differs in intensity. The herds in each of the two major categories of pedigree herds can be placed into a number of strata depending on their importance as a source of breeding material for the rest of the breed and also on their registration practices. For example, the Breeders' Herds can be subdivided into four strata. B.H.(1) are those at the top of the structure, B.H.(2) and B.H. (3) are intermediate strata and B.H. (4) are those that did not have their bulls used in other Breeders' Herds but whose bulls were used by Multipliers' Herds.

On the basis of the two categories as defined earlier, the 483 herds (in the 1969 Herd Book) can be subdivided into 105 Breeders' Herds (comprising the 4 categories outlined above) and 378 Multipliers' Herds. Of the 105 Breeders' Herds, 80 of them did not have their bulls appearing as sires in other Breeders' Herds. However, these 80 herds did contribute sires to the Multipliers' Herds. These 80 herds comprise the B.H. (4) stratum. The remaining 25 herds were analysed to find in which other Breeders' Herds (within that group of 25) their bulls had been used. It was found that 11 of these herds had their sires used by other Breeders' Herds. Hence, 14 herds were assigned to B.H. (3). The same process was repeated on the remaining 11 herds to obtain the herds in the two higher strata, B.H. (1) and B.H. (2) (see Figure 6.1). B.H. (1) was further subdivided into two sections: B.H. (1a), the major breeders' herds, and B.H. (1b) - herds in this category differ from those of B.H. (1a) in that their bulls were not used in the next stratum B.H. (2). There was, however, some reliance by B.H. (1b) on B.H. (1a) herds for sires.

The subclassifications of the Multiplier Herds (378 altogether) are more arbitrary and are based mainly on registration practices. They are as follows:

(i) M.H.(H) - herds that registered males, but whose bulls were used only in the herd in which they were bred, and presumably, in grade herds.

(ii) M.H.(N) - herds that registered males, but whose bulls did not appear as sires in any pedigree herd, thus distinguishing them from the B.H. and M.H(H) classifications.

(iii) M.H.(S) - herds that did not register males, and that did not appear among the B.H. OR M.H.(H).

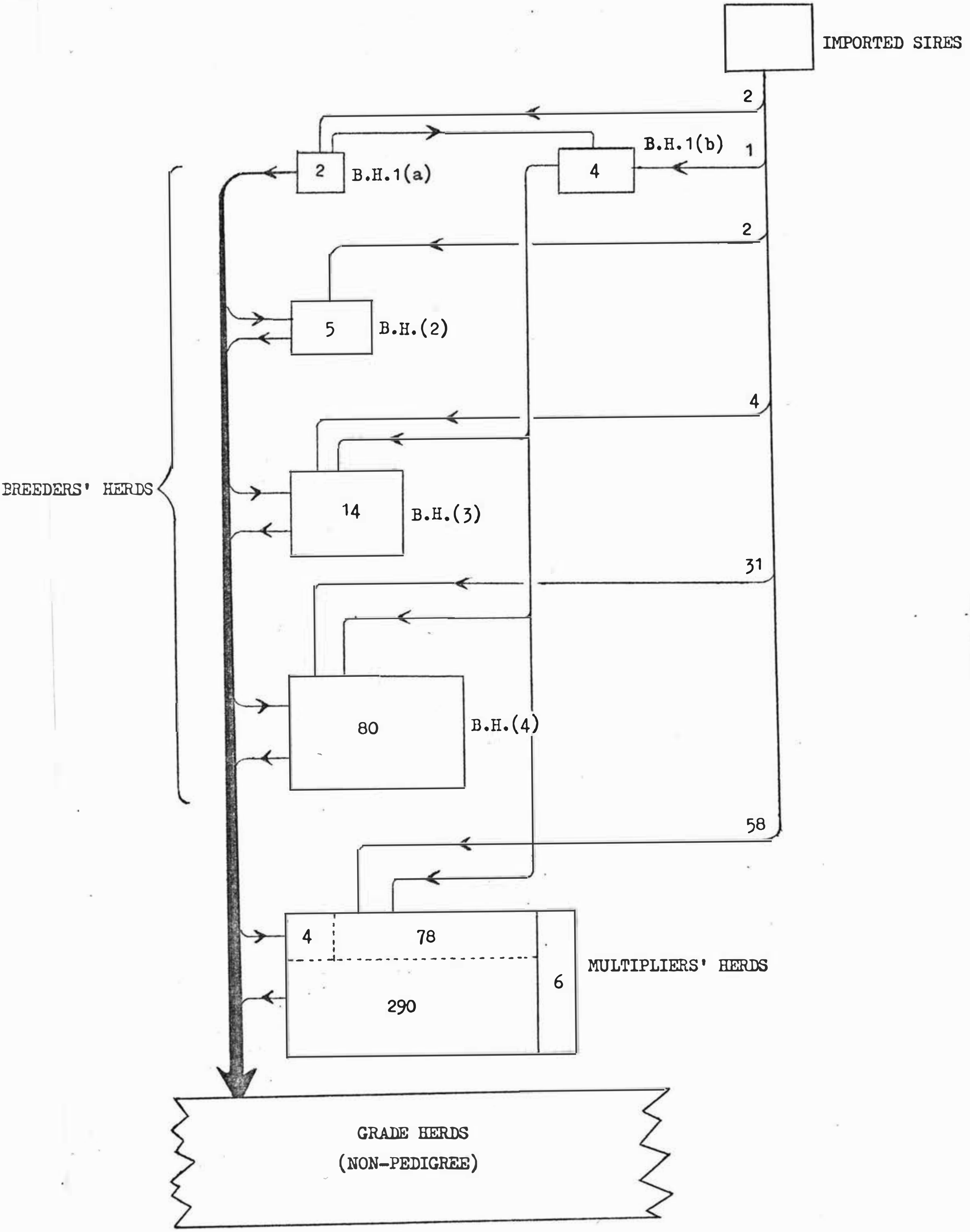
(iv) M.H.(M) - herds that registered males only.

Except for the home-bred bulls used in M.H.(H), the sires used in the Multiplier's Herds were bulls purchased from one or more of the

FIGURE 6.1

Diagrammatic representation of breed structure based on registration data in volume 61 of the New Zealand Aberdeen Angus Herdbook.

The figures in each block are the number of herds in that stratum that registered animals in the volume analysed. The top stratum is B.H. (1a) and B.H. (1b), the second is B.H. (2), etc. The figures on the lines from Imported sires are the numbers of herds in each stratum using these sires.


IMPORTED SIRES
2
1
B.H.1(b)
4
2
B.H.1(a)
2
B.H.(2)
5
4
14
B.H.(3)
31
80
B.H.(4)
BREEDERS' HERDS
58
4
78
290
6
MULTIPLIERS' HERDS
GRADE HERDS
(NON-PEDIGREE)

Breeders' Herds. Sires used in the Breeders' Herds were home-bred or purchased from another Breeders' Herd in the same or a higher stratum.

The breed structure obtained is shown in Figure 6.1. Briefly, the top stratum consists of a small self-contained group of herds supplying sires to each other and to herds in any stratum below it. The second stratum obtains sires from the top stratum only, but supplies sires to herds in any stratum below it. Likewise, the third stratum obtains sires from either of the top two strata and supplies to any below it, and so on. Differences between herds in the top and lower strata are largely determined by the number of strata through which genes have passed. Many breeders of grade cattle purchase their sires from the top group of herds and this short-circuiting may well result in many of the bulls in high grade herds being genetically superior to many of those born in herds in the lower pedigree strata. Because of changes over time, it is unlikely that the actual structure of the breed is as rigid as the diagram suggests; in fact, there are some herds which would be difficult to place exactly. Therefore, 'stratification' of herds in the Angus breed should not be visualized as a hard and fast division, but rather as several functional stages within the one population.

It should be stressed that the breed structure as indicated in no way reflects the actual genetic differences between herds. For example, the stratum into which any herd falls will depend on whether the breeder is able (or prepared) to turn his herd into a 'breeders' herd'. It must also depend on the willingness of other breeders to recognize the superiority, real or imagined, of one or more of their contemporaries.

Since many sires are bought from other herds and little improvement is possible by culling females, it follows that the great majority of breeders are relying on somebody else to do the job for them. So, each stratum depends on those above it to effect genetic improvement and the whole breed is therefore graded to the top stratum. Consequently, unless the top herds are constantly improving, whatever genetic superiority they may possess at any time is being continually reduced by the use of their bulls in the lower strata.

CHAPTER 7

REGISTRATION PRACTICES

In a rapidly expanding breed such as this, it would be expected that practically all females reared would be registered. This is not the case for males, and there is some selective registration of bull calves which is essentially culling of males from the pedigree breed. Over the period of time considered objective measures were seldom, if ever, employed by pedigree breeders in the selection of breeding animals. Moreover, the selection of males for registration would have largely been subjective, determined by conformity with breed type. Nevertheless, it does represent selection being applied by the breeders; animals considered of insufficient desirability being eliminated from the pedigree section of the breed. The ratio of females/males registered is then a direct measure of the degree of this selective registration of males.

The registration practices of the various strata are shown in Table 7.1. The average number of females registered per herd is an indication of herd size, as most females born probably will be registered. The most important herds (B.H. (1a)) are also, on the average, the largest herds, and average herd size decreases in order of decreasing importance of the strata. In the breed as a whole, over nine-tenths of the males born are not registered. The ratio of females to males registered is lowest for B.H. (1a) herds, which implies that these herds can dispose of most of their male progeny as registered animals. This is to be

TABLE 7.1

Herd types and registration practices of herds registering in volume 61 of the New Zealand Aberdeen Angus Herd Book

Type of Herd	Herds			Males Registered		Females Registered		Average No. of males registered per herd	Average No. of females registered per herd	Ratio females/ males registered
	No.	% of total	No. registering females only	No.	(%)	No.	(%)			
Breeders' Herds (1a)	2	0.41	—	42	6.92	114	1.77	21	57.0	2.7
Breeders' Herds (1b)	4	0.83	—	22	3.62	133	2.07	5.5	33.3	6.0
Breeders' Herds (1)	6	1.24	—	64	10.54	247	3.84	10.7	41.2	3.9
Breeders' Herds (2)	5	1.04	—	26	4.28	124	1.93	5.2	24.8	4.8
Breeders' Herds (3)	14	2.90	—	48	7.91	243	3.78	3.4	17.4	5.1
Breeders' Herds (4)	80	16.56	1	277	45.63	1568	24.40	3.5	19.6	5.7
Multiplier Herds (H)	4	0.83	—	5	0.82	55	0.86	1.3	13.8	11.0
Multiplier Herds (N)	78	16.15	—	178	29.32	1094	17.03	2.3	14.0	6.1
Multiplier Herds (S)	290	60.04	290	—	—	3094	48.16	—	10.7	—
Multiplier Herds (M)	6	1.24	—	9	1.48	0	0	1.5	—	—
Total	483	100	291	607	100	6425	100			
Average								1.3	13.3	10.6

expected as these are the major herds, that is, they are the most popular herds, and consequently their animals are sought after by other pedigree breeders. The average ratio increases with decreasing order of importance among the breeders' herds, except for B.H. (1b) which has the highest ratio. Over all strata, the highest ratio is shown by M.H.(H). The M.H.(S) herds, registering no males, are mainly small herds not considered of importance by other breeders. Presumably, they sell bulls to commercial herds, and do not consider it worthwhile to register these animals.

I HERD SIZE

The B.H. (1), (2), (3) and (4) are analyzed in detail in Table 7.2, using the number of female registrations per herd as an indication of herd size. Some allowance must of course be made for year-to-year fluctuations in numbers registered and for the fact that herds significant some years ago may have been dispersed or become less fashionable or popular by 1969-the year to which the last two tables refer. The importance of the 105 breeders' herds (21.7 per cent of all herds) is shown by the fact that they registered 68.5% of all males and 34.0% of all females. The distribution of herd sizes is also not very different from that shown in previous analyses of pedigree cattle breeds. In the present study the majority of herds have been shown to fall within the limitations of 1-20 cows (representing 13.6% of total breeders' herds). A disconcerting feature among those herds registering 10 or less animals is the low ratio (2.2) of heifers to bulls registered. There

TABLE 7.2

Analysis of Breeders' Herds (1), (2), (3), and (4) by numbers of females registered in volume 61 of the New Zealand Aberdeen Angus Herd Book

Female registrations per herd	Herds No.	Herds % of total	No. of males registered and per cent	No. of Females registered and per cent	Average No. of males registered per herd	Average No. of females registered per herd	Ratio females/males registered
51 and over	8	1.7	88 (14.5)	625 (9.7)	11.0	78.1	7.1
41-50	2	0.4	13 (2.1)	98 (1.5)	6.5	49.0	7.5
31-40	6	1.2	17 (2.8)	211 (3.3)	2.8	35.2	12.4
21-30	23	4.8	84 (13.8)	568 (8.8)	3.7	24.7	6.8
11-20	34	7.0	135 (22.2)	513 (7.9)	3.9	15.1	3.8
0-10	32	6.6	79 (13.0)	171 (2.7)	2.5	5.3	2.2
Total	105	21.7	416 (68.5)	2186 (34.0)			
Average					3.9	20.8	5.3

are two possible reasons for these small breeders registering such a high proportion of bulls to heifers. Many small herds belong to "new" breeders who endeavour to recover investments in their foundation pedigree stock as quickly as possible by the sale of pure bred bulls. Other small herds may belong to breeders of long standing, but they need to sell as many bulls as possible because of the high cost of their herd sires. The small breeder's selection difficulties are thus accentuated by financial considerations.

Donald and Itriby (1945), in discussing the significance of herd size in cattle, point out that small herds are seriously hindered in constructive breeding. The importance of random gene frequency fluctuations - one of the major difficulties in selective breeding - varies inversely as the number of breeding animals. Moreover, the smaller the herd, the more difficult it becomes to progeny test and to use the information obtained to best advantage. In one or two sire herds, as is often the case in the majority of pedigree herds, it is also hardly possible to discriminate promptly against an unsuccessful sire by disposing of all his progeny. So, it is clear that the majority of pedigree herds in New Zealand cannot follow any consistent breeding policy of their own, but act as multipliers of bulls bought from a very few important herds - multiplication being a necessary function of a proportion of herds in any breed of animals with a low reproductive rate.

It must also be realized that when the breed is structured into so many very small herds, and where A.I. is not practised, then a greatly increased number of bulls is needed for purebreeding with a consequent reduction in their quality (by whatever criterion quality is judged). While the existence of many small multiplier herds (they comprise some 78% of total herds in the 1969 registrations), each with its own bull, does not reduce the rate of genetic progress in the breed, it does lower the average quality of those sold by increasing the improvement lag within the breed (Bichard, 1971).

Within the smaller herds (those registering 30 or less females) shown in Table 7.2, it was found that selective registration increases as herd size increases. However, the relationship between herd size and the ratio females/males registered is not as simple for the larger herds (those registering 31 or more females). These herds have a ratio of 7.9, so that they are selectively registering only about one-eighth of the males born. In contrast to the smaller herds selective registration here decreases as herd size increases. Of the 16 herds comprising this latter group, the B.H. (1a) and B.H. (1b) strata each has one herd, 2 are B.H. (2), one is B.H. (3) and the remaining 11 are B.H. (4). The ratios for these strata are respectively 3.0, 6.7, 11.9, 4.8 and 11.1. The evidence here would suggest that within the top two strata of the Breeders' Herds, those lower in the breed structure are practising more selective registration. A similar trend persists, traversing from B.H. (3) and B.H. (4).

The smaller herds (registering up to 30 females) show a quite different pattern. The ratios for the different strata are B.H. (1a) 1.8, B.H. (1b) 4.7, B.H. (2) 2.2, B.H. (3) 5.1, and B.H. (4) 4.3. As indicated earlier (Table 7.1) the four B.H. (1b) herds show a high degree of selective registration, but among these smaller herds, the B.H. (3) also show this trend and may simply mean that they have not the market for registered males.

II THE USE OF IMPORTED STOCK BY NEW ZEALAND HERDS

The percentage of herds in each stratum using imported animals is shown in Table 7.3. All the B.H. (1a) herds use imported sires. In comparison, there is less emphasis by B.H. (1b) and B.H. (2) (25% and 40% respectively) on imported sires. However, little value can be placed on the figures obtained for these 3 strata since there are very few herds within each of these 3 categories. The herds in both the B.H. (1a) and (1b) strata share the same emphasis with regard to the use of imported dams. The breeders' herds in the remaining strata are apparently concentrating more on imported sires to increase their popularity since only a small percentage of herds in these strata use imported dams. Overall, the New Zealand Pedigree Angus is still depending very largely on imported animals for its development, as 20.5% of all herds use imported sires.

The ratio of females/males registered has been analyzed for B.H. (1), (2), (3) and (4) herds, classified according to whether or not they used imported sires. For all these herds, the ratios are 4.4 and 6.2 respectively. For the separate strata, the ratios for herds using imported sires are: 2 for B.H. (1b), 2.5 for B.H. (2), 4 for B.H. (3) and 5.4 for B.H. (4). Again, there is a general tendency among these herds for those lower in the structure to show increased selective registration of males. The ratios for herds not using imported sires are B.H. (1b) 6.9, B.H. (2) 10.9, B.H. (3) 6.0 and B.H. (4) 5.9.

TABLE 7.3

Numbers and percentages of herds in each stratum using imported sires and dams

Breed structure classification	No. of herds	Herds using imported sires		Herds using imported dams	
		No.	%	No.	%
B.H. (1a)	2	2	100.0	1	50
B.H. (1b)	4	1	25.0	2	50
B.H. (2)	5	2	40.0	1	20
B.H. (3)	14	4	28.6	1	7.1
B.H. (4)	80	32	40	11	13.8
M.H. (H)	4	1	25	0	0
M.H. (N)	78	15	19.2	3	3.8
M.H. (S)	290	39	13.4	1	0.3
M.H. (M)	6	-	0	0	0
All herds	483	99	20.5	21	4.3

Among these herds, B.H. (2) show the highest degree of selective registration of males. In general, the trend is towards a smaller ratio, or lower degree of selective registration, in those herds using imported animals. This could mean that such herds can more readily sell males as registered animals and consequently their importance is likely to increase.

III THE USE OF BULLS FROM PROMINENT NEW ZEALAND HERDS

The numbers of herds in each stratum using bulls from B.H. (1) herds are shown in Table 7.4. Mangatoro and Puketutu are the herds having the most influence on the breed. Bulls from B.H. (1) herds are used in herds at all levels of the structure so that the genetic differences between herds and the time taken for any genetic changes being made in B.H. (1) herds to be passed down through the breed will be less than in a classical hierarchy where breeders purchase animals only from other herds in their own stratum, or from the next highest one. Genetic differences between herds may be even less than one might expect, because of the very extensive movement of animals from herd to herd. This has been analysed from the random sample animals (as discussed in Chapter 4) in terms of the percentages of sires and dams bred in herds other than the one in which they are used. The results are given in Table 7.5.

TABLE 7.4

Numbers of herds in each stratum using bulls from B.H. (1) herds

Herd Name	Numbers of herds in which bulls have been used						
	B.H.(1a)	B.H.(1b)	B.H.(2)	B.H.(3)	B.H.(4)	M.H.	Total
B.H. (1a) herds							
Mangatoro	1	1	1	2	17	68	90
Puketutu	-	-	1	-	5	30	36
B.H. (1b) herds							
Purunui	-	-	-	1	2	2	5
Te Ohu	-	-	-	-	-	2	2
Turihaua	-	-	-	1	-	5	6
Woodley	-	-	-	-	1	1	2

TABLE 7.5

Percentages of sires and dams bred in herds other than the one in which they were used, in eight samples of the pedigree Angus breed in New Zealand.

Sample Year	Per cent of Sires	Per cent of dams
1900	59.1	9.1
1910	82.5	68.6
1920	70.7	34.1
1930	71.4	41.7
1940	75.9	36.7
1950	81.7	24.7
1960	81.4	43.1
1966/67	80.3	36.5

These figures for sires are generally comparable with previous studies (Robertson and Asker, 1951; Barker, 1957; Barker and Davey, 1960 and Davey and Barker, 1963) while those for dams are intermediate between those found in studies of the Jersey and Polled Hereford breeds in Australia (Barker, 1957; Barker and Davey, 1960).

IV HERD DURATION

Because cattle reproduce slowly relative to the working life of a breeder, time is obviously a factor of major importance. A study has therefore been made of the duration of breeding effort of the New Zealand pedigree Angus breeders. Two methods of approach have been adopted. The first consisted in obtaining a list of herds which were established during fixed periods of time and then determining how long each herd lasted. The second involves working backwards from herds in existence in 1969 to determine how long ago each of them had been founded.

Inspection of Table 7.6 shows that about two-thirds (as compared to 73% in the defunct herds) of the breeders in the 1969 Herd Book had been breeding stock for 15 years or less. It could well be that a considerable proportion of these herds may consist of animals which have either been purchased relatively recently or whose parents have been purchased. Thus, there has been insufficient time to develop and carry out a breeding programme.

Of the present herds, only 13 have been in existence for 46 or more years. The fact that a herd has been established for a long time is, of course, no guarantee that any constructive breeding has been done. For example, it is expected that the progress made by individual breeders would be maintained and added to by their successors. But in practice, of the several individual efforts, successes may well be largely counterbalanced by failures. This is because a change of herd ownership may be accompanied by a change in selection objectives so that whatever improvement there may have been may be negated by the efforts of the new owner. It is therefore reasonable to surmise that few breeders can hope to build

TABLE 7.6 : Percentage distribution of Angus breeders distributed according to duration of breeding effort.

Duration (years)	Herds now defunct		Present Herds	
	Number of Herds	Per cent of total	Number of Herds	Per cent of total
1 - 5	25	20.2		
6 - 10	43	34.7	188	34.5
11 - 15	23	18.5	173	31.7
16 - 20	10	8.1	50	9.2
21 - 25	16	12.9	40	7.3
26 - 30	4	3.2	25	4.6
31 - 35	1	0.8	39	7.2
36 - 40			9	1.7
41 - 45			8	1.5
46 - 50	2	1.6	3	0.6
51 - 55			5	0.9
56 - 60			1	0.2
61 - 63			4	0.7
TOTAL	124	100.0	545	100.0
AVERAGE HERD DURATION	12 years		16.5 years	

up and maintain genuinely superior herds in the face of the obstacles presented by small numbers (as pointed out in a previous section) and short herd-duration.

CHAPTER 8

DISCUSSION

As this study refers to a breed rather than individuals, it follows that the results obtained, and hence the picture presented of the entire breed, is to some extent dependent on the sampling process involved. Therefore, this is a factor to bear in mind for interpretations and conclusions to be in their proper perspective. Even in the most carefully conducted breed association, errors do creep into their pedigree records. Such errors would affect the conclusions from a study like this in different ways according to whether they were errors resulting either from carelessness or from fraudulent registration. However, few, if any, breeders today would fraudulently alter the pedigrees of their stock whereas errors in the records resulting from carelessness or neglect are much more common and are greatly increased if registration of animals is long delayed after their birth. Such errors would, for instance, tend to make prominent ancestors appear less prominent than they really were, merely because the prominent ancestors are few and the alternatives which may result from a clerical or typographical error are many. In the same way, such errors would tend to minimize the inbreeding and *inter se* relationship coefficients.

Errors arising from false registration would tend to affect the conclusions in the opposite direction since, wherever false statements were made it is likely that the registration numbers of popular sires or dams would be substituted. The effect of these two kinds of errors are in opposite directions, although it is unlikely that they are of equal magnitude. At any rate this study of the Angus breed has shown little influence even by the most prominent sires and only a moderate amount of inbreeding. If there were very many fraudulent registrations then the true situation must be that these individual animals have had even less influence than the figures indicate and that the actual amount of inbreeding in the breed is even less than was found.

The present study has shown that the New Zealand Angus breed is rapidly increasing in numbers and that one consequence of this is a somewhat diffuse but dynamic breed structure. The basic pattern of a structure similar to that found in other breed studies (Robertson and Asker, 1951; Stewart, 1952; Stewart, 1955; Barker, 1957; Barker and Davey, 1960, and Davey and Barker, 1963) has already developed, but there are a large number of multiplier herds registering females only, designated as M.H.(S). Some of these are newly established herds that have yet to find their level in the structure. Further, the analysis of important herds (Table 5.13) shows that these herds have changed their importance from one sample to the next. These changes in the relative ranking of herds and the number of herds in each stratum will presumably not affect the pattern of the structure.

The high ratio of females to males registered (Table 7.1) means that overall there is considerable selective registration of males. It has also been shown that there is a variation in the degree of this selective registration in different herd types.

Because of the breed structure and the use of bulls from B.H.(1) herds at all levels of this structure (Table 7.4) and because of the high percentages of sires and dams bred in herds other than the one in which they were used, it does not appear likely that much of the variation between herds would be genetic. It may also be surmised that genetic differences between herds in beef production characters, as for example, growth rate, may even be less than might be expected because among pedigree breeders, whatever selection that has been practised is based largely on subjective rather than objective criteria.

It is shown (Table 7.3) that the important herds in the breed structure have all used imported sires; 20.5% of all herds used such sires, and 4.3% used imported dams. This emphasis is further exemplified by the numbers of non-current inbreeding and *inter se* relationship ties contributed by such animals (Table 5.8), and in the analysis of the important herds of the breed. The latter suggests, however, that this reliance on imported breeding stock has been delcining steadily for some years (Table 5.13). In view of the considerable reduction in importations in recent years, breeders will now have to rely on the genetic material already available here - indeed, there should be a considerable gene pool by now to serve the needs of breed improvement in New Zealand. Besides, a policy of continued importation is, in a sense, a confession of failure on the part of the New Zealand breeder.

Some of the periods of importation clearly owe their importance in part to a few individual animals. This is particularly so in the case of the Foundation Stock and Lancer of Advie, Mistral, Fashion's Prince, Ralph of Careston and Baron Arradoul. However with the expansion of the breed it becomes difficult or even impossible for any one sire to secure such a pre-eminent reputation as it would have in a smaller breed. Hence, the inbreeding resulting from a general desire of many breeders to seek sons of particular sires to head their herds also falls off in amount. Partially opposing these two tendencies is the increased practice of deliberate line-breeding which many breeders undertake; this may perhaps occur to a greater extent in future owing to the decline in importations.

The prominent animals in the New Zealand pedigree Angus breed have direct relationships that are lower than that reported overseas (see Appendix VIII) and clearly demonstrates the lack of influence of any particular outstanding individual in the breed. The high rate of importation no doubt helped to prevent the development of high relationships as no one animal appears to have been singled out for line-breeding. This would be in marked contrast to, for instance, the Shorthorns (as reported by McPhee and Wright, 1925) where the relationship of the breed to the bull Favourite, rose to over 44% some 17 years after he was born and to 50% by the time the first herd book was published. The Shorthorn breed also had a relationship to the bull Champion of England, of about 45% by 1920.

That so many of the pedigress trace back to so few individuals in this and other studies is no evidence in itself that any particular foundation animal confers more merit upon his later descendants than any other. Nor is the fact that the apparently outstanding animals, with a marked influence in the breeds, are frequently males any direct evidence that the male has a greater influence than the female. As individuals the males have greater numbers of offspring and can be culled more heavily than the females. It is usually only when a dam has several sons that become widely used (e.g. the Holstein-Friesian cow De Kol 2nd - Lush, Holbert and Willham, 1936) that she can have any appreciable influence as shown by her frequency in the pedigrees of far-off descendants.

The levels of inbreeding found in the present study are about the same as in other breeds (see Table 3.4) of livestock, especially when considered as the average amount per generation (the general increase in homozygosity arising from inbreeding is about 0.5% per generation). The expectation that the relatively small number of foundation animals would lead to an unusually high amount of inbreeding was not borne out by the data. However, inbreeding was found to have been more intensive during the formative period of the breed than later. This could be the result of a tendency among the early breeders to linebreed to certain animals and this may also have been greatly facilitated by the relatively small number of herds present at that time. Furthermore, distance between herds would partially prevent completely random mating in the breed.

At present, the inbreeding coefficient is only 1.8% (1966/67) which is somewhat lower than estimates from other studies. It is reasonable to assume that if the base data for this study had been chosen to correspond to that in other studies, the amount of inbreeding found might have been nearly the same. This 1.8% inbreeding represents a decrease in heterozygosity of only 0.1% per generation during the 103 years from 1863 to 1966/67. This amount of inbreeding per generation is extremely mild and to put it into perspective, it may be contrasted with the 12.5% loss of heterozygosity per generation to be expected under half brother-sister mating. At the present rate, it will take some 600 years to change homozygosity as much as it would be changed by one generation of half brother-sister mating! Therefore, the rate of inbreeding found would be a powerful force if it occurred in nature over the long stretches of geologic time, but within the active lifetime of an average breeder, would accomplish very little.

It has previously been estimated (Chapter 5, Section II) that if mating was entirely at random, only about 125 bulls would have been needed to cause an increase of inbreeding at the rate found in the breed today (see Table 5.6). In practice, far less than 125 take so active a part that they exert a distinct influence on the breed even some generations after their death. In many instances (especially in pedigree breeding) particular sires may be favoured because of show-ring performance, successful breeding history or any other whims and fancies of the day. This leads to a further reduction in the effective number of males. It is of interest to reflect on the consequences of such a reduction.

Apart from its relation to reduction in heterozygosity, restricting the numbers of breeding animals may have an insidious effect. The effective size of a breeding population, N (Wright, 1931) is not just a matter of the number breeding at any time, but is also related to the number of present animals whose descendants will make up the breed or population in the future. In a small isolated herd or breed for instance, the future population might be descended exclusively from only very few of the animals now breeding, so that the future genetic situation would be derived from only a very small sample of the present one. Consequently, the opportunities for future selection would then be restricted; the population gene frequency would tend to drift purely as a result of random gene sampling and any deliberate selection would be less effective. Whether any of the small breeds present today have reached such a state is a matter for concern, as also is the number which might be approaching this dilemma.

To sum up, it is clear that importations have made a considerable contribution towards the establishment and improvement of the Angus breed in New Zealand. In fact, the major emphasis in breeding policy in this breed has been on the use of imported animals, their genetic contribution to the 1966/67 sample being 85.4%. This is particularly striking, as imported bulls comprise only 0.80% of all male registrations since 1863, and imported cows 0.13% of all female registrations. However, it is doubtful whether there is much more to be gained from further importations. In the 1969 registrations for example, the percentage of genes derived from importations since 1955 amounts to only 9%.

Another aspect to consider concerns the breed structure. It should be such as to allow rapid dissemination throughout the breed of any genetic progress made in the major breeders' herds. This requirement is met, provided that progress is being made in these herds. Since the major breeders' herds have in the past depended on imported animals, the ability of these herds to effect genetic improvement in the breed will depend on whether those imported animals are genetically superior to New Zealand stock. It is questionable whether they are because the rate of importation and dissemination of imported genes has been such that the New Zealand-bred Angus cattle would have been graded up to the level of imported stock.

As brought out in previous discussion (Tables 7.2 and 7.6) both the size and duration of most pedigree herds are ill-adapted to the task of constructive breeding. This therefore represents an obstacle to genetic progress. With regard to the genetic merit of the New Zealand pedigree Angus herds, it must be remembered that the scope of the present study does not allow any definite statements to be made. To date, some 43% of New Zealand pedigree Angus herds (C. A. Morris, personal communication) have enrolled in Beefplan. It will be possible to ascribe some meaningful estimates of genetic differences to these herds and relate them to the breed structure classification already outlined, if they could be persuaded to use some common reference sires through AB. Genetic herd differences would be estimated by comparing the progeny of home sires with those of the reference sires (using balanced groups of cows as mates for each bull). Use of reference sires would also show up unregistered bulls of high genetic merit.

Perhaps it may also be possible then to draw pedigree breeders' attention to the fact that there is considerable merit in having open rather than the closed herd books which are typical of most breeds in New Zealand. It is encouraging to note that many breed societies in Europe have open herd books which not only allow the entry of animals of superior performance, but also the culling of animals of below average merit. At worst, open books may allow a small possibility of undesirable genes being introduced. However, their chief effect is to permit favourable genes to be admitted through the high grades qualifying for entry. Furthermore, selective registration demanding superior qualifications on the part of the grades approaching admission would form a useful filter.

In the New Zealand context, having open herd books would enable the as yet untapped genetic potential of the non-registered cattle population to be exploited. This in fact is essentially the rationale behind group breeding schemes now in operation.

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APPENDIX I : Number of male and female registrations in each volume of the New Zealand Angus Herd Book

Volume	Males	Females	Total	Volume	Males	Females	Total
1	20	47	67	35	593	1584	2177
2	103	206	309	36	567	1763	2330
3	109	160	269	37	644	1737	2381
4	100	148	248	38	604	2007	2611
5	192	212	404	39	693	2054	2747
6	145	270	415	40	599	2172	2771
7	119	181	300	41	564	1945	2509
8	97	175	272	42	583	2164	2747
9	69	228	297	43	487	1888	2375
10	97	337	434	44	530	2122	2652
11	342	1459	1801	45	559	1881	2440
12	507	594	1101	46	606	2471	3077
13	293	450	743	47	632	2616	3248
14	183	390	573	48	581	2398	2979
15	175	517	692	49	808	2849	3657
16	187	408	595	50	872	3315	4187
17	224	510	734	51	777	3418	4195
18	239	524	763	52	823	4226	5049
19	276	599	875	53	799	3658	4457
20	358	557	915	54	727	4344	5071
21	319	632	951	55	761	4643	5404
22	397	791	1188	56	792	4999	5791
23	367	713	1080	57	705	5009	5714
24	308	605	913	58	771	3961	4732
25	216	604	820	59	642	5947	6589
26	196	856	1052	60	546	6401	6947
27	325	753	1078	61	618	6580	7198
28	487	1150	1637	62	570	6847	7417
29	484	1119	1603	63	741	7063	7804
30	520	1272	1792	64	639	6922	7561
31	661	1505	2166	65	633	7235	7868
32	709	1436	2145	66	684	7908	8592
33	528	1330	1858	67	551	8192	8743
34	526	1647	2173	68	587	8370	8957

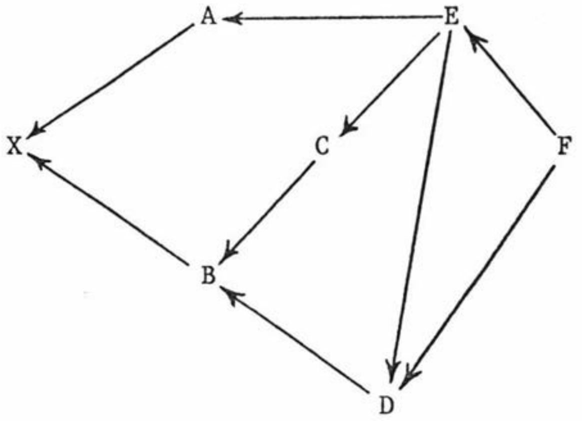
APPENDIX II : Number of female registrations and number of herds in each of the eight 10-year periods (1900-1970).

	1900	1910	1920	1930	1940	1950	1960	1970
Number of females registered	44	139	473	693	1603	1979	4291	7476
Number of herds	8	16	41	57	118	177	465	545

APPENDIX III

An example of the use of Wright's (1922) formula (see Page 9) for the computation of the coefficient of inbreeding.

Consider the pedigree below:



It is assumed that the inbreeding coefficient of individual E is $F_E = {}^1/_8$. In the analysis below, common ancestors are underlined. Inbreeding coefficients of individuals other than common ancestors need not be considered.

A-$\underline{E}$-C-B $\quad (\frac{1}{2})^4\ (1+{}^1/_8) = {}^9/_{128}$

A-$\underline{E}$-D-B $\quad (\frac{1}{2})^4\ (1+{}^1/_8) = {}^9/_{128}$

A-E-$\underline{F}$-D-B $\quad (\frac{1}{2})^5 = {}^1/_{32}$

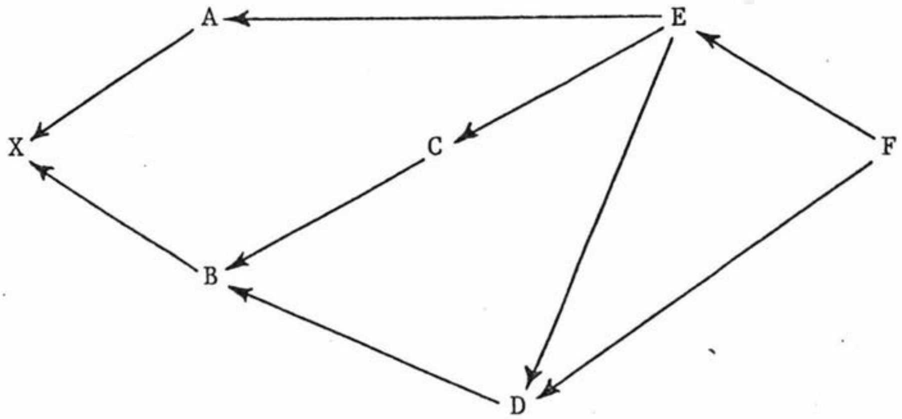
Inbreeding coefficient of X,

i.e. $F_X = {}^{11}/_{64}$

APPENDIX IV

An example of the use of coancestry for computing inbreeding coefficients.

Consider the pedigree below (which is the same as that shown in Appendix III):



It is assumed that individual F is not inbred and the inbreeding coefficient of E is $^1/_8$. An individual not appearing in the figure and unrelated to its mate is denoted by 0.

From the discussion on Page 15,

$f_{FF} = \frac{1}{2}(1+F_F) = \frac{1}{2}$

$f_{EE} = \frac{1}{2}(1+F_E) = \frac{1}{2}(1+{}^1/_8) = {}^9/_{16}$

Individual E is an offspring of F. Therefore,

$f_{EF} = f_{FO.F} = \frac{1}{2}(f_{OF} + f_{FF}) = \frac{1}{4}$ since $f_{OF} = 0$.

NOTE: $f_{FO.F}$ symbolises the coancestry coefficient between an offspring of the mating FxO and one of the parents, that is, F. The coancestry coefficient between parent and offspring equals the average of the coefficient of the parent itself (f_{FF}) and the coefficient of coancestry between the two parents (f_{FO}). Individual D is an offspring of E and F. Therefore,

$$f_{DE} = f_{ExF.E} = \tfrac{1}{2}(f_{EE} + f_{FE}) = \tfrac{1}{2}(9/16 + \tfrac{1}{4}) = 13/32, \text{ etc.}$$

Hence, using this approach, coefficients of coancestry for the whole pedigree can be compiled as shown in the table below:

Coefficients of coancestry

	A	B	C	D	E	F
A	½	11/64	9/64	21/128	9/32	1/8
B		75/128	45/128	53/128	11/32	29/128
C			½	13/64	9/32	¼
D				5/8	13/32	3/8
E					9/16	¼
F						½

Using the coefficient of coancestry of an individual with itself, the inbreeding coefficient can be estimated, as for example,

$$f_{DD} = \tfrac{1}{2}\,(1+F_D)$$

$$\text{or } F_D = 2f_{DD} - 1 = 2(5/8) - 1 = \tfrac{1}{4}$$

Simpler still is estimating inbreeding from the coancestry coefficient of the parents of the individual. For instance,

$F_D = f_{EF} = \frac{1}{4}$

or $F_X = f_{AB} = {}^{11}/_{64}$ (which is the same answer obtained by the application of Wright's formula, as demonstrated in Appendix III).

APPENDIX V : Number of male and female pedigree Angus cattle imported into New Zealand since 1863

Date of Importation	BULLS		COWS	
	Number	Country of Origin	Number	Country of Origin
1863	3	Great Britain	2	Great Britain
1875	2	"	3	"
1880	2	"		
1882	5	"	10	"
1883	1	"		
1892	3	"	8	"
1893	1	"		
1900	3	"		
1905	6	"	4	"
1906	1	"		
1908	1	"		
1910	3	"	2	"
1911	1	"		
1912	2	"		
1913	2	"		
1914	1	"	5	"
1915	3	"	3	"
1917	1	"		
1920	11	"	11	"
1921			8	"
1923	1	"	1	"
1930	3	Canada	5	Canada
1932	2	"		
1934	3	Great Britain		
1935	3	U.S.A.	6	U.S.A.
1936	15	5 from Great Britain 10 from U.S.A.	9	"
1937	6	1 from Great Britain 5 from U.S.A.	8	"
1938	5	2 from Great Britain 3 from U.S.A.	7	2 from U.S.A. 5 from Great Britai
1939	11	Great Britain	1	Great Britain
1940	3	"		
1946	4	"		
1947	3	"		
1948	2	"	10	"
1949	5	"	10	"
1951	6	"	4	"
1952	4	"	7	"
1953	12	"	5	"

APPENDIX V (Continued)

Date of Importation	BULLS		COWS	
	Number	Country of Origin	Number	Country of Origin
1954	8	Great Britain	9	Great Britain
1955	9	"	11	"
1956	1	"	6	"
1957	8	"	10	"
1958	8	"	4	"
1959	3	"	6	"
1960	9	"	3	"
1961	4	"	1	"
1962	16	"	5	"
1963	5	"	1	"
1964	4	"	11	"
1965	13	2 from Australia 11 from Great Britain	10	5 from Australia 5 from Great Britain
1966	6	Great Britain	4	Great Britain
1967	2	"		
1969	6	"	4	"
1970	4	1 from Australia 3 from Great Britain	3	Australia
1971	2	Great Britain		
1972	3	"		
1973	5	1 from Great Britain 4 from Australia		
1974			2	1 from Australia 1 from Great Britain

APPENDIX VI

List of Importations (1863-1976)

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1863	Druid	67	Britain	Australian & N.Z. Land Co.
1863	Imported Bull	69	Britain	Australian & N.Z. Land Co.
1863	Imported Bull	70	Britain	Australian & N.Z. Land Co.
1875	Robin Hood	-	Britain	Australian & N.Z. Land Co.
1875	Blackleg	68	Britain	Australian & N.Z. Land Co.
1883	Solomon	-	Britain	Australian & N.Z. Land Co.
1882	Solomon II	21	Britain	N.Z. Agricultural Co.
1882	Baron Formatine	8	Britain	N.Z. Agricultural Co.
1882	Knight of Fyvie	9	Britain	N.Z. Agricultural Co.
1882	Canny Chiel of Waimea	10	Britain	N.Z. Agricultural Co.
1882	Young Eric of Waimea	11	Britain	N.Z. Agricultural Co.
1880	Glenbarry	96	Britain	Hon. Matthew Holmes
1880	Knight of the Thistle	97	Britain	Hon. Matthew Holmes
1892	Baron Arradoul	180	Britain	Gladbrook
1892	Jove	190	Britain	Marainanga
1892	Hansard of Byres	189	Britain	Marainanga
1893	Lancer of Advie	181	Britain	Gladbrook
1900	Ralph of Careston	428	Britain	Gladbrook
1900	Mistral	429	Britain	Gladbrook
1900	Fashion's Prince	376	Britain	Gladbrook
1905	B.B.B.	535	Britain	Marainanga
1905	Protector of Auchterarder	536	Britain	Marainanga
1905	Esmond of Dalmeny	664	Britain	Kereone
1905	Pope Boniface	609	Britain	Annandale
1905	Heathen	525	Britain	Gladbrook
1905	Eblis of Ballindalloch	526	Britain	Gladbrook
1906	Justice of Hursley	647	Britain	Thorsby
1908	King of Standen	763	Britain	Gwavas
1910	Escovedo	804	Britain	Gladbrook
1910	Idric	805	Britain	Gladbrook

APPENDIX VI (Continued)

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1910	Bengal Light	948	Britain	Gwavas
1911	Darwin of Claverdon	889	Britain	Mount Royal
1912	Estro of Maisemore	892	Britain	Turihaua
1912	Premier of Dalmeny	887	Britain	Thorsby
1913	Prince Burnish of Ballindalloch	953	Britain	Gladbrook
1913	British Mark	954	Britain	Gladbrook
1914	Moose 2nd	955	Britain	Akitio
1915	Elato	1019	Britain	Mount Royal
1915	Quality of Maisemore	1012	Britain	Gwavas
1915	Ermitano	1051	Britain	Woodlands
1917	Example of Maisemore	1063	Britain	Ben Lomond
1920	Quality of Frampton	2161	Britain	Turihaua
1920	Mulben Elbow	2041	Britain	Waiterenui
1920	Moyness Punch	2031	Britain	Glenelg
1920	Nyanga	2030	Britain	Bywell
1920	Victor of Rarichie	2130	Britain	Mangatoro
1920	Evron of Ruthven	2214	Britain	Akitio
1920	Evistic of Ruthven	2215	Britain	Akitio
1920	Hayston Bright Print	2216	Britain	Akitio
1920	Plato of Ruthven	2371	Britain	Koiro
1920	Evereldo of Ruthven	2372	Britain	Koiro
1920	Eddy of Ruthven	2373	Britain	Koiro
1923	Eland of Bleaton	2677	Britain	Woodlands
1930	Glencarnock King 3rd	4567	Canada	Ngawaka
1930	Burgess of Glencarnock 8th	4570	Canada	Tautane
1930	Qualatum of Raydale	4571	Canada	Tautane
1932	Northlane of Black Marshall	5319	Canada	W. Clark
1932	Elton Glencarnock	5320	Canada	W. Clark
1934	Juror Eric	5728	Britain	Waiterenui
1934	Bachelor of Derculich	5783	Britain	Ngawaka
1934	Jerdin Eric	5819	Britain	Tautane
1935	Black Marshall Earl	6197	U.S.A.	Kaiwaka

APPENDIX VI (Continued)

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1935	Energy Barkley	6206	U.S.A.	Turihaua
1935	Barmar Quality	6295	U.S.A.	Beachlea
1936	Barmar Quality Again	6546	U.S.A.	Turihaua
1936	Brigandine of Banks	6595	Britain	W. Clark
1936	Gaffer Elvin	6596	Britain	W. Clark
1936	Blason	6597	Britain	W. Clark
1936	Epistos Barmar	6619	U.S.A.	Mangamaire
1936	Eric Bar 2nd	6620	U.S.A.	Turihaua
1936	Double Revolution 6th	6621	U.S.A.	Turihaua
1936	Barmar Escort	6623	U.S.A.	Springfield
1936	Quality Barmar	6740	U.S.A.	Matapihi
1936	Eston Bar	6933	U.S.A.	Tarangower
1936	Prizemere 371st	6934	U.S.A.	Tarangower
1936	Blackcap Echo Quality	6898	U.S.A.	Tauwhare
1936	Queenmere 232nd	6622	U.S.A.	Tautane
1936	Euxidor 7th	6840	Britain	Akitio
1936	Event of Froxfield	6841	Britain	Akitio
1937	Quality Bar	6936	U.S.A.	Moetohunga
1937	Jerkin Eric	6954	Britain	Woodlands
1937	Barson Quality	7269	U.S.A.	Turihaua
1937	Epistos Quality	7270	U.S.A.	Matapihi
1937	Enchanter Barmar	7434	U.S.A.	Newbury
1937	Black Rex of Bordulac	7445	U.S.A.	Taheke
1938	Briarcliff Bardo	7456	U.S.A.	Motuotaria
1938	Bestman Quality	7459	U.S.A.	Tarangower
1938	Baron Ensign 2nd	7597	U.S.A.	C. Blake
1938	Jimmie Jinks	7733	Britain	Mangatoro
1938	Etheridge of Tillyrie	7735	Britain	Ngawaka
1939	Blackman Quality 2nd	8137	U.S.A.	Heathfield
1939	Enterprise Master	8151	U.S.A.	Waitoru
1939	Blackman Quality	8152	U.S.A.	Waitoru
1939	Jeddo Eric	8184	Britain	Taumangi
1939	Embelesco	8185	Britain	Taumangi
1939	Event of Gallowhill	8186	Britain	Makaretu
1939	Pericles of Gallowhill	8187	Britain	Glen Aros

APPENDIX VI (Continued)

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1939	Eulogist 2nd of Kilham	8188	Britain	Waiterenui
1939	Hayston Elmore	8442	Britain	Akitio
1939	Mulben Embassy	8733	Britain	Mangatoro
1939	Belgrafton	8834	Britain	Moetohunga
1940	Enrique	8917	Britain	W. Clark
1940	Elorkin of Dalmeny	8949	Britain	Gladbrook
1940	Justice of Bywell	9352	Britain	Tautane
1946	Jogetcil of Dalmeny	12310	Britain	Gladbrook
1946	Evillaron of Dalmeny	12311	Britain	Tautane
1946	Elland of Rannagulzion	12312	Britain	Matapihi
1946	Racate of Douneside	12308	Britain	Te Whanga
1947	Paddy of Broadleys	12495	Britain	Akitio
1947	Hayston Primo	12496	Britain	Akitio
1947	Emperor Elect of Douneside	12733	Britain	Mangatoro
1948	Peteris of Dalmeny	13793	Britain	Te Whanga
1948	Ebelum of Leslie	14070	Britain	Ribbonwood
1949	Wavell of Haymount	14278	Britain	Heathfield
1949	European of Bruceton	14303	Britain	Mangatoro
1949	Eulijago of Kilham	14304	Britain	Mangatoro
1949	Euclid of Incheoch	14626	Britain	Gladbrook
1949	Matthew of Strathkinness	14698	Britain	Tautane
1951	Junalier of Dalmeny	15297	Britain	Cricklewood
1951	Prince Powerful of Hampton Lucy	15298	Britain	Cricklewood
1951	Empire of Incheoch	15298A	Britain	Cricklewood
1951	Janesslier of Dalmeny	15653	Britain	Gladbrook
1951	Euliwilly of Kilham	15712	Britain	Tautane
1951	Baronet of Rannagulzion	15728	Britain	Te Mania
1952	Bernard of Beaufort	16096	Britain	Ohiaroa
1952	Baron Bethoc	16053	Britain	Ribbonwood
1952	Parotian of Fordhouse	16105	Britain	Newbury
1952	Espuril of Fordhouse	16106	Britain	Newbury
1953	Erreth of Harviestoun	16514	Britain	Heathfield
1953	Newhouse Peranza	16569	Britain	Totaranui

APPENDIX VI (Continued)

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1953	Blizzard of Orchardlands	16864	Britain	Te Aratipi
1953	Jason of Barnoldby	16330	Britain	Akitio
1953	Blucher of Little Dean	16783	Britain	Kahika
1953	Brose of Broomhill	16315	Britain	Doone
1953	Evabor of Hampton Lucy	16427	Britain	Whakapirau
1953	Batman of Thorn	16513	Britain	Heathfield
1953	Eriebon of Spittal	16763	Britain	Brooklands
1953	Balgour Purdy	16764	Britain	Brooklands
1953	Proud Eric of Manorhill	16765	Britain	Brooklands
1953	Jamie Eric of Westdrums	16865	Britain	Te Aratipi
1954	Black Idol of Barnoldby	17002	Britain	Cricklewood
1954	Eldesco of Haymount	17446	Britain	Gladbrook
1954	Gilt of Ballintomb	16923	Britain	Parera
1954	Bruce of Greenyards	17108	Britain	Mangatoro
1954	Kronin of Lindertis	17107	Britain	Mangatoro
1954	Esam of Ballintomb	17312	Britain	Thornhill
1954	Newhouse Jewvill Eric	16994	Britain	Balfour
1954	Prince Mandor of Hampton Lucy	17502	Britain	Tautane
1955	Euro of Bleaton	17907	Britain	Waiterenui
1955	Proof of Maisemore	17909	Britain	Waiterenui
1955	Balgour Endor	17908	Britain	Waiterenui
1955	Engleberg of Haymount	18033	Britain	Tataramoa
1955	Prince Paul of Charterhouse	18044	Britain	Te Aratipi
1955	Baron Balfe	17789	Britain	Ribbonwood
1955	Erario of Fordhouse	17729	Britain	Newbury
1955	Prince Malan of Hampton Lucy	17823	Britain	Craigburn
1955	Exponent of Leckaway	17864	Britain	Mangawhero
1956	Evangelist of Westdrums	18691	Britain	Motere
1957	Elcomus of Leckaway	19509	Britain	Thornhill
1957	Stype Playboy	19055	Britain	Balfour
1957	Stype Gambol	18125	Britain	Parera
1957	Jasper Eric of Westdrums	19920	Britain	Glenmark
1957	Erisert of Harviestoun	19298	Britain	Ribbonwood

APPENDIX VI (Continued)

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1957	Georgic of Haymount	19066	Britain	Cricklewood
1957	Prince Pilot of Bywell	19283	Britain	Totaranui
1957	Ethelred 2nd of Spittal	19284	Britain	Totaranui
1958	Kelite of Lindertis	19842	Britain	Balfour
1958	Elegance of Charterhouse	20026	Britain	Mangatoro
1958	Stype Guardian	20027	Britain	Mangatoro
1958	Eskimo of Little Dean	20361	Britain	Kahika
1958	Enorman of Haymount	20440	Britain	Gladbrook
1958	Black Bandit of Barnoldby	20558	Britain	Turihaua
1958	Eregli of Harviestoun	19991	Britain	Heathfield
1958	Stype Master Brian	20298	Britain	Waiterenui
1959	Balgour Jumbo Eric	20762	Britain	Brackenfield
1959	Prince of Movement	21323	Britain	Totara Hills
1959	Bard of Crooklands	20909	Britain	Totaranui
1960	Baron Barrister of Harviestoun	22019	Britain	Sefton
1960	Kilmundie Erasmort	22071	Britain	Glen Garth
1960	Black Banner of Struthers	22080	Britain	Fuschia Creek
1960	Borodin of Fordhouse	21947	Britain	Brooklands
1960	Euripus of Wych Cross	21564	Britain	Heathfield
1960	Barometer of Cullisse	21563	Britain	Heathfield
1960	Ergo of Tisted	22342	Britain	Heathfield
1960	Kilmundie Embask	22121	Britain	Tataramoa
1960	Elfont of Gloagburn	22713	Britain	Tataramoa
1961	Gold Standard of Fordhouse	22122	Britain	Kahika
1961	Proctor of Westdrums	22437	Britain	Totaranui
1961	Ebony Master of Rowley	22653	Britain	Thornhill
1961	Newhouse Edwin Elric	22216	Britain	Balfour
1962	Edwin of Hungerford	23630	Britain	Waiterenui
1962	Erquand of Kinermony	22971	Britain	Cricklewood
1962	Gladhand of Kinermony	22972	Britain	Cricklewood
1962	Purist of Fordhouse	23143	Britain	Craigburn
1962	Wizard of Balhary	23015	Britain	Valhalla
1962	President of Tofts	23520	Britain	Glen Fruin

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1962	Islabank Joy Eric	23221	Britain	Zenith
1962	Eulihunter of Kilham	23518	Britain	Tawhara and Turiroa
1962	Kilmundie Peyote	23853	Britain	Elgin
1962	Erotic of Fordhouse	24139	Britain	Brooklands
1962	Janetic Eric of Tangier	24140	Britain	Brooklands
1962	Edwin Era of Balmyle	24295	Britain	Gladbrook
1962	Stype Dollar	24870	Britain	Omakere
1962	Everclad of Maisemore	24642	Britain	Glenmark
1963	Envoice of Incheoch	24245	Britain	Karaka
1963	Electronic of Lindertis	23857	Britain	Brackenfield
1963	Eustace of Derculich	23146	Britain	Mangatoro
1963	Newhouse Excelsior	24419	Britain	Waiterenui
1963	Newhouse Ellerman	23775	Britain	Overshiels
1963	Emulator of Haymount	25030	Britain	Tataramoa
1964	Escalator of Gloagburn	24484	Britain	Parera
1964	Jarryl Eric of Broadleys	24594	Britain	Dalby Partnership
1964	Jave Eric of Candacraig	24595	Britain	Dalby Partnership
1964	Parando of Fordhouse	24599	Britain	Delta Station
1964	Black Mark of Parkbeg	24617	Britain	Waihihi
1964	Islabank Major Benaud	24672	Britain	Hazeldell
1964	Evron of Wandel	24702	Britain	Holden Stud Ltd.
1964	Evrecom of Kinermony	24736	Britain	Korakonui
1964	Probard of Shawbury	24737	Britain	Korakonui
1964	Junyor Eric of Candacraig	24810	Britain	Rawhiti
1964	Jurotic Eric of Thorn	24871	Britain	Omakere
1964	Estort of Graden	24900	Britain	Woodley
1964	Balgour Perry	24932	Britain	Tarangower
1964	Newhouse Emeritus	24995	Britain	Winchester
1964	Elector of Burnton	25013	Britain	Aria
1964	Emanate of Haymount	25050	Britain	Waiterenui
1964	Error of Tangier	25077	Britain	Te Mania
1964	Elate of Tangier	26361	Britain	Moerangi
1964	Newhouse Perinthian	26362	Britain	Moerangi

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1965	Princibet of Kinermony	25431	Britain	Taimate
1965	Jeweltion Eric of Selden	25206	Britain	Balfour
1965	Erast of Wych Cross	25217	Britain	Barkla Downs
1965	Eudaron of Candacraig	25331	Britain	Brackenfield
1965	Jox Eric of Candacraig	25352	Britain	Stern
1965	Erasmus J. of Tangier	25360	Britain	Heathfield
1965	Black Bollard of Barnoldby	25462	Britain	Puketutu
1965	Ero of Wych Cross	25530	Britain	Totara Park
1965	Newhouse Edwin Eminent	25790	Britain	Gladbrook
1965	Native Point Bruce 31st	26136	Australia	Agadar
1965	Native Point Bruce 23rd	26137	Australia	Agadar
1965	Julius of Renmure	26749	Britain	Puketutu
1966	Lindertis Evidence	25956	Britain	Kingsclear
1966	Eric of Selden	25961	Britain	Atahua
1966	Purser of Eastfield	26075	Britain	Elgin
1966	Elomest of Kinermony	26115	Britain	Mangatoro
1966	Elsinore of Belladrum	26310	Britain	Thornhill
1966	Pampador of Haymount	27304	Britain	Craigburn
1965	Exigent of Leckaway	27865	Britain	Mangatoro
1967	Newhouse Jeweros Eric*	28173	Britain	Gladbrook
1969	Gaffer Defiance of Banks	27815	Britain	Oaklea
1969	Janko Eric of Candacraig	27862	Britain	Craigburn
1969	Jerry Eric of Lownie	27866	Britain	Mangatoro
1969	Jomogen Eric of Kinermony	27898	Britain	Totaranui
1969	Bassador of Greenyards	28043	Britain	Strathyre
1969	Black Ben of Kinchurdy	28085	Britain	Thornhill
1970	Newhouse Jewdax Eric	28506	Britain	Braeside
1970	Cherry Bow of Peebles	28646	Britain	Kai Iwi
1970	Jandic Eric of Buchaam	28462	Britain	Oaklea
1970	Connorville Dauntless	28925	Australia	Waitepipi
1971	Pronomac of Kinermony	29153	Britain	Brackenfield
1971	Jesenedus Eric of Douneside	29193	Britain	Braeside

*For A.I. service only

Date of Importation	Name of Bull	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1972	Ermine of Peebles	29954	Britain	Dunearn
1972	Templehall Prince Powerfull	29990	Britain	Matua
1972	Black Night of Tangier	29991	Britain	Matua
1973	Victoree Abaridy 152nd	30733	Australia	Omakere
1973	Ethnarch of Idvies	31188	Britain	Totaranui
1973	Delegate Quarter-Master	31206	Australia	Puketutu
1973	Barwidgee Potter	31239	Australia	Akitio
1973	Connorville Duke 10th	31514	Australia	Turihaua

(See next page for list of imported cows)

APPENDIX VI (Continued)

Date of Importation	Name of Cow	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1863	Minerva	158	Britain	Australian & N.Z. Land Co.
1863	Sunbeam	157	Britain	Australian & N.Z. Land Co.
1875	Nancy of East Mains	52	Britain	Australian & N.Z. Land Co.
1875	Sweet Grapes	54	Britain	Australian & N.Z. Land Co.
1875	Tillyfour Lass	160	Britain	Australian & N.Z. Land Co.
1882	Bella 2nd of Greystone	11	Britain	N.Z. Agricultural Co.
1882	Bella 5th of Greystone	12	Britain	N.Z. Agricultural Co.
1882	Bella 1st of Waimea	13	Britain	N.Z. Agricultural Co.
1882	Mabel	14	Britain	N.Z. Agricultural Co.
1882	Waterside Milkmaid	15	Britain	N.Z. Agricultural Co.
1882	Joan of Thomastown	16	Britain	N.Z. Agricultural Co.
1882	Lily 4th of Thomastown	17	Britain	N.Z. Agricultural Co.
1882	Lily 5th of Thomastown	19	Britain	N.Z. Agricultural Co.
1882	Lily 1st of Waimea	18	Britain	N.Z. Agricultural Co.
1882	Victoria 1st of Waimea	20	Britain	N.Z. Agricultural Co.
1892	Eclypta	347	Britain	Gladbrook
1892	Merry Maiden of Byres	349	Britain	Gladbrook
1892	Quetta	348	Britain	Gladbrook
1892	Jolliment	358	Britain	Gladbrook
1892	Kathleen 2nd of Drummuir	357	Britain	Gladbrook
1892	Celandine of Drummuir	404	Britain	Marainanga
1892	Rosella of Advie	405	Britain	Marainanga
1892	Vivacious	403	Britain	Marainanga
1905	Ericia	788	Britain	Marainanga
1905	Ermine of Pitpointie	789	Britain	Marainanga
1905	Pearl 2nd of Ballintomb	774	Britain	Gladbrook
1905	Kindness of Ballintomb	775	Britain	Gladbrook
1910	Dear Diana	1598	Britain	Mount Royal
1910	Jipsey Rose Bloom	1599	Britain	Mount Royal
1914	Pure Pride of Dalmeny	1768	Britain	Gwavas
1914	Eunice of Harviestoun	1766	Britain	Gwavas
1914	Elja 2nd	1767	Britain	Gwavas
1914	Elegia	1782	Britain	Mount Royal

APPENDIX VI (Continued)

Date of Importation	Name of Cow	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1914	Pride of Kyle	1781	Britain	Mount Royal
1915	Pride of Mulben 44th	1961	Britain	Woodlands
1915	Pride of Aberdeen 532nd	1962	Britain	Woodlands
1915	Proud Peggie	1963	Britain	Woodlands
1920	Country Lass	4368	Britain	Mangatoro
1920	Ettie 8th of Dalvey	4369	Britain	Mangatoro
1920	Erica of Clochie	4304	Britain	Mangatoro
1920	Parkhead Ruth 2nd	4302	Britain	Mangatoro
1920	Pride 31st of Dalvey	5301	Britain	Mangatoro
1920	Purity of Dalvey	4305	Britain	Mangatoro
1920	Queenly of Ballintomb	4370	Britain	Mangatoro
1920	Ruth 2nd of Congash	4367	Britain	Mangatoro
1920	Eerie	4580	Britain	Mangatoro
1920	Pride of Dallas	4581	Britain	Mangatoro
1920	Erma of Moyness 3rd	4582	Britain	Mangatoro
1921	Black Jilt of Philorth	4497	Britain	Akitio
1921	Patricia of Denoon	4496	Britain	Akitio
1921	Evelauna of Ruthven	4499	Britain	Akitio
1921	Emma of Ruthven	4500	Britain	Akitio
1921	Elcynetta of Ballindalloch	4793	Britain	Koiro
1921	Eugenie of Denoon	4794	Britain	Koiro
1921	Ermla of Ruthven	4795	Britain	Koiro
1921	Eleanor of Damside	4796	Britain	Koiro
1923	Bunty of Mulben	5620	Britain	Woodlands
1930	Karama of Glencarnock 6th	9417	Canada	Ngawaka
1930	Blackbird of Glencarnock 33rd	9418	Canada	Ngawaka
1930	Elba of Glencarnock 32nd	9419	Canada	Ngawaka
1930	Elba of Page 4th	9422	Canada	Tautane
1935	Blackcap M.K. 15th	13449	U.S.A.	Beachlea
1935	Blackcap Carmen M.K. 5th	13450	U.S.A.	Beachlea
1930	Blackbird Glencarnock 32nd	9423	Canada	Tautane
1935	Blackcap Empress M.K. 15th	13451	U.S.A.	Beachlea
1935	Elba M.K. 7th	13452	U.S.A.	Beachlea

APPENDIX VI (Continued)

Date of Importation	Name of Cow	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1935	Blackcap M.K. 12th	13453	U.S.A.	Beachlea
1935	Queens Viola 4th	13454	U.S.A.	Beachlea
1936	Ames Plantation Phloretta	14369	U.S.A.	Beachlea
1936	Ames Plantation Bernalda	14370	U.S.A.	Beachlea
1936	Erica Evergreen 2nd	14368	U.S.A.	Beachlea
1936	Briarcliff Jessie 9th	14371	U.S.A.	Beachlea
1936	Briarcliff Ebba 43rd	14372	U.S.A.	Beachlea
1936	Briarcliff Pride 35th	14373	U.S.A.	Beachlea
1936	Elgamere	14374	U.S.A.	Beachlea
1936	Elgamere 2nd	14375	U.S.A.	Beachlea
1936	Black Sophronelite	14376	U.S.A.	Beachlea
1937	Elwoods Elba	15762	U.S.A.	Turihaua
1937	Blackcap McHenry 465th	15761	U.S.A.	Turihaua
1937	Elbaress Quality	15951	U.S.A.	Beachlea
1937	Miss Burgess Hopley 6th	16004	U.S.A.	Moetohunga
1937	Bethel Blackbird 126th	16005	U.S.A.	Moetohunga
1937	Barbird Miss	16006	U.S.A.	Moetohunga
1937	Bethel Primrose 24th	16147	U.S.A.	Dunira
1937	Escora Marlene	16407	U.S.A.	Taheke
1938	Barmar Quality Lass 2nd	16498	U.S.A.	Greenbank
1938	Beta Quality 3rd	16680	U.S.A.	Greenbank
1938	Mavis of Bywell	16880	Britain	Burford
1938	Evelutine of Ballindalloch	16889	Britain	Mangatoro
1938	Perdita of Jardine	16890	Britain	Mangatoro
1938	Genista of Jardine	19193	Britain	Mangatoro
1938	Permita of Jardine	16892	Britain	Mangatoro
1939	Blackbird 12th of Dalvey	34164	Britain	Mangatoro
1948	Europa 13th of Dalmeny	34165	Britain	Te Whanga
1948	Petronella 13th of Dalmeny	34166	Britain	Te Whanga
1948	Kindly Pride of Leylodge	34167	Britain	Beachlea
1948	Peahen of Tullyraw	34168	Britain	Beachlea
1948	Print of Glen Farg	34169	Britain	Beachlea
1948	Eugene of Myreton	35299	Britain	Beachlea

Date of Importation	Name of Cow	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1948	Etala of Fordhouse	35301	Britain	Ribbonwood
1948	Rosota of Fordhouse	35300	Britain	Ribbonwood
1948	Elenco 2nd of Balfron	35302	Britain	Ribbonwood
1948	Eridema of Balfron	36149	Britain	Ribbonwood
1949	Eulima 54th of Kilham	36150	Britain	Glenmark
1949	Bouncing Maid of Gallowhill	36150	Britain	Glenmark
1949	Jusk Erica of Eynsham	36173	Britain	Craigburn
1949	Evanna of Ballindalloch	36174	Britain	Craigburn
1949	Pride of Mulben 141st	36175	Britain	Craigburn
1949	Easy of Derculich	36190	Britain	Mangatoro
1949	Betty Black of Gaidrew	36191	Britain	Mangatoro
1949	Paola of Gaidrew	36192	Britain	Mangatoro
1949	Erodie of Harviestoun	36367	Britain	Ribbonwood
1949	Jeffica Erica	36368	Britain	Ribbonwood
1951	Beaving Maid 4th of Dalmeny	39320	Britain	Ribbonwood
1951	Erotoa of Dalmeny	39321	Britain	Ribbonwood
1951	Barajara 8th of Dalmeny	41410	Britain	Gladbrook
1951	Black Melda of Bywell	41547	Britain	Tautane
1952	Pride 8th of Golford	42074	Britain	Westburn
1952	Jilt 38th of Maisemore	42695	Britain	Newbury
1952	Estelle 30th of Maisemore	42699	Britain	Newbury
1952	Pride of Maisemore 121st	42698	Britain	Newbury
1952	Evaka of Harviestoun	43302	Britain	Gladbrook
1952	Pride of Maisemore 119th	42697	Britain	Newbury
1952	Estelle 25th of Maisemore	42696	Britain	Newbury
1953	Ereena of Harviestoun	44562	Britain	Ribbonwood
1953	Ethana of Harviestoun	44561	Britain	Ribbonwood
1953	Pandora of Fordhouse	44244	Britain	Heathfield
1953	Poplin 5th of Tisted	45857	Britain	Te Aratipi
1953	Blackeyes of Gaidrew	43854	Britain	Tunui
1954	Pepita of Dalmeny	46369	Britain	Cricklewood
1954	Pearl of Dalmeny	46368	Britain	Cricklewood
1954	Beta Maid of Bankhead	46952	Britain	Strathyre
1954	Belle Maid of Fordhouse	46307	Britain	Balfour

APPENDIX VI (Continued)

Date of Importation	Name of Cow	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1954	Glenys of Menzies	46308	Britain	Balfour
1954	Eudocia of Incheoch	46309	Britain	Balfour
1954	Black Ruby of Broomhall	46187	Britain	Doone
1954	Ergana of Harviestoun	48226	Britain	Gladbrook
1954	Joyeda Erica	48227	Britain	Gladbrook
1955	Puree Purnell of Charterhouse	50379	Britain	Te Aratipi
1955	Erma of Dalmeny	50271	Britain	Waiterenui
1955	Pretty Pride of Dalmeny	50272	Britain	Waiterenui
1955	Pride of Majority	49450	Britain	Mangawhero
1955	Ernette of Shampston	50012	Britain	Mangawhero
1955	Bashful 2nd of Aske	50013	Britain	Mangawhero
1955	Ebony Kira of Rowley	51526	Britain	Forres
1955	Primwell of Balfron	51363	Britain	Balfour
1955	Kay Pride of Balfron	51364	Britain	Balfour
1955	Elpa 3rd of Balfron	51991	Britain	Glenmark
1955	Pomara of Fordhouse	49831	Britain	Newbury
1956	Eroba of Gloagburn	52011	Britain	Craigburn
1956	Georgenta of Cullaird	52565	Britain	Strathyre
1956	Poppet of Balfron	52567	Britain	Greenbank
1956	Jasmi Erica	52012	Britain	Craigburn
1956	Primrose of Rannagulzion	52023	Britain	Mangatoro
1956	Pearlband of Rannagulzion	52024	Britain	Mangatoro
1957	Enamorate of Gloagburn	54989	Britain	Craigburn
1957	Bosky of Broomhall	55367	Britain	Hingaia
1957	Josie Erica of Westdrums	55241	Britain	Ribbonwood
1957	Winnow of Haymount	55242	Britain	Ribbonwood
1957	Elisabeth of Balfron	55009	Britain	Mangatoro
1957	Princess Patricia of Spittal	55010	Britain	Mangatoro
1957	Bycora Maid of Advie	55226	Britain	Totaranui
1957	Jovie Erica of Bywell	55227	Britain	Totaranui
1957	Ethelreal of Spittal	55228	Britain	Totaranui
1957	Jolina Erica	55229	Britain	Totaranui
1958	Kind Princess of Ballindalloch	58580	Britain	Zenith

APPENDIX VI (Continued)

Date of Importation	Name of Cow	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1958	Eurekie of Candacraig	59495	Britain	Kahika
1958	Petronial 7th of Dalmeny	60295	Britain	Aria
1958	Evilina 11th of Dalmeny	60296	Britain	Aria
1959	Bengin Maid of Westdrums	60317	Britain	Te Aratipi
1959	Erinova of Broadleys	62516	Britain	Scotdale
1959	Edwiveena 27th of Charterhouse	61542	Britain	Brackenfield
1959	Prijeta of Kinermony	62010	Britain	Totaranui
1959	Barina Maid of Broadleys	61845	Britain	Strathspey
1959	Black Bess of Kilham	61970	Britain	Taimate
1960	Gammer Euda	68289	Britain	Totara Hills
1960	Entranina of Kinermony	68288	Britain	Totara Hills
1960	Aclurya Evatwin	66020	Britain	Heathfield
1961	Erbeta of Harviestoun	68780	Britain	Balfour
1962	Elandia 2nd of Calward	80558	Britain	Brooklands
1963	Pandura of Haymount	78588	Britain	Brackenfield
1962	Parma of Coulnakyle	80871	Britain	Woodley
1962	Evilira of Manorhill	80870	Britain	Woodley
1962	Heather Petal of Kinnudie	80872	Britain	Woodley
1962	Junita Erica of Wych Cross	84256	Britain	Totaranui
1964	Bride of Westmains	82958	Britain	Tunui
1964	Eurekar 2nd of Candacraig	82972	Britain	Sterling
1964	Stype Edwiveena 11th	83999	Britain	Craigburn
1964	Stype Ellerena 11th	83998	Britain	Craigburn
1964	Esperanza of Murdostoun	84198	Britain	Taimate
1964	Ellebet of Islabank	84199	Britain	Taimate
1964	Jinty Erica of Westdrums	84339	Britain	Holden Stud Ltd.
1964	Erotessa of Broadleys	84815	Britain	Matua
1964	Elincomo of Kinermony	84816	Britain	Matua
1964	Eve of Selden	86709	Britain	Aria
1964	Jungab Erica of Candacraig	86747	Britain	Te Ohu
1965	Black Bettina of Barnoldby	89146	Britain	Puketutu
1965	Pridellie of Bywell	89147	Britain	Puketutu
1965	Korosa of Manorhill	89148	Britain	Puketutu
1965	Proud Girl of Coulnakyle	91033	Britain	Aria

APPENDIX VI (Continued)

Date of Importation	Name of Cow	N.Z. Herd Book Number	Country of Origin	Name of Importing Stud
1965	Mesena Pride of Tangier	91061	Britain	Te Ohu
1965	Sarum Gaiety 5th	93318	Australia	Agadar
1965	Native Point Dell 3rd	93319	Australia	Agadar
1965	Native Point Even 5th	93320	Australia	Agadar
1965	Native Point Netta 4th	93321	Australia	Agadar
1965	Native Point Estelle 6th	93322	Australia	Agadar
1966	Prosy of Westdrums	93257	Britain	Craigburn
1966	Eroika of Westdrums	93258	Britain	Craigburn
1966	Jessone Erica of Westdrums	97192	Britain	Balmoral
1966	Jessena Erica of Westdrums	97193	Britain	Balmoral
1969	Maurvesa of Bywell	111799	Britain	Oaklea
1969	Even Girl 2nd of Kilham	112770	Britain	Totaranui
1969	Joppatty Erica of Candacraig	115291	Britain	Moerangi
1969	Junember Erica of Islabank	130252	Britain	Aria
1970	Connorville Queen 8th	122991	Australia	Waitepipi
1970	Connorville Sally 4th	122992	Australia	Waitepipi
1970	Connorville Jess 6th	122993	Australia	Waitepipi
1974	Carisbrook Faithful	148782	Australia	Glenbourke
1974	Purpuss of Eastfield	148883	Britain	Mangatoro

APPENDIX VII

Parent-offspring intervals of the New Zealand Pedigree Angus for eight sample years

1900								
Length of interval (years)	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No. of dam-daughter intervals	%
2			3	8.3			1	2.5
3	10	25.6	7	19.4	16	37.2	7	17.5
4	10	25.6	10	27.8	12	27.9	8	20.0
5	3	7.7	4	11.1	6	14.0	7	17.5
6	8	20.5	5	13.9	3	7.0	3	7.5
7			3	8.3	2	4.7	3	7.5
8	8	20.5	2	5.6			4	10.0
9			2	5.6	4	9.3	3	7.5
10							1	2.5
11							1	2.5
14							1	2.5
17							1	2.5
Total No. of Intervals	39		36		43		40	

1910								
Length of interval (years)	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No. of dam-daughter intervals	%
2	11	30.6	2	3.4				
3	11	30.6	16	27.1	4	11.1	5	9.6
4	3	8.3	11	18.6	1	2.8	11	21.2
5			12	20.3	7	19.4	11	21.2
6	10	27.8	4	6.8	2	5.6	7	13.5
7			4	6.8			6	11.5
8			2	3.4	7	19.4	2	3.8
9			5	8.5				
10	1	2.8	2	3.4			6	11.5
11			1	1.7				
12					15	41.7	2	3.8
13							1	1.9
15							1	1.9
Total No. of Intervals	36		59		36		52	

1920								
Length of interval	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No. of dam-daughter intervals	%
2	3	4.5	4	5.6	2	3.3		
3	5	7.5	20	28.0	9	14.8	9	13.9
4	18	26.9	9	12.5	6	9.8	6	9.2
5	9	13.4	14	19.4	14	23.0	7	10.8
6	12	17.9	9	12.5	4	6.6	1	1.5
7	1	1.5	5	6.9	10	16.4	4	6.2
8	9	13.4	6	8.3	1	1.6	13	20.0
9	3	4.5	3	4.2			7	10.8
10	1	1.5	1	1.4	5	8.2	8	12.3
11	3	4.5			2	3.3	4	6.2
12	1	1.5					2	3.1
13	1	1.5			3	4.9		
14			1	1.4	3	4.9	2	3.1
15					1	1.6	1	1.5
18					1	1.6	1	1.5
20	1	1.5						
Total No. of Intervals	67		72		61		65	

1930								
Length of interval (years)	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No of dam-daughter intervals	%
2	1	2.2	2	3.7			1	1.9
3	18	40.0	9	16.7	10	20.4	9	16.7
4	12	26.7	12	22.2	10	20.4	12	22.2
5	6	13.3	14	25.9	8	16.3	5	9.3
6			4	7.4	8	16.3	4	7.4
7	2	4.4	3	5.6	3	6.1	10	18.5
8	4	8.9	3	5.6	3	6.1	3	5.6
9	1	2.2	1	1.9	2	4.1	5	9.3
10	1	2.2	2	3.7	4	8.2		
11			3	5.6			1	1.9
12			1	1.9				
13							1	1.9
14							2	3.7
15					1	2.0	1	1.9
Total No. of Intervals	45		54		49		54	

1940								
Length of Interval (years)	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No. of dam-daughter intervals	%
2	2	4.7	3	5.9	3	6.9	1	2.0
3	10	23.3	15	29.4	5	11.6	5	10.0
4	7	16.3	7	13.7	7	16.3	9	18.0
5	5	11.6	5	9.8	5	11.6	4	8.0
6	9	20.9	6	11.8			9	18.0
7	2	4.7	6	11.8	1	2.3	8	16.0
8	2	4.7	1	1.9	3	6.9	5	10.0
9	5	11.6	6	11.8	3	6.9	3	6.0
10			1	1.9	5	11.6	3	6.0
11					5	11.6	1	2.0
12	1	2.3			2	4.7	1	2.0
13					3	6.9		
14			1	1.9			1	2.0
15					1	2.3		
Total No. of Intervals	43		51		43		50	

1950								
Length of interval (years)	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No. of dam-daughter intervals	%
2	14	24.6	9	15.3	1	1.6	3	5.1
3	18	31.6	11	18.6	13	21.3	8	13.6
4	10	17.5	8	13.6	5	8.2	9	15.3
5	8	14.0	10	16.9	7	11.5	8	13.6
6	2	3.5	9	15.3	3	4.9	3	5.1
7	1	1.8	5	8.5	9	14.8	7	11.9
8	1	1.8	4	6.8	4	6.6	7	11.9
9	1	1.8	1	1.7	4	6.6	7	11.9
10	1	1.8	2	3.4	6	9.8		
11							2	3.4
12					2	3.3		
13					1	1.6	2	3.4
14					3	4.9	1	1.7
15	1	1.8			1	1.6		
16					1	1.6	2	3.4
17					1	1.6		
Total No. of Intervals	57		59		61		59	

1960								
Length of intervals (years)	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No. of dam-daughter intervals	%
2	13	31.0	5	10.6			2	4.1
3	10	23.8	10	21.3	11	28.2	6	12.2
4	4	9.5	12	25.5	8	20.5	10	20.4
5	6	14.3	5	10.6	3	7.7	3	6.1
6	3	7.1	5	10.6	1	2.6	5	10.2
7	1	2.4	6	12.8	7	17.9	9	18.4
8	3	7.1	2	4.3			4	8.2
9	1	2.4	2	4.3	3	7.7	3	6.1
10	1	2.4			3	7.7	2	4.1
11					1	2.6	1	2.0
12					1	2.6	1	2.0
13							1	2.0
15					1	2.6	2	4.1
Total No. of intervals	42		47		39		49	

1966/67								
Length of interval (years)	No. of sire-son intervals	%	No. of sire-daughter intervals	%	No. of dam-son intervals	%	No. of dam-daughter intervals	%
2	10	18.9	8	13.1	2	3.7	1	1.7
3	11	20.8	11	18.0	13	24.1	12	20.0
4	10	18.9	12	19.7	8	14.8	9	15.0
5	10	18.9	3	4.9	5	9.3	9	15.0
6	7	13.2	7	11.5	7	13.0	5	8.3
7	1	1.9	3	4.9	4	7.4	3	5.0
8	1	1.9	5	8.2	4	7.4	2	3.3
9	3	5.7	1	1.6	3	5.6	5	8.3
10			7	11.5	3	5.6	3	5.0
11					3	5.6	3	5.0
12			3	4.9	2	3.7	2	3.3
13			1	1.6			1	1.7
14							2	3.3
15							3	5.0
Total No. of Intervals	53		61		54		60	

APPENDIX VIII

Prominent Animals From Studies of Various Cattle Breeds

Country	Breed	Author	Important Animals	Highest Recorded Direct Relationship to Breed (%)	Year Studied
U.S.A.	Shorthorn (Beef)	McPhee and Wright (1925)	♂ Favourite (252)	55.2	1920
			♂ Champion of England	45.5	1920
U.S.A.	Holstein-Friesian	Lush, Holbert and Willham (1936)	♀ De Kol 2nd	12.2	1928
U.S.A.	Brown Swiss	Yoder and Lush (1937)	♂ William Tell	9.4	1909
			♂ Junker	7.6	1929
U.S.A.	Hereford	Willham (1937)	♂ Beau Brummel	24.6	1930
			♂ Don Carlos	22.6	1930
			♂ Anxiety	18.5	1930
U.S.A.	Aberdeen-Angus	Stonaker (1943)	♂ Black Prince of Tillyfour	29.1	1910
			♂ Grey Breasted Jock	26.6	1910
			♂ Hanton	23.4	1930
Great Britain	Friesian	Robertson and Asker (1951)	♂ Albert 1306H	8.5	1931
			♂ Ceres 4497	7.4	1938
Denmark	Red Danish	Robertson and Mason (1954)	♂ Eske Brangstrup	26.5	1950
			♂ Højager	18.0	1950
Australia	Jersey	Barker (1957)	♂ Lord Twylish	7.0	1937
Australia	Polled Hereford	Barker and Davey (1960)	♂ Woodrow 1st	9.3	1949
Australia	Hereford	Davey and Barker (1963)	♂ Free Town Director	9.2	1949
New Zealand	Jersey	Stewart (1952)	♂ K.C.B.	8.0	1950