THE ESTIMATION OF PHENOTYPIC AND GENETIC PARAMETERS

FOR LIVEWEIGHT TRAITS OF RED DEER

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ABSTRACT

Data for this study were uplifted from Deerplan (the New Zealand deer performance recording scheme). The data consisted of 311 birth weight records from 4 herds, 2874 March weight (approximately 3 months of age) records from 28 herds and 1225 15-month weight records from 20 herds, for Red deer. Approximately half the March and 15-month weight records had an accompanying date of birth. Dam winter weight accompanied about one-third of the fawn weight records. The objectives of this study included: least squares estimation of non-genetic effects influencing birth, March and 15-month weights; estimation of heritability of these weight traits by Henderson's Method 3 and offspring-dam regression method; estimation of phenotypic and genetic correlations between these weight traits, and development of selection indices based on the estimated parameters.

The non-genetic effects found to significantly influence birth weight, with the approximate percentage of total variation each controlled given in parenthesis, were: herd (12%); sex (15%); age of dam (13%), and dam winter weight (18%). The effects of year and date of birth were small and were not considered to be of practical importance. Approximately 50% of the total variation in birth weight was accounted for by these non-genetic effects.

The non-genetic effects found to significantly influence March weight were: herd (11%); year (2%); sex (13%); age of dam or dam winter weight (10%), and age at March weighing (25%). Approximately 63% of the total variation in March weight was accounted for by these non-genetic effects.

The non-genetic effects found to significantly influence 15-month weight were: herd (6.0%); sex (70%); age at 15-month weighing (3%), and dam winter weight (3%). The effect of year on 15-month weight could not be tested. Approximately 80% of the total variation in 15-month weight was accounted for by these non-genetic effects.

The paternal-half sib heritability estimates of birth, March, and 15-month weights were high, 0.67 ± 0.29 ($\pm$ S.E), 0.77 ± 0.15, 0.60 ± 0.22, respectively.

The heritability of adjusted March weight estimated by the offspring-dam regression method was low, 0.15 ± 0.30.

The phenotypic correlation estimates between the adjusted fawn weights were consistently positive with moderate to strong magnitude. These estimates were 0.49 for birth and March weight, 0.34 for birth and 15-month weight and 0.51 for March and 15-month weight. The phenotypic correlation estimates between dam winter weight in adjacent years were strongly positive (0.49 to 0.97).

The genetic correlation estimates between the adjusted fawn weights were moderately to strongly positive, 0.93 ± 0.24 for birth and March weight and 0.32 ± 0.44 for March and 15-month weight.

Selection indices were developed for two objectives. One was to increase venison production at 15-months of age, and the other was to increase venison production at 27-months of age and 2 year old velvet antler weight. Due to the strongly positive correlations between liveweights, negative index weighting factors were obtained for March weight. These were considered unreasonable and indicated the need for further investigation. An economic gain per generation of $12.80 and $24.27 could be achieved for the two objectives respectively. The economic gain in the first objective was reduced to $12.53 by restricting genetic gain in birth weight to zero. There was little advantage in recording actual birth weights.

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LIST OF ABBREVIATIONS

Abbreviation	Meaning
age at mwt	age at the March weighing
age at wt	age at the 15-month weighing
ANOVA	analysis of variance
β	regression coefficient
bwt	birth weight
D.F.	degrees of freedom
EMS	expected mean square
kg	kilogram
kgDM/ha	kilograms of dry matter per hectare
LSE	ordinary least squares estimate
LSM	ordinary least squares mean
mwt	March weight
n	number of records in each sub-class
N	total number of records for that model
na	not applicable
NS	not significant (P>0.05)
P	probability
R^2	coefficient of determination
S.D.	standard deviation
S.E.	standard error
SIGN.	significance level
ylg	15-month weight
%VC	percentage of variation controlled

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CHAPTER 1

INTRODUCTION

The farming of Red deer began in New Zealand officially in 1970, when the first licence was issued (Yerex, 1982). The impetus was provided by the high returns for exported feral venison and the poor returns from sheep farming. At this time deer farming was seen as a profitable means of using poor quality land with little, if any, improved pasture. However, farmers quickly realized that it was more profitable to run deer on good quality land. Their experience soon revealed that, although deer in the natural state could survive on poor country in a harsh climate, they grew more rapidly and produced a higher fawning rate when they were given access to good feed all year round. Deer farmers introduced, from their experience with sheep, techniques of mating management, weaning and grazing control, so that the early system of simply enclosing deer (a form of ranching) quickly gave way to farming in the true sense of the word (Yerex, 1982). Deer are now farmed in all areas of New Zealand.

After the initial boom in deer farming in the 1970's, partly due to the high interest shown in New Zealand as a source of velvet antler, industry growth slowed during the 1980's, bringing with it the inevitable fall in live sale prices which had been the main source of income for most deer farmers. The industry's route began to swing back towards venison production, as it was realized that this was the product which offered the best marketing opportunity for the steadily expanding national herd (Yerex and Spiers, 1987). The reduction in prices for live deer applied pressure on farmers to achieve good performance levels in their herd as economically as possible.

The number of farmed deer in New Zealand has increased dramatically during the 1980's. A survey carried out by the Ministry of Agriculture and Fisheries prior to the 1980 fawning season, showed a total farmed deer population of approximately 104,000 deer, with 60 percent of the national herd being female. The latest Department of Statistics census, to 30 June 1987, shows that there are now 500,397 deer being farmed on 4316 farms (MAFCorp, 1988). Thus, farmed deer numbers have increased by approximately 380 percent in the seven years between 1980 and 1987. It has been predicted that the New Zealand farmed Red deer population is likely to exceed 1 million by 1991 (Spiers, 1987).

The above total population figures include all breeds of farmed deer, that is, Red, Wapiti or Elk and Fallow deer. Red deer are the most common breed farmed in New Zealand and account for 79 percent of the total farmed deer population (MAFCorp, 1988). Virtually all of the base stock for Red deer farms were captured from feral herds.

Red deer primarily provide venison and velvet. While many other products are obtained from deer (for example, skins, sinews and pizzles), venison, velvet antler and the sale of live animals represent the major proportion of returns to the deer farmer.

Since the inception of deer farming, much interest has been shown in the genetic improvement of productive traits in Red deer (see, for example, Yerex, 1982; Dick and Dodd, 1985; Fennessy, 1986). Until the initiation of a national performance recording scheme for deer (Deerplan) in 1985, insufficient data for the estimation of the necessary parameters for the development of effective breeding plans was available either in New Zealand or elsewhere in the world. The Chinese, who farm Red and Sika deer for velvet, had published a limited number of genetic parameters on velvet production (Zhou and Wu, 1979).

The objective of this study was to estimate phenotypic and genetic parameters on the liveweight traits of Red deer, thereby providing some of the information essential in formulating effective breeding plans for the New Zealand deer industry.[1]

The retention of a selected group of individuals for breeding purposes is a fundamental aspect of any selection programme. While the actual methods used to select individuals may vary, they all aim to identify individuals with the

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1   Please note that throughout this study female Red deer were referred to as hinds, male Red deer were referred to as stags and their offspring were referred to as fawns. Conventionally, Red deer offspring are referred to as calves. However, due to comparisons made between parameters estimated for cattle and deer throughout this study the terms fawn and fawning were used to prevent confusion between the two species.

highest genetic merit. An effective selection policy, combined with a complementary mating plan, forms the basis of a breeding programme designed to maximize genetic gain in each generation of selection.

Most of the economically important characters in farm animals are quantitative and in most cases their inheritance is polygenic. The phenotypic manifestation of such characters is subject to considerable modification by environmental influences. It is therefore important to try to account for any known environmental differences, through the use of correction factors, when making a genetic assessment of a certain trait.

Breeding objectives can involve the improvement of one or several traits simultaneously (for example, using selection indices). With a dual purpose breed, such as the Red deer, an aggregate breeding value may be predicted to use as a basis for discerning between individuals. Furthermore, it is of interest to know how the productive traits under selection pressure can be expected to change in future generations. These factors are dependent on such parameters as the heritability of the individual trait, the genetic and phenotypic correlation between traits and the relative economic value assigned to each trait.

This study utilized relevant data on farmed Red deer collected through Deerplan on birth weight, March weight and 15-month weight, in order to:

(i)   Estimate non-genetic effects which could be used to adjust data for differences induced by environmental factors such as sex and age of dam.

(ii)   Estimate heritabilities of the above liveweight traits and the phenotypic and genetic correlations between traits.

(iii)   Develop likely selection indices from the estimated genetic parameters and derived relative economic weights.

CHAPTER 2
LITERATURE REVIEW

2.1 INTRODUCTION

The purpose of this chapter is to review: non-genetic effects known to influence birth, March and 15-month weight and velvet antler weight of Red deer and the comparable traits of beef cattle; heritability estimates for the above liveweight traits of Red deer and beef cattle; heritability estimates for velvet antler traits in deer; phenotypic and genetic correlation estimates between liveweight traits for Red deer and beef cattle; and the phenotypic and genetic correlation estimates between liveweight traits and velvet antler traits in deer.

2.2 NON-GENETIC EFFECTS

The accurate evaluation of productive differences between animals is fundamental to the genetic improvement of economically important traits. Differences in performance are caused by both genetic and environmental effects. The latter is defined as all the variation in the trait which is non-genetic in origin. The contribution of environmental variation to total variation is important because it is not transmitted from parent to offspring. Its effect is to obscure that part of the variation due to genotype. Reduction of the environmental influence can be achieved either physically or statistically.

Statistical control involves the estimation of the magnitude of non-genetic effects on the recorded trait, and adjustment of the record through the use of factors derived from non-genetic effect estimates.

Adjustment for non-genetic effects is important at the population level, where a major component affecting the rate of genetic gain in the population is the accuracy with which breeding value is predicted, particularly through estimation of the heritability of the specified trait.

Statistical adjustment factors are applied to reduce the contribution of environmental variance to total phenotypic variation relative to that of genetic

variation, with consequent increases in the accuracy of, and rate of response to, selection within the population.

This section will discuss non-genetic effects which have been identified in Red deer and cattle for birth weight, weaning weight and 15-month or yearling weight, and velvet antler weight.

2.2.1 Birth Weight

2.2.1.1 Date of birth

Date of birth (in terms of the time of the fawning season a fawn was born) has been shown to influence fawn birth weight in some studies. Blaxter *et al.* (1974) in Scotland found that fawn birth weight increased by 0.33 kg if it was born a month late, that is, an increase of 0.011 kg per day. Adam and Asher (1986) commented that fawn birth weight was positively associated with birth date for farmed Red deer in New Zealand. However, other studies, Asher and Adam (1985) and Guinness *et al.* (1978a) have found no significant relationship between fawn birth weight and date of birth.

The inconsistent results may be a reflection of the spread of the fawning period in the above studies. Red deer are short-day breeders and conceive under natural conditions in autumn. However, Red deer hinds are polyoestrus, that is, they can have up to five or six cycles in a mating season should they fail to conceive at any one oestrus. Commonly, there is a concentrated annual peak of rutting activity which results in a concentrated fawning. Thus, the majority of fawns are born over a four to six week period (Asher and Adam, 1985).

Date of birth has been shown to significantly influence calf birth weight in a number of beef cattle studies. Carter (1971) found that later born calves were heavier than those born earlier. Ahunu and Makarechian (1986) found that in two out of three cattle lines examined, the linear effect of date of birth was highly significant. In a study of Hereford calves, Koch and Clark (1955a) found the regression of birth weight on weaning age was -0.08 pounds per day, calves born later in the calving season were slightly heavier at birth. They suggested that this slight difference was due to either better pasture conditions or to variation in gestation length of cows.

In a review of beef cattle studies, Sewell *et al.* (1963) showed that a longer gestation length accounted for between five and eight percent of the difference in calf birth weights. Lasley *et al.* (1961) found that length of gestation (days between insemination and birth) was not significantly different for calves born at different times during the calving season but date of birth did have a significant (P<0.01) effect on birth weights.

It appears that date of birth may have an influence on the birth weight of fawns and calves but the extent of this influence probably depends on the spread of the fawning/calving season within the herd. In Red deer herds that have a concentrated fawning this effect on birth weight is not likely to be of consequence.

2.2.1.2 Sex of offspring

The sex of the fawn has consistently been shown to have a significant influence on its birth weight. In farmed Red deer populations males are commonly about 0.5 kg (8 - 10%) heavier than females at birth (Blaxter *et al.*, 1974; Kelly and Whateley, 1975; Hamilton and Blaxter, 1980; Asher *et al.*, 1981; Asher and Adam, 1985). Similar weight differences have also been found in wild Red deer populations in Scotland (Mitchell, 1971; Mitchell and Lincoln, 1973; Guinness *et al.*, 1978a; Clutton-Brock *et al.*, 1981, 1982; Clutton-Brock, 1985).

These findings are consistent with those of beef cattle (Woldehawariat *et al.*, 1977; Koch *et al.*, 1973; Richardson *et al.*, 1978; Ahunu and Makarechian, 1986).

Pabst *et al.* (1977) showed that sex was the greatest source of variation in calf birth weights and that differences due to sex tend to increase with the size of the breed. From the beef cattle literature reviewed, it appears that within a beef cattle breed or line, males are 6 to 10% heavier than female calves at birth.

These results show the importance of adjusting birth weight for the non-genetic effect of sex before genetic comparisons are undertaken.

2.2.1.3 Age of dam

There are few studies in Red deer that have considered the effect of age of dam on birth weight. In Scottish farmed Red deer, Blaxter *et al.* (1974) found that 2 year old hinds (n=41) produced fawns that were approximately 1 kg lighter than 3 year old hinds (n=6). During studies of the wild Red deer population on Rhum in Scotland, Guinness *et al.* (1978a) found that mean fawn birth weight increased with dams age from first breeding at 3 years of age to a peak in dams of 9 to 10 years of age and then subsequently declined. In contrast with the Scottish findings, Asher and Adam (1985) found that 2 year old farmed Red deer hinds in New Zealand (n=3) produced fawns which were nearly the same weight (0.05 kg heavier) on average as older hinds (n=174). However, due to the very small number of 2 year old hinds in this study the results should be treated with caution.

Numerous beef cattle investigations have shown the importance of age of dam influences on calf birth weights. Woldehawariat *et al.* (1977) summarized many of these studies. On average, first calving cows commonly produced the lightest calves at birth, with a steady rise at each age until maturity at approximately 6 to 9 years of age, followed by a decline for cows 10 years of age and older. Similar results have been found in later studies, although the age of dam at which birth weights peak appears to vary among populations of beef cattle. For instance, Ahunu and Makarechian (1986) found that in a crossbred line of cattle, birth weight increased significantly with the increase in age of dam up to 4 years but in the Hereford and Synthetic Breed lines this increase continued to 5 years of age. They found no decline in birth weight with age of dam up to 9 years of age in these lines. Reimer *et al.* (1986) found that calf birth weights were highest for offspring of 9 to 13 year old dams and lowest for those of two year old dams.

Sewell *et al.* (1963) reported that some studies have shown age of dam to have no effect on birth weight while others indicated that maximum birth weight was not reached until cows are 9 to 10 years of age. Thomson (1968) found a steady rise in birth weight of Angus cattle with increasing age of dam to 8 years, then a steady decline.

Elzo *et al.* (1987) study of 839,292 Simmental records, found large age of dam effects for birth weight for young dams relative to mature (5 - 8 year old) dams. Age of dam effects relative to mature age were largest between heifers and

mature cows with the differences decreasing as females matured. Age of dam effects past maturity were again negative. This trend is probably a reflection of a greater ability by mature cows to provide the foetus with the necessary nutrients and environmental conditions for its development. These results also suggest a reduction of this ability in cows older than 8 years of age.

The studies on Red deer show that age of dam can be expected to affect birth weight. The studies on beef cattle clearly show the importance of the effect of age of dam on birth weight, particularly in relation to young dams versus mature dams. These results suggest that the non-genetic effect of age of dam on birth weight should be adjusted for before genetic comparisons are undertaken.

2.2.1.4 Dam liveweight

Although age of dam information is usually readily available at fawning/calving, age *per se* is not the factor being adjusted for. Age of dam merely provides an easily recognizable, albeit closely related, parameter of those aspects of maturity such as development of the mammary gland, milk yield and maternal ability. Body size or liveweight of the dam is also a reflection of maturity.

Several studies in Red deer have shown that hind liveweight, either at the time of the rut or fawning, has a significant influence on fawn birth weight. In the study of Asher and Adam (1985) they found that if fawn birth weight had been previously adjusted for dam pre-rut liveweight then there was no longer any effect of dam age on birth weight. Blaxter and Hamilton (1980) also found that there was no effect from age of hind on fawn birth weight that could not be explained by hind body weight. They calculated that an increase of 20 kg in hind body weight at the time of the rut would increase fawn birth weight by 1.05 kg. Fennessy (1982a) and Adam and Asher (1986) also reported that fawn birth weight was positively associated with hind liveweight.

Several studies in beef cattle have also shown an effect of dam liveweight on calf birth weight. Gregory *et al.* (1950) noted that the cows that were heavier than the mean weight at calving tended to give birth to calves that were heavier than the mean birth weight of all calves. Jeffery and Berg (1972) found that the birth weight of the calf was positively correlated with the body weight and skeletal measurements of its dam. They also found that within breed and age of

dam categories the birth weights of calves were positively correlated with cow-size variables. In the review of Sewell *et al.* (1963) it was reported that the weight of dam at calving was related to the birth weight of the calf to about the same extent as age of dam.

Both age and liveweight are indicators of maturity, however the use of age of dam correction factors to account for differences in dam maturity may be preferable to using liveweight of the dam, as the dam liveweight and offspring birth weight are genetically correlated. Thus, some of the genetic as well as environmental variation would be removed when comparing adjusted birth weight records. The importance of this will depend on the strength of the genetic correlation.

2.2.1.5 Year of birth

The effect of year on fawn birth weight has been shown to be significant in a number of studies of wild Red deer populations in Scotland (Albon *et al.*, 1983a, 1987; Clutton- Brock *et al.*, 1982). These authors postulated that variation in fawn birth weights between years was a consequence of climatic differences, particularly in spring weather conditions, and that these were mediated through the dams weight and condition in spring prior to the birth of the fawn. Studies involving farmed Red deer have noted some differences between years in fawn birth weights but these do not appear to have reached significance (Blaxter *et al.*, 1974; Asher *et al.*, 1981; Asher and Adam, 1985). These studies only involved small numbers of records over a two year period, which may account for the lack of significance. Mitchell (1971) and Guinness *et al.* (1978a) studying wild Red deer also commented on year differences in fawn birth weight but noted their sample sizes were too small to show overall significant differences.

While year of birth has been shown to significantly influence calf birth weights, this effect has not reached significance in all beef cattle studies. For instance, Ahunu and Makarechian (1986) found that year was highly significant (P<0.01) in the Hereford and Synthetic Breed lines but not in the crossbred line. Bailey and Lawson (1986) found that year did not have a significant effect on the birth weights in the Angus and Hereford lines studied. However, Itulya *et al.* (1987) noted that there was a large variation in Hereford birth weights between years.

Generally, most beef cattle studies have found year of birth to be a significant effect on birth weight (for example, Baker *et al.*, 1974; Pabst *et al.*, 1977; Richardson *et al.*, 1978; Wilson *et al.*, 1986).

To overcome differences between years in birth weight, which may be caused by either genetic or environmental trends, some beef cattle studies have been analysed on a within year basis, such as in the study by Baker *et al.* (1974). If birth weights are to be compared across years preliminary analysis of the data should be undertaken to test the significance and importance of this non-genetic effect. If year differences need to be accounted for then BLUP (Best Linear Unbiased Prediction) techniques can be utilized.

2.2.1.6 Herd

In the one study involving a number of herds of Red deer found in the literature, herd was found to have a significant effect on fawn birth weight (Asher and Adam, 1985). In some studies involving wild Red deer populations the effect of region has also been shown to have an effect on average birth weights (Guinness *et al.*, 1978a). In contrast, Mitchell and Lincoln (1973) found there to be no differences in birth weights between areas in Scotland.

In beef cattle studies within breed or strain where data has been drawn from more than one herd, herd effects on calf birth weight are usually found to be significant (Baker *et al.*, 1974; Pabst *et al.*, 1977; Wilson *et al.*, 1986). However, Koch *et al.* (1959) found that the average birth weights between six research stations for several breeds of cattle were similar.

If birth weights are to be compared across herds then preliminary analysis of the data should be undertaken to determine the significance and importance of this non-genetic effect. Ideally, the most accurate adjustments of birth weight will be those developed in the herd in which they are to be applied.

2.2.1.7 Interactions

No significant interactions among the non-genetic effects have been found in the literature concerning the birth weights of Red deer. However, the existence of a number of interactions have been published for beef cattle.

Chapman *et al.* (1972), studying 7 years of Hereford records from 4 herds, found a highly significant (P<0.01) herd by year interaction. In this case the interaction was apparently due to fluctuations in the rank of two herds.

Ahunu and Makarechian (1986) found the year by sex interaction was an important source of variation in calf birth weights in the Synthetic Breed and crossbred lines of cattle studied but not in the Hereford line. They postulated that this interaction was due to a gradually improving environment in which the males expressed greater superiority relative to females.

Where sex by age of dam interactions were tested they were found to be non-significant for birth weight in beef cattle (Koch and Clark, 1955a; Baker *et al.*, 1974; Ahunu and Makarechian, 1986). However, Elzo *et al.* (1987) reported that in Simmental cattle the age of dam effects were smaller for female calves than male calves but that the difference between the age of dam effects on males and females tended to disappear as cows reached mature age.

Chapman *et al.* (1972) found that the interactions of herd by sex and year by sex were not significant in their analysis of Hereford records. No other reports of interactions among non-genetic effects influencing birth weight were found in the literature for beef cattle. Thus, it appears that single sets of correction factors can be established within each breed for each of the major non-genetic effects, although the possible presence of interactions should be tested for.

2.2.2 Weaning Weight

2.2.2.1 Age at weaning

Once the decision has been made to separate offspring from their dams it is convenient for the breeder to wean all offspring in one operation. Since dates of birth will have differed within the herd, the ages of the offspring at weaning will vary. A positive relationship between weaning weight and the age at which weaning occurs should be apparent. However, the nature of this relationship and the relative contribution of age at weaning to the total variation in weaning weight may not be so evident.

The age of the fawn at weaning has been shown to have a major effect on fawn weaning weight. Fennessy (pers. comm.) found that age at weaning controlled approximately 37% of the total variation in weaning weight in 1985 and 1986 in the study of one herd in New Zealand. Blaxter and Hamilton (1980) noted that date of birth, and hence the duration of the suckling period, was the main determinant of weaning weight in farmed Scottish Red deer. Most workers in Red deer have assumed growth to be linear between birth and weaning. Kelly and Drew (1976) reported growth rates of 318 and 287 grams per day for male and female Red deer calves, respectively. Asher and Adam (1985) reported an average figure for both sexes of 310 grams per day and Fennessy (pers. comm.) calculated average growth rates of 378 and 311 grams per day from 1985 and 1986 data, respectively. Asher and Adam (1985) found that the regression of weaning weight on age at weaning was not significant (P>0.10, n=473) after prior adjustment for dam liveweight and birth weight, even though fawning was spread over three months.

Adam and Moir (1987) showed that fawn growth rate varied with the age of the fawn. They weighed 66 fawns at 2 weekly intervals from birth to 14 weeks of age. From 0 to 2 weeks of age, mean fawn liveweight gain was 546 grams per day. Liveweight gain declined steadily to be 262 grams per day between 12 to 14 weeks of age. The overall mean liveweight gain was 367 grams per day. However, these results were in contrast with those of Loudon et al. (1984) who found that fawns tended to maintain their growth rate from birth to 14 weeks of age. Loudon et al. (1984) weighed the fawns at 10-day intervals from 0 to 100 days of age. Over this period, there was a slight but steady decline in fawn liveweight gain within each of the three nutritional treatment groups. All three groups maintained a growth rate of 300 - 400 grams per day during the first 30 days. Between days 30 and 70, the liveweight gains of fawns were considerably greater for those fawns whose dams were grazed on improved pastures than for those fawns whose dams were grazed on indigenous Scottish hill pasture. However, between days 70 and 100 liveweight gains of calves on the indigenous pasture were greater than those on the improved pastures. The mean fawn liveweight gains form 0 to 100 days were 283, 319 and 369 for the indigenous pasture, improved pasture maintained at 1500 kgDM/ha and improved pasture maintained at 2000 kgDM/ha, respectively.

From these studies it appears that fawn liveweight gain may not be linear from birth until weaning at 12 to 14 weeks of age and that the amount of curvilinearity is affected by the nutritional conditions to which the dam is subjected. Therefore, it is conceivable that, mean fawn growth rates will vary among herds and even within paddocks within farms. This will affect the magnitude and type of correction factor to be applied for the age of the fawn at weaning. Practically, it is probably adequate to calculate the mean growth rate from birth to weaning or use the regression coefficient of age at weighing on weaning weight.

Most studies have shown that the growth of beef calves tends to be linear in the period of 5 to 8 months of age, the time at which weaning generally occurs (Nicoll, 1975). Swiger *et al.* (1962) reported that the liveweight gains of 2739 beef calves were linear up to 130 days of age, but curvilinear from 130 to 220 days of age. Rhodes *et al.* (1970) found significant negative quadratic values were obtained for the regression of age at weaning on weaning weight which indicated that the rate of weight gain declined with increasing age. Marlowe *et al.* (1965) believed that seasonal and age effects were confounded in the study of Swiger *et al.* (1962), and they maintained that after removal of seasonal influences, growth of the calves was generally linear from 120 days to weaning. Baker *et al.* (1974) using the growth data of 4893 calves, from the Waikeria and Waikite experimental beef breeding locations of New Zealand, failed to establish any departure from linearity in the regressions of age at weaning on weaning weight over several years.

The relative contribution of age at weaning to the total variation in weaning weight has generally been regarded to be of importance in beef cattle. Carter (1971) observed age differences accounted for 15 to 30% of the variation in liveweights at weaning in an investigation of selection on performance in beef cattle in New Zealand. Vesely and Robison (1971) noted the importance of age at weaning in 1692 Hereford weaning records, although sex of calf was found to be a more important source of variation in weaning weight based on the proportions of total sum of squares. Baker *et al.* (1974) concluded that the most important single source of variation was that due to the regression of weaning weight on age at weaning which accounted for between 23 and 29% of the total variation in weaning weight. Nicoll and Rae (1977) also found that the regression of weight on age at weaning was the most important single source of variation in the weaning weights of 7771 Hereford and 16666 Angus calves.

Other studies have also shown the significant influence of age at weaning on weaning weight but have not indicated the relative importance of this effect (Magee *et al.*, 1961; Harwin *et al.*, 1966; Rhodes *et al.*, 1970; Singh *et al.*, 1970; Jeffery *et al.*, 1971).

These studies on Red deer and beef cattle clearly show the need for adjustment of weaning weight for age at weaning.

2.2.2.2 Sex of offspring

Differences in weaning weight due to sex have been shown in several studies of farmed Red deer with stag fawns always being heavier than hind fawns. In New Zealand farmed Red deer, Asher and Adam (1985) observed a difference of 2.7 kg (6.9%) between the sexes in 176 records and Fennessy (1986b) noted a difference of 5 kg (10 - 12%) over several sets of farm records. A difference of 3.9 kg (11.5%) was derived from the study of Adam and Moir (1987) for 66 Scottish farmed Red deer fawns.

The magnitude of sex differences of beef cattle for weight at weaning in the reviewed literature has varied from herd to herd, but in all cases the weaning weights of males have exceeded those for females when ages at weaning have been at least 180 days, except Gregory *et al.* (1950) who found no significant differences due to sex in either 150- or 200-day weaning weight in 237 beef cattle records. This was attributed to the fact that large variations in weights and gains had occurred at both stations involved in this study.

Rhodes *et al.* (1970), Baker *et al.* (1974), Anderson and Wilham (1978), Leighton *et al.* (1982) and Wilson *et al.* (1986) have all found that sex of calf exerted a highly significant influence on calf weaning weight. Koch and Clark (1955a) found Hereford male calves to be nearly 12 kg heavier than females for weaning weight adjusted to 182 days of age. Lasley *et al.* (1961) found with Hereford cattle in Arizona that bull calves weighed an average of 12 kg more than heifer calves at weaning at an average of 210-days of age. Thomson (1968) found that Angus bulls in the United Kingdom were 21% heavier than heifers at 200 days of age. Srinivasan and Martin (1970) found that bull calves were 8.2 and 18.2 kg heavier than heifer calves at 120- and 210-day weight respectively.

Singh *et al.* (1970), Nicoll and Rae (1977), Ahunu and Makarechian (1986) and Itulya *et al.* (1987) all found that males were heavier than females at weaning regardless of beef cattle type in the study.

Cundiff *et al.* (1966a) reported sex to be the most important factor influencing weaning weight, accounting for 17% of the total variation in weight adjusted to 205 days of age in Angus and Hereford cattle. Baker *et al.* (1974) found the effect of sex to be highly significant (P<0.01) accounting for 7.3 and 3.9% of the variation at the Waikeria and Waikite locations of New Zealand, respectively. Pabst *et al.* (1977) showed that sex was the main source of variation in 200-day weight. They found that differences due to sex tended to increase with the size of breed.

These studies on Red deer and beef cattle clearly show the need for adjustment of weaning weight for the non-genetic effect of sex.

2.2.2.3 Age of dam

Few studies of Red deer have involved the investigation of the effect of age of dam on fawn weaning weight *per se*. Asher and Adam (1985) reported that 2 year old hinds (n=3) produced fawns that were 5.1 kg (13.3%) heavier than older dams (n=173). However, due to the small number of 2 year old dams involved in this study this estimate should be treated with caution. Fennessy (1986b) notes that from the analysis of records from several herds, fawns reared by 2 year old hinds were about 10% lighter than fawns from older hinds, even at the same hind weight.

Numerous investigations in beef cattle have drawn attention to the importance of age of dam influences on the weight of the calf at weaning. Such studies have shown that the maximum production in terms of calf weaning weight appears to be attained when the dams are approximately 6 to 9 or more years of age (Thomson, 1968; Rhodes *et al.*, 1970; Srinivasan and Martin, 1970; Woldehawariat *et al.*, 1977; Anderson and Wilham, 1978; Simm *et al.*, 1985; Elzo *et al.*, 1987).

Pabst *et al.* (1977) found that calves from 2 year old dams had 200-day weights that were 5 to 11% lower, depending upon the breed, than calves from dams between 5 and 8 years of age. Similarly, calves from 3 year old dams had 200-

day weights between 2 and 9% lower than calves from 5 to 8 year old dams. They found no consistent pattern in the breeds studied for the effect of age of dam above 5 years of age although there was a tendency for some breeds to decline after 10 years of age. The effect on 200-day weights of calves due to age of dam in older cows is very dependent upon the culling and selection policies amongst the cows in the particular populations (Brinks *et al.*, 1962; Swiger *et al.*, 1962; Swiger *et al.*, 1963).

Nicoll and Rae (1977) with 7771 Hereford records found that the weaning weights of calves out of dams 2, 3, 4, 5 and 10 years of age and older deviated from those of calves out of mature dams (6 to 9 year old) by 33.3, 17.6, 8.7, 3.8 and 2.2 kg, respectively. For the 16666 Angus records the deviations were 22.7, 15.2, 7.9, 5.4 and 1.4 kg, respectively.

Several authors have postulated that it is the milk production of the dam that has the major effect on the weaning weight of the calf rather than dam age *per se* (Neville, 1962; Thomson, 1968; Elzo *et al.*, 1987; Itulya *et al.*, 1987). As cows mature, they become heavier, produce more milk and raise faster-gaining calves. From the study of Jeffery *et al.* (1971) it can be inferred that physiological changes associated with maturity other than size of dam could have some influence on preweaning performance of progeny. This may be largely a reflection of an association between maturity and milk production, independent of size.

Jeffery *et al.* (1971) considered the effect of milk yield of dam and found it to explain about 60% of the variation in average daily gain from birth to weaning and 40 to 50% of the variation in weaning weight. Breed of dam explained a further 23% of the total variance in average daily gain from birth to weaning in this study. The authors postulated that most of which was accounted for by breed differences in milk yield.

Neville (1962) found that no important influence for age of dam was found when age of dam differences were adjusted for variations in liveweight and milk production of dams. In this study milk production of the dam was found to control 66% of the total variance in 8 month weight of the calf.

Several authors have pointed out that the calculation of age of dam correction factors may be biased since cows are retained in a herd because of their ability to produce heavy calves at weaning (Swiger *et al.*, 1962; Cundiff *et al.*, 1966a). Thus, age of dam estimates are biased downward slightly in the younger age groups and upward slightly in the older age groups due to selection for cow productivity. Lush and Shrode (1950) have shown that such a bias can exist, when corrections are computed by comparing averages of records made at each age of dam. However, Marlowe *et al.* (1965) computed age of dam correction factors by either comparing the averages of all records at all ages or by comparing the records of mature cows (6 years of age and older) with their own records at younger ages. They concluded that either little selection was made for cow productivity or that selection was not very effective. In view of these findings it does not seem necessary to adjust age of dam estimates for the effect of selection. This is particularly so for Red deer, as little dam selection will have been undertaken due to the rapid increase in farmed Red deer numbers.

Age of dam effects have been shown to be an important influence on the weaning weight of calves (Magee *et al.*, 1961; Cunningham and Henderson, 1965; Sellers *et al.*, 1970; Singh *et al.*, 1970; Srinivasan and Martin, 1970; Nicoll and Rae, 1977; Leighton *et al.*, 1982). Dam age accounted for between 19 and 37% of the variation in bulls weaned at 168 days of age (Simm *et al.*, 1985). Cundiff *et al.* (1966a) found dam age to account for 7% of the total variation in weaning weight. Pabst *et al.* (1977) found dam age to account for between 1.8 and 2.8% of the variation in weaning weight depending upon the breed. Baker *et al.* (1974) found age of dam to account for 9.8 and 6.0% of the variation in the Waikeria and Waikite locations of New Zealand, respectively.

2.2.2.4 Dam liveweight

Several studies on Red deer have shown that the liveweight of the hind at the time of the rut has an effect on the subsequent preweaning average daily gain and weaning weight of the fawn. Blaxter and Hamilton (1980) found this to be a positive relationship, from five years of data in Scotland, however the effect was only significant in the good pasture growth year (1976) but not in the poor pasture growth year (1978). Asher and Adam (1985) found there to be a positive relationship between dam liveweight taken in March at the previous weaning and her offsprings liveweight gain from birth to weaning and weaning weight

(P<0.05), with regression coefficients of 0.624 grams per day and 0.074 kg, respectively, for each 1 kg increase in dam March liveweight. In their study, dam age was not significant for either of these traits, although there was only a very small number of first-fawning hinds included and the remainder of the age groups were classified together.

Several beef cattle studies have also shown a positive effect of dam liveweight on subsequent calf performance. For example, Gregory et al. (1950) noted that cows that were heavier than the mean weight at calving tended to wean calves that were heavier than the mean weight of all calves. However, this relationship was not consistent for both herds in the study. They also considered changes in cow liveweight over lactation and found that the cows making the smallest gains during the nursing period tended to produce calves that made the greatest gains. Jeffery et al. (1971) included cow summer weight gain and winter weight loss in their regression model for weaning weight. They found that these variables contributed little toward explaining additional variance in preweaning performance over and above milk yield of the dam and concluded that these variables could be omitted from the model. They also found that cow age (linear and quadratic) alone accounted for 59% of the total variance in post calving weight of the cow. The relationship was essentially linear as cow age squared only added 3.4 and 1.1% in explaining total variance in post-calving cow weight over cow age for 1966 and 1967, respectively. Jeffery et al. (1971) found that a 10 kg increase in post calving cow weight, independent of milk yield and cow age resulted in approximately a 0.7 kg increase in weaning weight of calf. Similar results were reported by Jeffery and Berg (1972).

Thus, from the results of Jeffery et al. (1971) it appears that there is little advantage in using either cow liveweight or change in cow liveweight during lactation in preference to age of dam as a predictor of non-genetic effects mediated through the maternal environment.

2.2.2.5 Year of birth

Only one study on Red deer found in the literature considered whether year of birth effects influence weaning weight. This is largely because most investigations of farmed Red deer have been conducted on a within year basis. Hamilton and Blaxter (1980) found that year of birth had a significant effect on growth from birth to weaning in farmed Red deer in Scotland.

The year in which beef calves are born can be expected to have an important influence on their liveweights at weaning, as reported by Neville (1962), Cunningham and Henderson (1965), Harwin *et al.* (1966), Sellers *et al.* (1970), Singh *et al.* (1970), Srinivasan and Martin (1970), Nicoll and Rae (1977), Pabst *et al.* (1977), Ahunu and Makarechian (1986), Bailey and Lawson (1986) and Itulya *et al.* (1987).

Baker *et al.* (1974) found year effects accounted for 4.9 and 0.8% of the total variation in weaning weight at the Waikeria and Waikite locations of New Zealand, respectively. Nicoll (1975) found year effects accounted for 2.7 and 2.5% of the variation in weaning weights of Hereford and Angus cattle, respectively. Dodd (1977) found year effects to be important for weaning weight in Friesian-cross calves, accounting for about 6% of the total variation, but year was not significant for Angus calves. Simm *et al.* (1985) found that year/season of birth accounted for up to 31% of the variation in liveweight in a study of 235 performance tested Hereford bull calves.

Variation among weights at weaning should not only be attributed to the environmental effects of year *per se*, but also to any change in genetic merit of the herd for weaning weight caused by culling. Using the average weaning weights of all calves born within a year as a basis for adjustment would not differentiate between genetic and yearly influences. There have been few attempts to eliminate the confounding of genetic change with year effects on weaning weight in beef cattle. Sewell *et al.* (1963) endeavoured to remove genetic change from estimated year adjustments by using the average weaning weights of calves from 19 cows that were producing in all but the first (1951) and last (1961) years considered in the study. The weights of calves from these cows were averaged by years and used as adjustment factors to adjust weaning weights to a base year (1953). Itulya *et al.* (1987) used a similar technique to standardize age adjusted weaning weight to the average of 7 year old dams in 1975 to account for large significant variation due to year, age of dam and their interaction. Commonly, year effects on beef cattle weaning weights have been regarded in the literature as a reflection of the variation in environmental conditions from year to year, either within- or between-herds.

The inability inherent in least squares analyses to completely separate the confounding effects of genetic and environmental trends in yearly variation must limit the advisability of computing year of birth adjustment factors for weaning

weights or any other weights. Over short time spans, say one generation, this is unlikely to be important as annual genetic gain is comparatively small, only 1 to 2% of the mean. Unlike other non-genetic influences affecting weaning weight such as sex of calf, where adjustments can be based on the male sex for example, it would be difficult to determine the most suitable year on which to base adjustments for year of birth. Consequently the computation of adjustment factors for year of birth is not usually practiced. Recommendations normally rely on the comparison of weaning weights adjusted for age and age of dam within years. This is usually adequate as selection on individual weaning weight performance is commonly practiced on a within year basis. If year differences need to be accounted for then BLUP analyses can be utilized.

2.2.2.6 Herd

Only one study involving a number of herds of Red deer was found in the literature. Asher and Adam (1985) found the effect of herd on weaning weight to be significant. Two confounding situations were apparent in this study, namely, the level of nutrition prior to and during the fawning/lactation period and the genetic origins of the stock.

Herd effects have been shown to significantly influence beef cattle weaning weights in a number of studies (Cunningham and Henderson, 1965; Chapman *et al.*, 1972; Nicoll and Rae, 1977; Wilson *et al.*, 1986). Other studies have attempted to combine data from several herds which are similar in performance level (Pabst *et al.*, 1977) or on regional basis, on the assumption that preweaning management and climate are similar throughout the region (Schaeffer and Wilton, 1974a).

The significance of the effect of herd reflects differences in genetic potential for postpartum maternal traits in the dams and for growth capability in the calves, and differences in management and feeding levels.

Ideally, the most accurate adjustments of weaning weight for non-genetic effects will be those developed in the herd in which they are to be applied. However, for the estimates of non-genetic effects to act as reliable adjustment factors, particularly within years (Baker *et al.*, 1974), the herd size should be relatively large.

2.2.2.7 Interactions

No significant interactions among the non-genetic effects have been found in the literature concerning the weaning weights of Red deer. However, the existence of a number of interactions and heterogeneous regressions between fixed effects and covariates have been published for beef cattle.

Swiger *et al.* (1961) noted that the regression of weaning weight on age of calf was heterogeneous between sexes (P<0.01) but the regressions of weaning weight on age of calf were homogeneous between years and age of dam classes. This meant the bulls and heifers grew at different rates up to weaning. This effect has been shown in some other investigations (see, for example, Koch *et al.*, 1959; Sewell *et al.*, 1963). Harwin *et al.* (1966), from a preliminary investigation of Hereford cattle data, found that the age of calf by year regression could be an important source of variation and suggested the use of within-year regressions on individual daily gain to adjust calves to a constant age.

An interaction between sex and age of dam has been shown to be significant in a number of studies (Harwin *et al.*, 1966; Sellers *et al.* 1970; Srinivasan and Martin, 1970; Baker *et al.*, 1974; Schaeffer and Wilton, 1974a; Anderson and Wilham, 1978; Leighton *et al.*, 1982; Elzo *et al.*, 1987; Itulya *et al.*, 1987). However, in other studies, the sex by age of dam interaction was non-significant (Koch and Clark, 1955a; Swiger, 1961; Cunningham and Henderson, 1965; Minyard and Dinkel, 1965; Cundiff *et al.*, 1966a; Nicoll and Rae, 1977). Baker *et al.* (1974) found that the sex by age of dam interaction controlled 0.2 and 0.4% of the total variation in weaning weight at the Waikeria and Waikite locations, respectively. They found that male calves from 2 year old dams were 31 kg (23%) lighter at 6-months of age than those from mature dams at the Waikite location. The corresponding difference for female calves being 17 kg (14%). Ahunu and Makarechian (1986) found a significant sex by age of dam interaction in the crossbred line but not in the Hereford and Synthetic Breed lines in their study. Harwin *et al.* (1966), Anderson and Wilham (1978) and Elzo *et al.* (1987) postulated that the sex by age of dam interaction may be occurring because young cows, and cows past maturity, meet the maintenance and preweaning growth requirements of female calves to a larger extent than

those of male calves. Although there does not seem to be a sex by age of dam interaction in all herds, it appears sufficiently common to justify separate age of dam adjustment factors for each sex.

Cunningham and Henderson (1965) found that the sex by year interaction bordered on significance at the 5% level, but did not include it in their model as it did not appear to a have a large effect on weaning weight. Harwin *et al.* (1966) found that there was a trend for the sex by year interaction to be a significant source of variation, especially in good pasture growth years. Srinivasan and Martin (1970) found that year by sex was a significant source of variation affecting 210-day weight. Baker *et al.* (1974) reported significant year by sex interactions at both locations in their study. Ahunu and Makarechian (1986) showed a significant year by sex interaction in the crossbred line of cattle. This they believed, was due to males expressing a greater superiority relative to females for preweaning average daily gain and weaning weight as environmental conditions gradually improved. As most comparisons are commonly conducted on a within-year basis, this interaction is not considered to be of great importance.

Schaeffer and Wilton (1974a) reported a significant sex by level of herd performance interaction, where herds were categorized into high, average and low levels of weaning weight performance. Chapman *et al.* (1972) and Baker *et al.* (1974) found the herd by sex interaction to be non-significant in their studies. Nicoll and Rae (1977) found the herd by sex interaction to be important for the Angus breed but not for the Hereford breed from New Zealand records. Nicoll and Rae (1977) felt that this interaction may have arisen through differential preweaning management policies giving the males a greater opportunity to realize their superior growth potential. As comparisons are commonly conducted on a within-herd basis this interaction is not considered to be of great importance.

Significant age of dam by year interactions have been noted in some studies (Swiger, 1961; Koger *et al.*, 1962; Harwin *et al.*, 1966; Itulya *et al.*, 1987). However, other studies have found this interaction to be non-significant (Cunningham and Henderson, 1965; Srinivasan and Martin, 1970; Nicoll and Rae, 1977). Baker *et al.* (1974) showed that the significant (P<0.01) age of dam by year interaction accounted for 1.9 and 1.2% of the total variation in 6-month

weight of beef calves at the Waikeria and Waikite locations, respectively. Both Harwin *et al.* (1966) and Itulya *et al.* (1987) postulated that the significant year by age of dam interaction results from younger cows being more adversely affected than older cows in poor versus good environments. Moreover, as Itulya *et al.* (1987) pointed out, it is possible that the relatively poor performance of older cows in years during which young cows performed well indicates decreased ability to take full advantage of abundant forage.

Schaeffer and Wilton (1974a) showed a significant age of dam by level of herd performance interaction in which increases in cow age apparently resulted in smaller increases in calf gains at higher herd performance levels than at lower herd performance levels. Baker *et al.* (1974) did not find the age of dam by herd interaction to be significant. Simm *et al.* (1985) pointed out that differences in the age structure of herds may have caused confounding of dam age and herd effects in some of the published results.

Important herd by year interactions have been reported in the studies of Chapman *et al.* (1972), Baker *et al.* (1974) and Nicoll and Rae (1977) for Hereford and Angus cattle data. The possibility of a large between-year variation among herds suggests the limited applicability of standardized adjustment factors in some years. The existence of such an interaction would indicate that weight comparisons, to be accurate, should be made on a within-herd-year basis for selection of the improvement of calf weaning weights.

The importance of a number of interactions between the non-genetic effects for weaning weight suggests that age of dam effects should be calculated for each herd and year separately, and possibly for each sex. Baker *et al.* (1974) also recommended the estimation of an approximate regression coefficient for age at weaning within each herd-sex-year group as a basis for adjustment of age effects. Koger *et al.* (1962) commented that although sex effects were less affected than age of dam effects by environmental factors, indiscriminate use of correction factors, especially for age of dam, may introduce more serious errors than working with unadjusted data. Clearly, adequate numbers of calves within each herd-year group would be needed to provide reliable estimates.

A further non-genetic effect that should be noted is that of a mating paddock effect. This has been shown to account for up to 15% of the variation in weaning weight (Carter, 1971). Baker *et al.* (1974) also note that paddock

differences in feed availability could account in part for the interactions between years and herds, as herds were not always grazed together in their study, and between years and sexes, as sexes were separated after weaning.

2.2.3 15-Month Weight

There has been very little investigation of the effects which influence 15-month weight in Red deer. This weight is important as most males are slaughtered for venison between 14- and 17-months of age and females are mated for the first time under farming conditions. Reports of beef cattle studies considering the influence of non-genetic effects on yearling to 18-month weight will be reviewed as a guide to the likely importance of these effects in Red deer.

2.2.3.1 Age at weighing

No studies of this effect were found in the literature concerning Red deer. Few studies of beef cattle have considered this influence *per se*. Instead age effects have been excluded in the majority of investigations by conducting the study at a set age, for example, 400-day weight (Pabst *et al.*, 1977).

Brinks *et al.* (1962) found age to significantly (P<0.01) affect final weight of Hereford bulls at approximately 376 days of age, at the end of a 196-day performance test. They found the regression coefficient of final weight on age of 0.86 kg was similar to the average preweaning daily gain of 0.88 kg. Baker *et al.* (1974) also found that regression of 13-month weight on age to be significant (P<0.01) at both the Waikeria and Waikite locations of New Zealand. This regression accounted for 14.3 and 15.0% of the total variation at each location, respectively. This was the most important single source of variation, indicating that it is a very important effect at 13-month age in Hereford and Angus cattle and their cross. It should be noted that the contribution of this regression in accounting for variation had declined from 6-month weight, and continued to decline to 18-months of age, but its effect remained significant and important to that stage.

Nicoll and Rae (1978) studied 4703 Hereford and 10226 Angus 18-month weight records in New Zealand. They found the regression of 18-month weight on age at weighing to be highly significant (P<0.001). However, this effect did

not control as much variation when estimated within breed and sex as it had for weaning weight, as herd and herd by year effects had become relatively more important.

In contrast to these results the investigation of Koch and Clarke (1955a) on the 18-month weight of Hereford heifers appeared to indicate that regression of weight on age was of no practical importance. The range of days of age appeared to be small in the study as indicated by the standard deviation of 13 days for age at weaning. This may have contributed the lack of importance of age at weighing.

The effect of age at weighing on 12- to 18-month weight is often significant, but not always of practical importance. The importance may be affected by the range of ages found within the herd. If there is a wide range of ages when the 15-month weight is taken then adjustment for age at weighing appears to be necessary.

2.2.3.2 Sex

Red deer studies concerning 15-month weight in both hinds and stags have consistently found that stags are heavier than hinds. Fennessy (1983) calculated that by 15-months of age, farmed Red deer hinds would have reached about 75% of their mature body weight, and stags about 55%, due to hinds having a lower growth rate from weaning to 15-months of age. Adam and Asher (1986) also noted that males have a higher average daily gain from weaning to 15-months of age and 15-month liveweight than females. Suttie *et al.* (1987) found that intakes and growth rates between the sexes were similar to 6-months of age but after that time males grew faster. In their study, 15-month old stags were 34 kg (41%) heavier than hinds of the same age.

Thompson (1968) found Angus bulls in the United Kingdom to be 37% heavier than heifers at 300 days of age and 40% heavier at 400 days of age. In beef cattle Baker *et al.* (1974) found that the effect of sex was highly significant (P<0.001), controlling up to 11.3% of the total variation in 13-month weight. Differences in weight due to sex effects increased from birth to 18-months of age (Baker *et al.*, 1974). Pabst *et al.* (1977) found sex to be the main source of variation in both

200- and 400-day weights. The effect of sex increased with age. They found that heifers were 8% lighter than bulls at 200-days and 30% lighter by 400-days of age.

From these studies it appears that sex has a major effect on 15-month liveweight. Due to large differences between sexes at this time and as males and females tend to be run separately from weaning, and selection is within sex, some studies analysed the sexes separately (see, for example, Nicoll and Rae (1978)).

2.2.3.3 Age of dam

No studies involving the effect of age of dam on 15-month liveweight in Red deer were found in the literature. Several studies have considered this effect in beef cattle and have found that age of dam continues to exert a significant influence on yearling to 18-month liveweights.

Brinks *et al.* (1962) found age of dam to be highly significant for 376-day weight of performance tested Hereford bulls, with the age of dam constants being very similar to those of weaning weight. This implies that there was little compensatory growth from weaning to 375-days of age due to preweaning maternal environment.

Thompson (1968) found that there was a steady rise in adjusted 400-day weights of Angus bulls and heifers as age of dam increased up to 5 years. He did not find any further effect as age of dam increased past 5 years of age.

Baker *et al.* (1974) found age of dam to have a highly significant (P<0.01) effect on the 13-month weight of Angus and Hereford cattle and their crosses. Although, as calves grew older the relative contribution of age of dam declined. In their study, dam age accounted for 2.5 and 1.4% of the total variation at the two locations, respectively. They found that in absolute terms, the average handicaps incurred by calves from younger dams declined from weaning to 12-months of age, but thereafter showed little change through to 18-months of age. Age of dam classes were only significant for 2 year old versus older dams at 13-months of age. Baker *et al.* (1974) also noted that age of dam correction factors for 6- to 13-month liveweight gain showed that calves out of cows younger than 5 years of age grew faster than calves out of 5 year old and older cows over this period, thus providing evidence for compensatory gain.

Nicoll and Rae (1978) examined the 18-month weight records of Angus and Hereford cattle within breed and sex and found that age of dam was a highly significant (P<0.001) source of variation and was of practical importance. They found age of dam influences to be of the same magnitude as those on weaning weights reported by Nicoll and Rae (1977). They also concluded that post-weaning growth does not always compensate for preweaning maternal environment.

Koch and Clarke (1955a) showed that the effect of age of dam at yearling age was smaller than that at weaning. They postulated this was due to the tendency of calves to grow more rapidly following periods of limited feed supply, in their case possibly because of differences in milk supply. They found that yearling weight varied in a similar manner to weaning weight for age of dam effects up to dams of 6 years of age, but that yearling weight continued to increase with dam age over 6 years of age, unlike weaning weight which declined. This may possibly be due to sampling errors.

Pabst *et al.* (1977) showed that age of dam had a less pronounced effect on 400-day weights of calves than at 200-days, but was still significant and accounted for 1.2% of the total variation. The effect of age of dam influences were similar to that for 200-day weight, with calves born out of 2- and 3-year old dams having the lowest 400-day weights. Pabst *et al.* (1977) also noted that the relative size of the constants in relation to the means was lower, reflecting compensatory growth of calves between 200- and 400-days of age.

As these studies consistently show an age of dam influence on yearling to 18-month weights of beef cattle, albeit reduced from the influence shown at weaning, it appears necessary to consider adjusting later weights for this effect.

2.2.3.4 Dam liveweight

No studies regarding the environmental effect of dam liveweight on offspring liveweight at 15-months of age were found in the literature for either Red deer or beef cattle. From the previous discussion of this influence on weaning weight (Section 2.2.2.4) it is possible that this may have some effect at later weights, but it is likely to be of smaller magnitude, as shown by age of dam effects on later weights.

2.2.3.5 Year of birth

No studies regarding the importance of year effects on 15-month weight were found in the literature for Red deer. However, a number of studies have shown this effect to be of importance for yearling to 18-month weight in beef cattle.

Baker *et al.* (1974) found year to be highly significant (P<0.01) for 13-month weight. Year controlled 8.8 and 20.2% of the variation at the Waikeria and Waikite locations, respectively. Pabst *et al.* (1977) found that year of birth had a significant influence on 400-day weight in most but not all of the breeds in their study. Nicoll and Rae (1978) also found significant (P<0.001) year of birth effects for 18-month weights in Angus and Hereford records gathered over 8 years.

2.2.3.6 Herd

No studies regarding the effect of herd on 15-month weight were found in the literature for Red deer. Baker *et al.* (1974) found that the effect of herd was not significant in their studies of 13-month weight in beef cattle from two herds. In contrast, Nicoll and Rae (1978) found herd to be a highly significant (P<0.001) source of variation for 18-month weight in Angus (33 herds) and Hereford (16 herds) beef cattle data. In their study, herd was the most important single source of variation. Differences due to herd would be expected, due to genetic and environmental differences between herds as discussed for weaning weight in Section 2.8.2.6.

2.2.3.7 Interactions

No interactions among the non-genetic effects were found in the literature concerning the 15-month weights of Red deer. However, several interactions have been noted in yearling to 18-month weight studies of beef cattle.

Sex by year interactions were found to be significant (P<0.01) in the study of Baker *et al.* (1974) at both locations, accounting for approximately 4.3% of the total variation in 13-month weight. The sex by herd interaction was also significant (P<0.01) in that study but only accounted for 0.4% of the total variation. In one of the two herds the sex by age of dam interaction was significant and controlled 0.3% of the total variation.

Significant age of dam by year interactions for 13-month and later weights have been reported by both Baker *et al.* (1974) and Nicoll and Rae (1978). This effect controlled 1.1 and 0.6% of the total variation in 13-month weight at the Waikeria and Waikite locations, respectively (Baker *et al.*, 1974). Nicoll and Rae (1978) found this interaction significantly affected the weights of Hereford males and Angus females only.

Nicoll and Rae (1978) found herd by age of dam interactions to be significant (P<0.05) in all groups in their study except for Hereford males. Baker *et al.* (1974) did not find this interaction to be significant.

Both Baker *et al.* (1974) and Nicoll and Rae (1978) have reported significant herd by year interactions. In the study by Nicoll and Rae (1978) this interaction was sufficiently large to be considered of practical importance. In their study, this interaction controlled as much variation as age at weighing, second only to herd effects.

Baker *et al.* (1974) noted that regression coefficients for age were not significantly different between years in their study of 13-month weight in beef cattle.

Due to the presence of a number of interactions among the non-genetic effects, particularly those involving herd and year effects, correction factors should be calculated on a within herd and year basis. Nicoll and Rae (1978) also

recommended that animals be compared on a within sex basis due to large weight differences between sexes in cattle by 18-months of age.

2.2.4 Velvet Antler Weight

2.2.4.1 Spiker velvet antler weight

Antler growth begins with pedicle initiation in stags at approximately 8 - 9 months of age (Fennessy, 1982a). Should the antler be harvested while still in velvet, the product is known as spiker velvet. Due to the small quantity and low quality, spiker velvet is not usually harvested. Instead, the antlers are removed when they have hardened at approximately 12 - 13 months of age. As spiker velvet has not been considered to be of economic importance, few investigations of the non-genetic effects influencing spiker velvet have been conducted.

In a study of 100 wild yearling Red deer stags, in Scotland from 1970 to 1976, Clutton-Brock *et al.* (1982) found that hard antler length at 16 months of age was significantly related to birth date and weight. Therefore, male fawns born after the median birth date or below the median birth weight had smaller antlers as yearlings than those born before the median date or above the median weight. From this study it can be surmised that age at velvet harvest and liveweight (at harvest or at the commencement of antler growth) will have an effect on spiker velvet weight. If liveweight has an effect on spiker velvet weight, then those non-genetic effects identified for March weight and/or 15-month weight, may be of relevance to spiker velvet weight.

2.2.4.2 Two year old velvet antler weight

In order to provide a high quality uniform product and to compare stags within the same age, velvet antler is commonly harvested at the same stage of growth. As the commencement of velvet growth (casting of the old antler stubs) varies between stags, the actual date of harvest will also vary. However, practical considerations on farms may mean that velvet antler from 2 year old stags is not all harvested at the same stage of growth. Two year old stags are probably run in for velvet antler harvest on only one or two occasions. In order to standardize

for the stage of growth, Fennessy (1983) calculated a set of correction factors which standardized yield to a '60-day growth period'. These are multiplicative factors based on the actual number of days of growth (Table 2.2.4.2.1).

Table 2.2.4.2.1: Multiplicative adjustment factors for velvet growth of 2 year old stags (from Fennessy, 1983).

Growing period (days from casting to harvest)	Adjustment factor
40	1.9
45	1.6
50	1.3
55	1.1
60	1.0
65	0.9

These adjustment factors assume that all 2 year old stags have been run in the same environment and are compared on a within herd and year basis. Huxley (1931) studying wild stags in Europe and the United Kingdom, noted that presumed rates of antler growth between casting and final weight were more different between stags than the final size of antlers attained. The importance of this has yet to be determined for velvet production, as velvet harvest should be completed before mineralization of the antler begins. There is some evidence that level of nutrition in late winter may affect casting and velvet antler yield (Fennessy, 1982a). Huxley (1931) noted that there was a marked seasonal effect (year effect) on antler growth. Hyvarinen *et al.* (1977) also noted that year had a marked effect on hard antler weight of 1 to 4 year-old experimental stags in Scotland.

Body weight has been shown to affect antler weight (Huxley, 1931; Hyvarinen *et al.*, 1977; Zhou and Wu, 1979). Hyvarinen *et al.* (1977) found that hard antler weight was more related to body weight at the end of the velvet growth period than to body weight gain from pre-cast to hard antler. They concluded that

antler growth depended not only on the stags nutrition and weight gain during the summer months but also on the size and the state of maturity reached by the stag at the commencement of antler growth.

The effect of liveweight on velvet production has yet to be determined for farmed Red deer, particularly within age groups.

2.2.4.3 Later ages

Hard antler weight increases with age, to reach a maximum at approximately 7 to 9 years of age in Red deer (Huxley, 1931; Blaxter *et al.*, 1974). Zhou and Wu (1979) found that velvet antler weight increases to 7 years of age in Sika deer, and then gradually declines. However, antler production was relatively steady between 4 and 11 years of age.

Clearly, if the velvet production of young stags is to be compared with older stags, or antler weights are to be adjusted to a mature age basis, then adjustment for the age of the stag is required.

2.3 ADDITIVE VERSUS MULTIPLICATIVE CORRECTION FACTORS

Once estimates of the environmental effects are obtained, they can be utilized as either additive or multiplicative adjustments. Records are additively adjusted by adding the differences between the mean values of the base and remaining subclasses. Multiplicative adjustments are the ratios of the mean value of a subclass to a base subclass (Brinks *et al.*, 1961).

When the difference between the subclass means changes proportionally with changes in the means, multiplicative corrections should be used. The phenotypic record is multiplied by the correction factor, adjusting the records to a common level of non-genetic effect. Additive correction factors are used when the differences between subclass means remain constant (Schaeffer and Wilton, 1974b). The phenotypic records are adjusted to a common level of non-genetic effect by adding the correction factor.

Additive correction factors do not alter the variance of the subclasses, whereas multiplicative factors do alter the subclass variances (Brinks *et al.*, 1961; Cundiff *et al.*, 1966b). Multiplicative corrections change the variance in proportion to the square of the ratio used (Cundiff *et al.*, 1966b).

Lush and Shrode (1950) noted that age correction factors for milk fat production could be either gross age comparisons (averages of all records made at each age) or successive age comparisons (records made by the same cows at two successive ages are compared). They suggested that the former procedure may overestimate the age effect because some of the cows with a low producing ability would normally be culled at each age. An opposite bias is introduced if the average inherent productivity of the dairy population is increasing. In this way the effects of any genetic time-trends in inherent productivity may be confounded with the effects of age (Lush and Shrode, 1950). The latter method seeks to avoid the effects of selection on cows, but also introduces a bias from selection because of incomplete repeatability of records by the same cow (Koch and Clark, 1955a). Thus, the average comparison of two records by the same cow will be biased downward from the true age effect. Koch and Clark (1955a) showed that the true age effect was between these two methods. They suggested the two procedures could be combined by weighting the estimates by p/1-p, where p is approximated by the repeatability of adjacent records.

Bean *et al.* (1982) examined beef cattle data corrected by the two methods of assessing age of dam effects. They demonstrated that little difference will result from using either of the methods for selection purposes assuming that selection was based on ranking procedures.

The equalization of the means of the subclasses and the within-subclass variances are common criteria for assessing the effectiveness of correction factors (Anderson and Wilham, 1978; Nicoll and Rae, 1978). Cundiff *et al.* (1966b) utilized this criterion to assess whether to adjust beef cattle weaning weights additively or multiplicatively. They found that both multiplicative and additive correction factors equalized the means of age of dam classes reasonably well. However, their results indicated that additive adjustments were more appropriate because although additive adjustments could not equalize the variances, they did not cause further divergence as did the multiplicative adjustments in some age of dam classes. Nicoll and Rae (1977) reported similar

findings. Koch *et al.* (1959), Schaeffer and Wilton (1974b) and Anderson and Wilham (1978) also recommended the use of additive correction factors for age of dam effects on weight records. Baker *et al.* (1974) found little difference between additive and multiplicative correction factors for age of dam, but preferred additive adjustments as these were similar over the two locations involved in their study, whereas multiplicative were not. Pabst *et al.* (1977) also found no clear preference for either type of adjustment factor for age of dam effects on weaning weights of beef calves.

Koch *et al.* (1959) recommended additive adjustments be made for age of dam effects when standard deviations were equal and multiplicative adjustments be made when coefficients of variation were equal. Searle and Henderson (1960) questioned the use of a coefficient of variation as a criterion for judging age correction factors on the basis that it should also be used as a criterion for other types of corrections, for example, those for environmental trends, and they thought this unreasonable.

Minyard and Dinkel (1965) found that variation of ranch-year subclasses for weaning weight was greater among the bull calves. However, the coefficients of variation for the two sexes were similar suggesting that a multiplicative adjustment would be more effective for sex influences. They found that both additive and multiplicative methods of adjustment reduced sex differences to a non-significant level. However, the multiplicative adjustment resulted in the greatest reduction therefore, its use was preferred. Cundiff *et al.* (1966b) also indicated that multiplicative corrections were more appropriate than additive corrections in adjusting for sex. Nicoll and Rae (1977) found that multiplicative adjustment for sex was satisfactory for Hereford calves, but failed to fully equalize the variances for Angus calves. However, variances were more nearly equalized under multiplicative than under additive adjustment methods.

Searle and Henderson (1960) considered several criteria for judging the effectiveness of correction factors for age on dairy production. These were: repeatability, coefficient of variation, interaction of herd by age, and regressions with herd, year and season of age-corrected yield on age. They concluded that no single criterion or combination of criteria seemed adequate and the criterion used should depend upon the purpose for which the correction factors are to be used.

2.4 HERITABILITIES

No heritability estimates for birth weight, March weight or 15-month weight of Red deer, or other members of the Cervidae family, were found in the literature examined. Sections 2.4.1, 2.4.2 and 2.4.3 review the literature for the estimates of heritability for these traits, or their equivalent, in beef cattle.

2.4.1 Birth Weight

In a summary of 68 paternal half-sib estimates for beef cattle Woldehawariat *et al.* (1977) presented an average weighted estimate of 0.45, from a range of 0.05 to 0.94. The weighting was based on either the number of sires involved in each estimate or the estimated number of sires based on the average number of offspring per sire. Preston and Willis (1970), who also summarized a number of heritability estimates, found it to be around 0.40. More recent published estimates for beef cattle are given in Table 2.4.1.

Knights *et al.* (1984) published an estimate of 0.70 which was estimated using REML methodology. Alenda and Martin (1987) calculated the heritability of birth weight, by intraclass correlation methods, to be 0.51 and 0.41 for male and female Angus calves, respectively. Bertrand and Benyshek (1987) calculated the heritability of direct genetic effects for birth weight to be 0.22 and 0.25 for Limousin and Brangus cattle, respectively.

From the literature examined it appears that birth weight in beef cattle is of medium to high heritability.

Table 2.4.1: Paternal half-sib estimates of the heritability of birth weight, weaning weight and yearling weight in beef cattle not included in the review of Woldehawariat *et al.* (1977).

Birth	WEIGHT TRAIT Weaning	Yearling	CODE	SOURCE
0.28	0.20	0.45		Baker *et al.* (1975)
	0.12-0.31	0.07-0.21	m	Schaeffer and Wilton (1981)
	0.15-0.40	0.17-0.52	f	Schaeffer and Wilton (1981)
0.35	0.69	0.66	m	Bourdon and Brinks (1982)
0.43	0.63	0.73	f	Bourdon and Brinks (1982)
0.33				Cundiff *et al.* (1982b)
	0.46			Knights *et al.* (1984)
0.37				MacNeil *et al.* (1984)
	0.48			Nadarajah *et al.* (1985)
0.45	0.39			Reimer *et al.* (1986)
0.41	0.13		H	Wilson *et al.* (1986)
0.19	0.16		A	Wilson *et al.* (1986)
0.53	0.05		Hm	Itulya *et al.* (1987)
0.52	0.18		Hf	Itulya *et al.* (1987)

where code: A = Angus
H = Hereford
m = male
f = female
blank = mixture of breeds and sexes

2.4.2 Weaning Weight

Woldehawariat *et al.* (1977) summarized 72 paternal half-sib estimates of the heritability of weaning weight in beef cattle. The weighted average of these estimates was 0.26, with a range of -0.01 to 0.81. The summary of 11 regression of offspring on parent estimates yielded a weighted average of 0.31 (Woldehawariat *et al.*, 1977). Preston and Willis (1970) who also summarized heritability estimates of weaning weight in beef cattle concluded that it was of moderate inheritance and presented an average value of 0.30.

More recent paternal half-sib estimates are given in Table 2.4.1. Alenda and Martin (1987) estimated the heritability of birth weight, by intraclass correlation methods, to be 0.30 and 0.21 for male and female Angus calves, respectively. Bertrand and Benyshek (1987) calculated the heritability of direct genetic effects for weaning weight to be 0.16 and 0.28 for Limousin and Brangus cattle, respectively.

The low estimates published by Wilson *et al.* (1986) (0.13 and 0.16) may have been due to the inclusion of a dam variance component in the denominator of the equations to estimate heritability. This would have reduced their heritability estimates compared to other published estimates. Itulya *et al.* (1987) reasoned that the low heritability estimates for weaning weight in their experiment (0.05 and 0.18), particularly when compared to their estimates of birth weight heritability (0.53 and 0.52), may have been caused by increased environmental variation due to inadequate nutrition and other stresses.

In summary, it appears that the heritability of weaning weight varies across populations, although most estimates indicate weaning weight to be of moderate heritability in beef cattle.

2.4.3 Yearling Weight

Woldehawariat *et al.* (1977) summarized 18 paternal half-sib estimates of the heritability of yearling weight in beef cattle. The weighted average of these estimates was 0.44, from a range of 0.10 to 0.83.

More recent paternal half-sib estimates of the heritability of yearling weight are given in Table 2.4.1. Alenda and Martin (1987) estimated the heritability of yearling weight, by intraclass correlation methods, to be 0.36 and 0.18 for male and female Angus cattle, respectively.

In summary, these estimates indicate a medium to high heritability for yearling weight in beef cattle.

2.4.4 Velvet Antler Weight

No published estimates of the heritability of velvet antler weight for Red deer were found in the literature examined. Chinese research on Sika deer estimated the heritability of velvet antler weight to be 0.35 (Zhou and Wu, 1979) from sire-son regressions. However, from the English translation of this paper, the specific traits used for the regressions were unclear and the number of records used were very low. Therefore this estimate should be treated with caution. As Red and Sika deer are closely related genetically, it is reasonable to expect that the heritability of velvet antler weight in Red deer will be of similar magnitude to that of Sika deer.

The repeatability of fresh 3-branch velvet antler weight in Sika deer was 0.79 (Zhou and Wu, 1979). This calculation was based on three successive records from 4 to 6 years of age on 8 stags, and therefore must be treated with caution.

2.5 CORRELATIONS

No phenotypic or genetic correlation estimates between liveweight traits of Red deer, or other members of the Cervidae family, were found in the literature examined. Therefore, this section will review the correlation estimates of liveweight traits of beef cattle, except for Section 2.5.1.4 which reviews correlations between liveweight and antler weight traits of deer and Section 2.5.1.5 which reviews correlations between antler traits of deer.

2.5.1 Phenotypic Correlations

2.5.1.1 Birth weight and weaning weight

Woldehawariat *et al.* (1977) summarized 26 estimates of the phenotypic correlation between birth weight and weaning weight of beef cattle. The average of these estimates was 0.38, from a range of 0.09 to 0.64. More recent estimates of this phenotypic correlation are given in Table 2.5.1.1.

In summary, the reviewed phenotypic correlation estimates between birth weight and weaning weight in beef cattle were consistently positive and of moderate magnitude.

TABLE 2.5.1.1: Phenotypic and genetic correlation estimates between birth and weaning weight, birth and yearling weight, and weaning and yearling weight in beef cattle not included in the review of Woldehawariat *et al.* (1977).

TYPE OF CORRELATION		CODE	SOURCE
Phenotypic	Genetic		

Birth weight and weaning weight

0.354	0.50	Hm	Koch *et al.* (1974a,b)
0.434	0.47	Hf	Koch *et al.* (1974a,b)
0.38	0.63	m	Bourdon and Brinks (1982)
0.41	0.60	f	Bourdon and Brinks (1982)
0.35	0.59	Am	Knights *et al.* (1984)
0.34	0.57	Am	Alenda and Martin (1987)
0.40	0.36	Af	Alenda and Martin (1987)
0.25	0.52	H	Itulya *et al.* (1987)

Birth weight and yearling weight

0.36	1.12		Trial *et al.* (1971)
0.43	0.70	Hm	Koch *et al.* (1974a,b)
0.51	0.50	Hf	Koch *et al.* (1974a,b)
0.41	0.69	m	Bourdon and Brinks (1982)
0.40	0.55	f	Bourdon and Brinks (1982)
0.43	0.57	Am	Knights *et al.* (1984)
0.37	0.75	Am	Alenda and Martin (1987)
0.35	0.45	Af	Alenda and Martin (1987)
0.23	0.32	H	Itulya *et al.* (1987)

Weaning weight and yearling weight

0.73	0.72	Hm	Koch *et al.* (1974a,b)
0.74	0.70	Hf	Koch *et al.* (1974a,b)
	0.63-0.91		Schaeffer and Wilton (1981)
0.76	0.89	m	Bourdon and Brinks (1982)
0.76	0.90	f	Bourdon and Brinks (1982)
0.71	0.79	Am	Knights *et al.* (1984)
	0.79	A	Aaron *et al.* (1986)
0.77	0.89	Am	Alenda and Martin (1987)
0.71	0.90	Af	Alenda and Martin (1987)
0.70	0.90	H	Itulya *et al.* (1987)

where code: A = Angus
H = Hereford
m = male
f = female
blank = mixture of breeds and sexes

2.5.1.2 Birth weight and yearling weight

Woldehawariat *et al.* (1977) summarized 13 estimates of the phenotypic correlation between birth weight and final feedlot weight in beef cattle. The average of these was 0.43, from a range of 0.36 to 0.60. Some additional estimates of the phenotypic correlation between birth weight and yearling weight are given in Table 2.5.1.1.

In summary, the reviewed phenotypic correlation estimates in beef cattle were consistently positive and of moderate magnitude.

2.5.1.3 Weaning weight and yearling weight

Woldehawariat *et al.* (1977) summarized 6 estimates of the phenotypic correlation between weaning weight and yearling pasture weight in beef cattle. The average was 0.64, from a range of 0.19 to 0.81. The average of 18 estimates of the correlation between weaning weight and final feedlot weight was 0.70, from a range of 0.07 to 0.84. Jensen and Anderson (1984) found the phenotypic correlation between weight at 42- and 336-days of age to be 0.52 over 2217 bulls from 296 sires at a Danish performance testing station.

In summary, the estimates of the phenotypic correlation between weaning weight and yearling weight in beef cattle are moderately to strongly positive.

Moore *et al.* (1988), studying the records of 97 farmed Red deer stags in New Zealand, found that liveweight at 3-months of age accounted for approximately 44% of the variation in 15-month liveweight, but only 25 and 21% of the variation in 26- and 38-month liveweight, respectively. These results indicate that there is a correlation between liveweights in Red deer and that these are positive.

2.5.1.4 Liveweight and velvet antler weight

Zhou and Wu (1979) estimated the correlation coefficient between total velvet antler weight and body weight of Sika deer to be 0.98. The estimate was derived from 25 stags between 6 and 8 years of age which were classified into five

weight categories ranging from 70 to 150 kg body weight. The correlation coefficient between average weight of 3-branch antler (approximately equivalent to velvet antler harvest weight for Red deer in New Zealand) and body weight was 0.973. However, due to the small number of records analysed their study the results should be treated with caution.

In New Zealand, Moore *et al.* (1988) conducted a study on 97 Red deer stags from 3 months to 3 years of age with 36 of these continuing to be studied until 5 years of age. They found that in the group recorded to 5 years of age, late summer liveweight increased linearly at 29 kg/year and antler weight increased linearly by 62g for a 10kg increase in late summer liveweight. Over the three groups, Moore *et al.* (1988) estimated the correlation coefficient between adult velvet antler weight and 3-month liveweight, 15-month liveweight, growth rate between 9- and 15-months of age and liveweight at pedicle initiation to be 0.386, 0.534, 0.349 and 0.209, respectively. The correlation coefficient between adult velvet antler weight and LWTSP (the combination of 15-month liveweight and hard spiker antler weight weighted by the ratio of their standard deviations) was estimated to be 0.571. Thus, LWTSP was the best indicator of adult velvet antler weight, although 15-month liveweight showed a similar relationship.

2.5.1.5 Spiker antler traits and adult velvet antler weight

From the data of 97 farmed Red deer stags in New Zealand, Moore *et al.* (1988) calculated the correlation coefficient between adult velvet antler weight and hard spiker antler weight and hard spiker antler length to be 0.388 and 0.293, respectively. These results indicate that the spiker antler measurements, taken on yearling Red deer stags, are not good phenotypic indicators of adult velvet antler production, although the relationships are positive and of moderate magnitude.

Spiker antler weight controlled 27.6 and 21.7% of the variation in 2- and 3-year old velvet antler weight, respectively (Moore *et al.*, 1988). However, 2 year old velvet weight controlled 62.3% of the variation in 3 year old velvet weight. In the group of stags studied to 5 years of age, the percentage of variation accounted for by the previous years velvet antler weight remained relatively constant between 2 and 4 years, at approximately 60% (Moore *et al.*, 1988). These results indicate that the correlation between velvet production in two consecutive years from 2 to 5 years of age in Red deer is strongly positive.

2.5.2 Genetic Correlations

2.5.2.1 Birth weight and weaning weight

Woldehawariat *et al.* (1977) summarized 25 estimates of the genetic correlation between birth weight and weaning weight in beef cattle. The weighted average of these estimates was 0.54, from a range of 0.21 to 0.99. The weighting was based on appropriate sire-weighted averages determined by the 'Z' transformation method of Snedecor (1956 cited Woldehawariat *et al.*, 1977). More recent estimates are given in Table 2.5.1.1.

In summary, the genetic correlation estimates between birth weight and weaning weight in the beef cattle studies reviewed were positive and of moderate magnitude.

2.5.2.2 Birth weight and yearling weight

Woldehawariat *et al.* (1977) summarized 13 estimates of the genetic correlation between birth weight and final feedlot weight in beef cattle. The weighted average of these estimates was 0.60, from a range of 0.44 to 0.78. More recent estimates are given in Table 2.5.1.1.

In summary, the genetic correlation between birth weight and yearling weight was moderately to strongly positive in the literature reviewed for beef cattle.

2.5.2.3 Weaning weight and yearling weight

Woldehawariat *et al.* (1977) summarized 5 estimates of the genetic correlation between weaning weight and yearling weight in beef cattle. The weighted average of these estimates was 0.67, from a range of 0.10 to 0.75. The weighted average of 18 estimates of the genetic correlation between weaning weight and final feedlot weight was 0.71, from a range of 0.33 to 0.98 (Woldehawariat *et al.*, 1977). Jensen and Anderson (1984) estimated the genetic correlation between 42- and 336-day weight to be 0.62 for bulls at a Danish performance testing station.

In summary, the estimates reviewed in the literature examined indicated that the genetic correlation between weaning weight and yearling weight is strongly positive in most populations of beef cattle.

2.6 BEEF CATTLE SELECTION EXPERIMENTS

Long term selection experiments in beef cattle have shown that selection for high or low weights, or weight gain, at any particular age, results in concomitant changes in weights at all other ages (Baker and Morris, 1984; Mrode, 1988), as would be expected from the positive genetic correlations between liveweight traits in beef cattle.

After 16 years of selection in two Angus cattle lines, where one was selected for weaning weight (WW) and the other for yearling weight (YW), Aaron et al. (1986) found the genetic responses in the WW line were 1.45 and 2.10 kg/year for weaning and yearling weight, respectively. The genetic responses in the YW line were 1.52 and 3.50 kg/year, respectively. Thus, the correlated response in weaning weight from selection for yearling weight was greater than the response obtained directly for weaning weight. Conversely, the indirect selection for yearling weight from selection for weaning weight was only 60% as effective as direct selection for yearling weight. Positive correlated responses of 0.24 and 0.45 kg/year were observed for birth weight in the WW and YW lines, respectively. Similar results from a 14 year selection experiment in Hereford cattle were reported by Frahm et al. (1985b). Both sets of authors concluded that some attention should be given to minimizing the correlated response of increased birth weight in selection programs designed to increase growth performance.

Baker and Morris (1984) reviewed correlated responses to weight selection in beef cattle. They concluded that in temperate environments, selection for growth almost invariably resulted in increased birth weights and in some cases an increased incidence of calving problems and calf mortality. These problems are most likely due to disproportion between calf birth weight and the dam's pelvic size and liveweight (Barlow, 1978). The fact that correlated responses in calf birth weights occur a generation ahead of those for cow traits aggravates the possible disproportion. It is well documented that there is an intermediate

optimum for birth weight and that above 'threshold' values there can be large increases in dystocia and calf mortality (Baker and Morris, 1984). In a more recent review of beef cattle selection experiments, Mrode (1988) refutes that selection for increased weight or growth rate has significantly increased birth weights or that the incidence of dystocia and calf mortality has increased. Further investigation is required to clarify the influence of increased birth weight on calving problems and calf mortality.

Genetic correlations between early growth and mature weights are strongly positive (Koch et al., 1982). This may be undesirable if bigger cows eat more and if the extra returns from heavier cows are less than the increased associated costs. Although information from selection experiments on the correlated responses in cow weights is somewhat fragmentary, preliminary results indicate that selection for early growth leads to increased cow weights (Baker and Morris, 1984). Luesakul-Reodecha et al. (1986) reported positive but non-significant trends of 0.35 and 4.12 kg/year for 205-day and 54-month eight in an Angus line selected for 365-day weight.

Cow weight, like calf birth weight, perhaps should be optimized rather than maximized and it is likely that this optimum will vary with breed, management system and climate. However, Morris and Wilton (1976), in a review of the association between cow size and biological efficiency of reproduction, concluded that when all post-weaning food requirements are added to the cow herd food costs, herd efficiency is little affected by cow size unless reproductive performance also changes.

2.7 RESTRICTED SELECTION INDICES

One method of preventing the concomitant change in birth weight or mature weight from selection for increased weaning or yearling weight is through the use of a restricted index. A selection index may be restricted by requiring that the genetic change it produces in one (or more) trait equals zero, or some predetermined value, or are of specified sign (Morley, 1955; Kempthorne and Nordskog, 1959; Cunningham et al., 1970).

An alternative method for restricting genetic change in a particular trait would be to use an unrestricted index while giving that trait a suitable artificial economic weighting in the aggregate genotype, which is usually a heavy negative economic value (Cunningham *et al.*, 1970). Cunningham *et al.* (1970) showed that the index produced by this method is identical to that obtained by incorporating the restriction explicitly in the index equations, however, this is not the case for intermediate degrees of restriction.

The use of explicit restrictions will, in general, be preferable to the manipulation of economic values, even where absolute restriction of a trait is desired. This is because arbitrary economic weights give the aggregate genotype an arbitrary definition and make predictions of genetic gain less useful. Explicit restriction is also simpler, in that a single set of uncomplicated equations yields the required index and the genetic cost of the restrictions can be readily calculated (Cunningham *et al.*, 1970).

Kempthorne and Nordskog (1959) pointed out that the economic value given to a restricted trait had no effect on the index obtained. Cunningham *et al.* (1970) noted that it does however, have an effect on the correlation of the index and aggregate genotype and should therefore be chosen so that this correlation can be used for meaningful estimation of the effect of the index. Usually, zero will be the most suitable relative economic value for a trait that is to be restricted.

Restricted selection indices were first mentioned by Morley (1955), who showed that clean fleece weight in Australian Merino sheep could be improved while holding crimps per inch constant.

Cunningham and Gjedrem (1970) presented an example of using the restricted index to limit ewe body weight (EBW) in indices including weaning weight, fleece weight and number of lambs born. They found that the restriction to zero genetic change in EBW caused a drastic reduction in the overall response to selection, if EBW was not measured. If EBW was measured and included in the index, then it could be restricted to zero with little loss in overall response. They also found that if EBW was not being restricted, it had little value in the index. Cunningham and Gjedrem (1970) also examined the effects of partially restricting EBW, which was expressed on a percentage scale from 0 to 100% (i.e. from unrestricted to complete restriction). They found that as EBW was

gradually restricted the rate of genetic change in the other traits altered in an almost linear fashion, but they were not greatly affected. The lower the correlations with EBW and other traits the less the overall effect of restricting EBW in the index. When EBW was restricted but not measured, the alteration in the rate of genetic gain for each trait and for the aggregate genotype was proportional to the degree of restriction of EBW (Cunningham and Gjedrem, 1970).

Eisen (1977) presented the results of using restricted index selection to maximize genetic change in postweaning weight gain from 3 to 6 weeks of age in mice, while keeping genetic response in feed intake at zero. This was successful in that correlated responses in postweaning gain were significant (P<0.01) in the intended direction in feed intake. However, once genetic change in postweaning gain had reached about one absolute phenotypic standard deviation (after approximately four generations), subsequent genetic change in feed intake tended to follow the direction of response in postweaning gain, although this was not significant.

Mendoza and Slanger (1985) utilized within-herd restricted indices so that the expected changes in the chosen traits were proportional to one another. In the three-trait indices (birth, weaning and mature weight) birth weight, maternal effects for weaning weight and mature weight were restricted. In the two-trait indices (birth and weaning weight) birth weight and mature weight were restricted. They found that the three-trait indices were much more successful in reducing gains in mature weight than were the two-trait indices. Reducing mature weight gain also reduced gains in weaning weight (direct effects) and yearling weight. Mendoza and Slanger (1985) concluded that maternal effects for weaning weight can be improved (even if maternal effects are negatively correlated with birth weight, direct effects on weaning weight and yearling weight) with reasonable genetic gains in the economically important growth traits using restricted selection indices.

Simm et al. (1986) constructed selection indices to improve the efficiency of lean meat production in cattle which were derived with an aggregate breeding value that included growth rate, food conversion efficiency, killing-out proportion and carcass lean proportion. They derived two indices. One with a restriction to zero genetic change in birth weight, and the other without

restriction. The correlation between the index and the aggregate breeding value was 0.53 for the restricted index and 0.57 for the unrestricted index. The maximum proportional reduction in expected economic response, due to complete restriction was about 0.08.

A Montana beef cattle selection experiment (Urick *et al.*, 1981 cited by Baker and Morris, 1984) confirmed the theoretical expectation that yearling weight selection alone (Y), or with an index which genetically restricted birth weight (YB) would lead to different growth curves from birth to 12-months of age. The 5 year-groups of YB sires were 3.6kg lighter than Y sires at birth, but of little percentage difference in yearling weight. The YB calves were correspondingly lighter at birth (1.3 to 1.6kg for all dam ages) with a 1.1 to 2.6kg margin in values for 2 year old heifers leading to lower calf mortalities (8% less) and lower assistance levels (4 to 11% less).

The effects of restricting birth weight and/or mature weight in beef cattle have also been considered by Fitzhugh (1976) and Alenda and Martin (1987). In both cases the expected genetic response in yearling weight was decreased by restricting birth weight.

Restricted indices are an effective method of preventing genetic changes in traits which are regarded as being at optimum levels. However, some loss in response for total economic merit may result from the use of restricted selection indices.

CHAPTER 3
MATERIALS AND METHODS

3.1 SOURCE OF DATA

The Deerplan recording scheme was introduced in 1985 (Fennessy, 1985) with the initial objective of collecting basic data on farmed Red deer in New Zealand. The deer breeders who joined Deerplan were asked to supply the following information:

- pedigree (parentage) of the fawn,
- sire and dam breed,
- fawn birth date,
- fawn weaning or March weight,
- fawn 15-month weight,
- hind annual liveweight during spring or autumn,
- stag two year old casting and velvet harvest dates,
- stag antler weight and characteristics, and
- stag annual mid-winter liveweight.

The recording of birth weight was not mandatory but was carried out in conjunction with the accurate recording of birth date on some farms. If birth date was not recorded to the day, by tagging fawns at or near birth, breeders were asked to estimate the date of birth to within seven days. However, many of the March weight records did not have an accompanying date of birth.

Data up to and including August 1986, were uplifted from the New Zealand Meat Producers Board via Beefplan through which the scheme was run. Although recording of data through Deerplan commenced with the 1984 fawning season, some deer breeders had been collecting suitable information from the 1982 fawning season onwards. Where possible this information was added to the Deerplan files before they were uplifted. No data on antler traits was uplifted due to the insufficient number of adequate records for analysis at this time.

The records of approximately 3200 fawns were made available from 28 herds throughout New Zealand. The most northern herd was located in North

Auckland and the most southern in Southland. A maximum of four years data were available on fawn March weight and up to three years data for other fawn and hind liveweight traits.

3.2 DEFINITIONS

Fawning season   - The year/season the fawn was born. For example,
   (year)   fawns born between November 1984 and February
                         1985 are classified as being born in the 1984 fawning
                         season.

Birth weight   - The liveweight in kilograms of the fawn taken within
   (bwt)   24 hours of birth.

March weight   - The liveweight in kilograms of the fawn recorded in or
   (mwt)   near the month of March following birth. This is
                         usually the weaning weight but it is the policy of some
                         breeders to wean post-rut in June or July.

Age at March weighing - The number of days between birth (where known) and
   (age at mwt)   the March weighing.

15-month weight   - The liveweight in kilograms of theanimal taken in
   (ylg)   March approximately 15 months after birth.

Age at 15-month weighing - The number of days between birth (where known)
   (age at wt)   and the 15-month weighing.

Dam age   - The age of the dam in years when the fawn was born.

Dam pre-fawning winter weight - The liveweight in kilograms of the dam
                         usually recorded in or around June after the rut and
                         before the foetal weight has a significant effect on dam
                         liveweight. For two year old dams this weight
                         corresponded to their 15-month weight.

Dam post-fawning winter weight - The liveweight in kilograms of the dam taken after the fawn is weaned, normally about June. For two year old dams this weight corresponded to their 2 1/2 year old liveweight.

3.3 PRELIMINARY EDITING

All fawns that had not been reared by the fawn's natural mother, as noted in the fate code, were removed from the data set. This included any fawns that were fostered, hand-reared or had been suckling more than one hind. In one herd, the initial fawn weights had not been recorded until October instead of the required March weighing. These records were removed from the data set.

All records were then scrutinized for possible inaccuracies and where possible these were checked against the original on-farm records for confirmation. Any records that remained unverified, and were obviously misrecorded, were removed from the data set.

In the original data two subspecies of the genus *Cervus elaphus* (Red deer and Wapiti) were represented and a small number of crossbred animals from these strains. The total number of deer other than Red deer in the original data was 244. The Bartlett's test of homogeneity of variance (Snedecor and Cochran, 1980) and Levene's test of homogeneity of variance (Snedecor and Cochran, 1980) which is less sensitive to the distribution of the data, were conducted on the various 'breed groups' for March weight. The variance of the 'breed groups' were found to be significantly different (P<0.05) for March weight. Due to the small numbers of crossbred and Wapiti deer and the significantly different variances for each of the 'breed groups', these records were deleted from the study. As a number of the hinds and breeding stags in the study were captured feral stock, and since Red deer and Wapiti freely interbreed, it is possible, if not likely, that some fawns in this study contain a percentage of Wapiti genes. The percentage is probably very small as Red deer and Wapiti usually have very different physical appearances, and the breeders were required to give an approximate breed description of hinds and stags included in the data set. As Wapiti deer are larger and heavier than Red deer at all ages (average mature

female weight being 210 kg and 110 kg, respectively (Dratch and Fennessy, 1985)), this would tend to increase the liveweights of the fawns concerned and may have increased the variance of the Red deer liveweights in this study.

The number of records and contributing herds remaining for each trait after the preliminary editing was completed and the number of records that had the corresponding date of birth recorded are given in Table 3.3.1.

TABLE 3.3.1: Number of records (N) for each liveweight trait and the number of herds contributing to that data base ($Herds_N$) and the number of records for each trait that had the corresponding date of birth recorded on the fawn (DOB) and the respective number of herds contributing to that data base ($Herd_{DOB}$).

TRAIT	N	$Herds_N$	DOB	$Herds_{DOB}$
Birth weight	311[a]	4	311	4
March weight	2874[b]	28	1671[c]	21
15-month weight	1225	20	546	14
Number of March weight records with:				
Dam 2 year weight	291	12	153	9
Dam 3 year weight	197	11	140	9
Dam 4 year weight	178	9	110	7
Dam 5 year weight	104	9	95	8
Dam 6 year weight	82	8	26	7
Dam 7 year weight	63	5	19	4
Dam 8 year weight	59	7	25	6
Dam 9 year weight	20	4	20	4
Dam 10 year weight	19	3	19	3
Dam 11-13 year weight	13	3	13	3

where:

a - 1 record did not have an accompanying dam age,

b - 158 records did not have an accompanying dam age, and

c - 75 records did not have an accompanying dam age.

3.4 STATISTICAL METHODS

The objectives of the analysis included the calculation of adjustment factors for non-genetic effects, the estimation of heritabilities and phenotypic and genetic correlations.

The ordinary least squares method of fitting constants was used (Hazel,1946; Searle, 1971). The basis of the method is the minimization of the sums of squares of the deviations of the observations from their expected values under the model. A preliminary analysis of variance was carried out including all expected non-genetic effects as the first step in determining the importance of various effects in accounting for the observed variation in each measured variable. The non-significant effects were excluded and solutions found for the model of best fit. Variance and covariance components were then computed from these models and heritabilities and genetic correlations calculated.

3.4.1 Non-genetic Effects

The non-genetic effects for birth weight, March weight and 15-month weight were determined by fitting all likely effects (herd, year, sex and age of dam) and regressions (age at weighing and dam winter weight) and testing for their significance or homogeneity, respectively. The significant effects ($P<0.05$) and heterogeneous regressions remained in the model. All first order interactions between the remaining main effects were then included in the model. These were excluded if they were non-significant ($P>0.05$) or were assumed to be unimportant when they controlled less than 2 percent of the total variation. The proportion of the total variance each effect controlled was estimated by the reduction in the coefficient of determination (R^2) when that effect was excluded from the model.

As the data had unequal subclass numbers (i.e. unbalanced) the order of fitting the effects influenced the sum of squares of each effect. The order of fitting dam age and the dam winter weights was examined to determine the change of significance and proportion of total variance each controlled.

As the method of estimating the non-genetic effects was the same for all models, only Model 5 (Section 4.3.1) will be described in detail.

For March weight (Model 5) the following model was fitted:

$$y_{ijklm} = \mu + h_i + t_j + s_k + d_l + b_2 a_{ijklm} + e_{ijklm} \qquad (3.1)$$

where:

y_{ijklm} is the observation on the mth individual recorded in the ith herd, in the jth year, of the kth sex and born to a hind of the lth age,

μ is the general mean,

h_i is the fixed effect of the ith herd
($i = 1,\ldots,11$),

t_j is the fixed effect of the jth birth year
($j = 1, 2, 3, 4$ where $1 = 1982$, $2 = 1983$, $3 = 1984$, and $4 = 1985$),

s_k is the fixed effect of the kth sex
($k = 1, 2$ where 1 is a male and 2 is a female),

d_l is the fixed effect of the lth dam age
($l = 1, 2, 3, 4$ where 1 is 2 year old dam, 2 is a 3 year old dam, 3 is a 4 year old dam and 4 is a 5 year old or older dam),

b_2 is the regression coefficient of the animal's age (a_{ijklm}) in days, on its weight (y_{ijklm}) in kilograms, and

e_{ijklm} is a random residual effect unique to the mth individual of the ith herd, in the jth year, of the kth sex and born to a hind of the lth dam age. The residual effects are assumed to be uncorrelated and normally distributed with mean zero and variance σ^2_e.

The number of dam age classes in each model was determined by amalgamating the oldest dam ages together where these were not significantly different from each other ($P>0.05$), and where there was little change in the coefficient of

determination (R^2) of the model, that is, a less than 2 percent change. In Model 5, four distinct dam age classes remained, 2, 3, 4 and 5 year old and older dams. Within the birth weight models, Models 1, 2 and 4 had 3 and 4 year old dams amalgamated into one class, and Model 3 had 2, 3 and 4 year old dams amalgamated into one class. The number of significant dam age classes varied between models depending on the liveweight trait, the number of records for that trait, and the distribution of data among the dam age classes for that model.

The model for birth weight was equivalent to equation (3.1), except $b_2 a_{ijklm}$ was replaced with $b_1 z_{ijklm}$, where b_1 was the regression coefficient of fawn's date of birth (z_{ijklm}) in days from 1 November, on the fawn's weight (y_{ijklm}) in kilograms.

The model for 15-month weight was equivalent to equation (3.1), except that age of dam was not significant (P>0.05) and was therefore not included. There was only one years data and $b_2 a_{ijklm}$ was replaced with $b_3 x_{ijklm}$, where b_3 was the regression coefficient of age at 15-month weighing (x_{ijklm}) in days from birth, on its 15-month weight (y_{ijklm}).

In models which included either/both dam pre-fawning winter weight or/and dam post-fawning winter weight, $b_4 w_{ijklm}$ and $b_5 u_{ijklm}$ were added to equation (3.1) when appropriate. In these models, b_4 was the regression coefficient of the fawn's dam pre-fawning winter weight (w_{ijklm}) in kilograms, on the fawn's weight (y_{ijklm}) in kilograms and b_5 was the regression coefficient of the fawn's dam post-fawning winter weight (u_{ijklm}) in kilograms, on the fawn's weight (y_{ijklm}) in kilograms.

3.4.2 Heritability

A preliminary investigation into the significance of the various factors in the model as in Section 3.4.1 was undertaken. This formed the basis of choosing an appropriate model for each liveweight trait.

The paternal half-sib estimates of the heritability of the liveweight traits were calculated using the sire nested within herd and error variance components obtained from Henderson's Method 3 (Henderson, 1953). The models fitted

were the same as for the non-genetic effects except that they contained a random effect for sires nested within herds. Standard errors of these estimates were calculated using the method outlined by Swiger *et al.* (1964). The method of Kempthorne (1957) was used for calculating the standard error of March weight heritability when the random x fixed effect interaction, (sire nested within herd x dam age), was included in the model.

Paternal half-sib estimates of the heritability of March weight using MIVQUE (minimum variance quadratic unbiased estimation), ML (maximum likelihood) and REML (restricted maximum likelihood) were also calculated using the method as given by Hartley *et al.* (1978), Hemmerle and Hartley (1973) and Patterson and Thompson (1971), respectively.

The heritability of March weight was also calculated using the regression of offspring on dam described by Becker (1984). Consideration was given as to whether or not the regression should be calculated on an intra-sire basis, or whether sires should be ignored. Since the accuracy of an estimate is dependent upon the number of observations (pairs) and the small progeny groups would have to be eliminated, it was decided that sires would be ignored. Standard errors of these estimates were calculated using the method outlined by Falconer (1981). Due to insufficient data it was not possible to calculate the heritability of birth weight or 15-month weight by this method.

3.4.3 Correlations

The phenotypic correlations between pairs of traits on the same animal were calculated using the method described by Turner and Young (1969). Phenotypic correlations were calculated between traits adjusted for herd nested within year only and between pairs of records adjusted for known sources of variation from preliminary analyses. The significance of these correlations was established using the two-tailed significance levels of the correlation coefficient table presented in Snedecor and Cochran (1980).

The genetic correlations between birth weight, March weight and 15-month weight were calculated using the method described by Becker (1984). The variance and covariance components were estimated using Henderson's Method

3. The standard errors of the genetic correlations were calculated using the formula given by Tallis (1959).

3.4.4 Selection Indices

Selection indices were computed using SELIND (Cunningham, 1970), a Fortran computer program for genetic selection indices. The version used in this study had been modified by Dr. D.L. Johnson (pers. comm.), to improve inputting of required parameters, and D. Garrick (J. Rendel, pers. comm.) to enable the program to be run on a personal computer. Reduced and restricted indices were computed using SELIND.

3.4.5 Computer Software

Analyses were primarily undertaken using REG, a generalized linear models package (Gilmour, 1985) with some recourse to SAS (SAS Institute Inc., 1985), a statistical analysis system, when the number of levels in the model being analysed exceeded the capacity of REG. This occurred when calculating the heritability of March weight with three random effects (Section 5.3.1). March weight heritability estimates calculated using ML, REML and MIVQUE methods were obtained using SAS. Selection indices were computed on an IBM personal computer using a modified version of Cunningham's (1970) SELIND program.

CHAPTER 4
NON-GENETIC EFFECTS

4.1 INTRODUCTION

The magnitude of a metric character is conditioned not only by the animal's genotype but also by its environment. Many of the differences in environment to which animals are subjected cannot be specified. Variation due to these effects cannot be separated, unless repeat observations are possible, from that due to errors of observation and measurement of the character concerned.

Environmental factors mask genetic differences between individuals. While the environmental component is usually complex it is, in some cases, possible to identify some specific non-genetic effects. Adjustment of production records for non-genetic effects decreases the environmental variance component thereby decreasing the phenotypic variance. This decrease in phenotypic variance results in the heritability of the adjusted trait being higher than that of the unadjusted trait, allowing greater genetic gain through improved accuracy of selection.

The purpose of this chapter was to identify non-genetic effects which significantly control variation in the birth, March and 15-month liveweights of farmed Red deer in New Zealand.

4.2 BIRTH WEIGHT

4.2.1 Model 1

The non-genetic effects of herd, year, sex, age of dam, and date of birth were fitted to birth weight. From the original database of 311 birth weights, 257 observations were chosen that met the following criteria:

    (i)   number of records in any given herd-year combination > 9,

    (ii)   dam age grouped into three classes: 2, 3&4, 5+ years, and

    (iii)   each herd required a minimum of 2 dams in each dam age class.

The number of observations by herd, year, sex, and dam age are given in Table 4.2.1.1. A detailed presentation of the data set is given in Appendix 1, Table 9.1.1.

TABLE 4.2.1.1: Number of records in each class of non-genetic effect in Model 1. (N = 257)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	120	1982	15	male	138	2 year	49
2	137	1983	64	female	119	3&4 year	138
		1984	128			5+ year	70
		1985	50				

A linear model with birth weight as the dependent variable and herd, year, sex, age of dam, and all first order interactions was fitted. Date of birth was also fitted as a covariate in this model.

Date of birth was not significant (P=0.36) and was removed from Model 1.

When the first order interactions among the fixed effects were included in the model, the following were not significant: (herd x year)(P=0.51), (herd x dam age)(P=0.07), (year x sex)(P=0.19), (year x dam age)(P=0.78), and (sex x dam age)(P=0.11). These interactions were therefore excluded from Model 1.

The ANOVA based on the model resulting from the above discussion is given in the Table 4.2.1.2, with the percentage of variation each of the non-genetic effects controlled. The least squares estimates and means are presented in Tables 4.2.1.3 and 4.2.1.4.

TABLE 4.2.1.2: Analysis of variance for birth weight and the percentage of variation controlled (%VC) by each of the non-genetic effects using Model 1.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	1	55.5	***	11.9
Year	3	8.1	***	5.2
Sex	1	36.3	***	7.8
Dam Age	2	25.8	***	11.0
(herd x sex)	1	15.2	***	3.2
Error	248	1.2		60.9
Total	256			100.0

$R^2 = 39.1\%$

The results shown in Table 4.2.1.3 indicated that males were generally 9.2% heavier than females at birth, given that all other non-genetic effects are equal. However, due to the presence of the (herd x sex) interaction, the magnitude of the difference varied between herds. As sires are confounded with herds it is possible that this is a sire effect rather than a herd effect. These results also indicated that fawns from 2 year and 3&4 year old dams were 14.7% and 7.4% respectively, lighter at birth than fawns from 5 year old and older dams, given that all other non-genetic effects are equal.

TABLE 4.2.1.3: Ordinary least squares estimates (LSE) and means (LSM) for sex, dam age, and (herd x sex) interaction, with their respective standard errors (S.E.) for Model 1. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	0.389	0.070	9.24	0.13
	female	-0.389	0.070	8.46	0.12
Dam Age	2 year	-0.698	0.117	8.15	0.17
	3&4 year	-0.007	0.104	8.84	0.11
	5+ year	0.705	0.113	9.55	0.16
(herd x sex) interaction					
Herd 1	male	0.255	0.070		
	female	-0.255	0.070		
Herd 2	male	-0.255	0.070		
	female	0.255	0.070		

TABLE 4.2.1.4: Combined ordinary least squares estimates of sex and (herd x sex) interaction for Model 1.

HERD NUMBER	SEX	
	MALE	FEMALE
1	0.645	-0.645
2	0.134	-0.134

The results of Model 1 indicated that herd, year, sex of fawn, and age of dam all cause significant differences in birth weight. The significant (herd x sex) interaction indicated that adjustment factors for sex should be calculated on a within rather than across herd basis.

4.2.2 Model 2

This model was fitted to test the usefulness of dam pre-fawning winter weight as an adjustment factor for birth weight. The non-genetic effects of herd, year, sex, age of dam, date of birth, and dam pre-fawning winter weight were fitted to birth weight. From the original database of 311 birth weights, 54 observations were chosen that met the following criteria:

(i)   each record required a dam pre-fawning winter weight,

(ii)   number of records in any given herd-year combination > 9,

(iii)   dam age grouped into three classes; 2, 3&4, 5 years, and

(iv)   each herd required a minimum of 2 dams in each dam age class.

The pre-fawning winter weight for the 2 year old dams corresponded to their 15-month weight. There were no dams older than 5 years of age. The number of observations by herd, year, sex, and dam age are given in Table 4.2.2.1. A detailed presentation of the data set is given in Appendix 1, Table 9.1.2.

TABLE 4.2.2.1: Number of records in each class of non-genetic effect in Model 2. (N = 54)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	54	1984	14	male	33	2 year	10
		1985	40	female	21	3&4 year	25
						5 year	19

A linear model with birth weight as the dependent variable and year, sex, age of dam and all first order interactions as the independent variables was fitted. Date of birth and dam pre-fawning winter weight were also fitted as covariates in this model.

Year was not significant (P=0.42) and was removed Model 2. Date of birth was not significant (P>0.37) regardless of the order of fit of dam age, dam pre-fawning weight, and date of birth. Therefore, date of birth was removed from

Model 2. Both dam age and dam pre-fawning winter weight were highly significant (P<0.001) regardless of the order of fit of these two variables.

When the first order interaction among the fixed effects, (sex x dam age), was included in the model it was significant (P<0.05) and controlled greater than 2% variation. This interaction therefore remained in Model 2.

The regression of birth weight on dam pre-fawning winter weight was homogeneous between sexes (P=0.49) and dam ages (P=0.55).

The ANOVA resulting from the above discussion is presented in Table 4.2.2.2, with the percentage of variation each of the non-genetic effects controlled. The least squares estimates and means are presented in Tables 4.2.2.3 and 4.2.2.4

TABLE 4.2.2.2: Analysis of variance for birth weight and the percentage of variation controlled (%VC) by each of the non-genetic effects using Model 2.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Sex	1	15.8	***	20.7
Dam age	2	6.1	***	16.0
Dam pre-fawning weight	1	12.7	***	16.6
(sex x dam age)	2	3.8	**	10.1
Error	47	0.6		
Total	53			100.0

$R^2 = 63.4\%$

The results shown in Table 4.2.2.3 indicated that, in general, males were 8.4% than females at birth, given that all other non-genetic effects were equal. However, the presence of the (sex x dam age) interaction indicated that the direction and magnitude of the difference varied between dam age classes. In general, 2 year old dams produced fawns that were 5.6% heavier than 5 year old dams, and 3&4 year old dams produced fawns that were 8.6% lighter than 5 year old dams.

TABLE 4.2.2.3: Ordinary least squares estimates (LSE) and means (LSM) for
sex, dam age and (sex x dam age) interaction, and the regression coefficient for
dam pre-fawning winter weight, with their respective standard errors (S.E.) for
Model 2. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	0.403	0.119	10.43	0.14
	female	-0.403	0.119	9.62	0.20
Dam age	2 year	0.671	0.255	10.70	0.33
	3&4 year	-0.772	0.166	9.30	0.16
	5 year	0.101	0.183	10.13	0.19
Dam weight(kg/kg dam wt)					
		0.062	0.013		
(sex x dam age) interaction					
2 year	male	-0.694	0.194		
	female	0.694	0.194		
3&4 year	male	0.278	0.150		
	female	-0.278	0.150		
5 year	male	0.417	0.158		
	female	-0.417	0.158		

TABLE 4.2.2.4: Combined ordinary least squares estimates of dam age, sex, and (sex x dam age) interaction for Model 2.

DAM AGE	SEX	
	MALE	FEMALE
2 year	0.380	0.962
3&4 year	-0.091	-1.453
5 year	0.921	-0.719

The results of Model 2 indicated that sex, dam age, and dam pre-fawning winter weight caused significant differences in birth weight. The (sex x dam age) interaction may be caused by differential treatment of dam age groups. That is, first fawning hinds (2 year old dams) were better fed throughout pregnancy than older hinds and as a result produced heavier fawns than mixed age hinds. Further work is required in this area as this is a very small data set from one herd only therefore, the results should be treated with caution.

4.2.3 Model 3

This model was fitted to test the usefulness of dam post-fawning winter weight as an adjustment factor for birth weight. The non-genetic effects of year, sex, age of dam, date of birth, and dam post-fawning winter weight were fitted to birth weight. From the original database of 311 birth weights, 106 observations were chosen that met the following criteria:

(i)   each record required a dam post-fawning winter weight,

(ii)   number of records in any given herd-year combination > 9,

(iii)   dam age grouped into two classes; 2&3&4, 5 years, and

(iv)   each herd required a minimum of 2 dams in each dam age class.

There were no dams older than 5 years of age. The number of observations by herd, year, sex, and dam age are given in Table 4.2.3.1. A detailed presentation of the data set is given in Appendix 1, Table 9.1.3.

TABLE 4.2.3.1: Number of records in each class of non-genetic effect in Model 3. (N = 106)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	106	1983	12	male	66	2&3&4 yr	86
		1984	45	female	40	5 yr	20
		1985	49				

A linear model with birth weight as the dependent variable and year, sex, age of dam, and all first order interactions as the independent variables was fitted. Date of birth and dam post-fawning winter weight were also fitted as covariates in this model.

Year was not significant (P=0.56) and was removed from Model 3. Date of birth was just significant (P=0.05) when fitted before dam post-fawning winter weight, but was significant (P<0.05) if fitted after dam post-fawning winter weight. As date of birth controlled 4.1% variation it remained in Model 3. Dam age was highly significant (P<0.01) regardless of the order of fit of dam age, date of birth, and dam post-fawning winter weight.

When the first order interaction among the fixed effects, (sex x dam age), was included in the model it was not significant (P=0.55) and was therefore excluded from Model 3.

The regression of birth weight on dam post-fawning winter weight was homogeneous between sexes (P=0.91) and dam ages (P=0.41). The regression of birth weight on date of birth was also homogeneous between sexes (P=0.60) and dam ages (P=0.68).

The ANOVA resulting from the above discussion is presented in Table 4.2.3.2, with the percentage of variation each of the non-genetic effects controlled. The least squares estimates and means are presented in Table 4.2.3.3.

TABLE 4.2.3.2: Analysis of variance for birth weight using Model 3 and the percentage of variation controlled (%VC) by each of the non-genetic effects.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Sex	1	30.6	***	14.9
Dam age	1	18.8	***	9.1
Dam post-fawning weight	1	41.3	***	20.1
Date of birth	1	8.7	**	4.2
Error	101	1.1		
Total	105			100.0

$R^2 = 48.3\%$

The results shown in Table 4.2.3.3 indicated the males were 13.1% heavier than females at birth, given that all other non-genetic effects were equal. Younger dams, 2&3&4 years of age, produced fawns that were 8.2% lighter than 5 year old dams, given that all other non-genetic effects were equal.

TABLE 4.2.3.3: Ordinary least squares estimates (LSE) and means (LSM) for sex and dam age, and the regression coefficients for dam post-fawning winter weight and date of birth, with their respective standard errors (S.E.) for Model 3. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	0.599	0.103	10.34	0.15
	female	-0.599	0.103	9.14	0.18
Dam age					
	2&3&4 year	-0.418	0.103	9.32	0.11
	5 year	0.418	0.130	10.16	0.23
Dam post-fawning winter weight (kg/kg dam wt)					
		0.068	0.010		
Date of birth (kg/day)					
		0.028	0.010		

The results of Model 3 indicated that sex, dam age, dam post-fawning winter weight, and date of birth caused significant differences in birth weight.

4.2.4 Model 4

This model was fitted to test the possible usefulness of concurrently adjusting for both dam pre- and post-fawning winter weight. The non-genetic effects of year, sex, age of dam, date of birth, dam pre-fawning winter weight, and dam post-fawning winter weight were fitted to birth weight. From the original database of 311 birth weights, 53 were chosen that met the following criteria:

(i)   each record required both dam pre- and post-fawning winter weight,

(ii)   number of records in any given herd-year combination > 9,

(iii)   dam age grouped into three classes: 2, 3&4, 5 years, and

(iv)   each herd required a minimum of 2 dams in each dam age class.

The pre-fawning winter weight for the 2 year old dams corresponded to their 15-month weight. There were no dams older than 5 years of age. The data set was identical to that used in Model 2, except that there was one less 5 year old dam as this dam did not have both a pre- and post-fawning winter weight. Refer Model 2, Table 4.2.2.1, for the number of observations noting that there is one less record in 1985 and that this was a female fawn. A detailed presentation of the data set is given in Appendix 1, Table 9.1.4.

A linear model with birth weight as the dependent variable and year, sex, age of dam, and all first order interactions as the independent variables was fitted. Date of birth, dam pre-fawning winter weight, and dam post-fawning winter weight were also fitted as covariates in this model.

Year was not significant (P=0.48) and was removed Model 4. Date of birth was not significant (P>0.05) regardless of the order of fit of dam age, dam winter weight, and date of birth. Date of birth was therefore removed from Model 4. Dam age was highly significant regardless of the order of fit of the independent variables. These results were expected given the findings of Model 2.

The order of fit of the two dam weights was important. The dam weight fitted first in the model was always significant and the second always non-significant (P>0.05). Dam pre-fawning winter weight controlled a greater percentage of variation (1.6% reduction in R^2) than did dam post-fawning winter weight (0.7% reduction in R^2). Therefore dam post-fawning winter weight was excluded from Model 4.

When the first order interaction among the fixed effects, (sex x dam age), was fitted, it was significant (P=0.005) and controlled greater than 2% variation. This interaction therefore remained in Model 4.

The regression of birth weight on dam pre-fawning winter weight was homogeneous between sexes (P=0.17) and dam ages (P=0.57).

The model resulting from the above discussion was identical to that of Model 2. The only difference between the two models is that Model 4 had one less complete record in the data set.

As expected, the results of the ANOVA of the two models are nearly identical, as were the derived least squares estimates and means for the non-genetic effects, and regression coefficient for dam pre-fawning winter weight. A detailed presentation of the results is given in Model 2, Tables 4.2.2.2, 4.2.2.3, and 4.2.2.4. A brief summary of results of both Model 2 and Model 4 are given in Table 4.2.5.1.

The results of Model 4 indicated that sex, dam age, and dam pre-fawning winter weight caused significant differences in birth weight. There was a non-significant increase in the amount of variation controlled in birth weight by Model 4 when both dam winter weights were included. Therefore, a single adjustment for dam winter weight, using pre-fawning winter weight, is appropriate if records are to be adjusted for this effect.

4.2.5 Summary of Models for Birth Weight

The results of the four models for birth weight are summarized in Table 4.2.5.1.

TABLE 4.2.5.1: Analysis of variance summary for birth weight using Models 1, 2, 3 and 4.

| EFFECT | MODEL | | | |
	1	2	3	4
N^a	257	54	106	53
R^{2b}	39.1	63.4	48.3	63.2
S.D.^{c}	1.07	0.77	1.03	0.78
HERD				
% VC^d	11.9	na	na	na
YEAR				
% VC	5.2	NS	NS	NS
SEX				
LSE^e male	0.389	0.403	0.599	0.394
LSE female	-0.389	-0.403	-0.599	-0.394
% M > F^f	9.2	8.4	13.1	8.2
% VC	7.8	20.7	14.9	19.9
DAM AGE				
LSE 2 year	-0.698	0.671	(	0.657
LSE 3 year	(-0.007	(-0.772	(-0.418	(-0.779
LSE 4 year	(	(	(	(
LSE 5+ year	0.705	0.101	0.418	0.122
% VC	11.0	16.0	9.1	17.2
DAM PRE-FAWNING WINTER WEIGHT				
β^g (kg/kg dam wt)	na	0.062	na	0.061
% VC		16.6		16.4
DAM POST-FAWNING WINTER WEIGHT				
β (kg/kg dam wt)	na	na	0.068	NS
% VC			20.1	
DATE OF BIRTH				
β (kg/day)	NS	NS	0.028	NS
% VC			4.2	
(HERD X SEX)				
% VC	3.2	na	na	na
(SEX X DAM AGE)				
% VC	NS	10.1	NS	9.7

where:

a = the total number of records in the data set,

b = the coefficient of determination,

c = the standard deviation of birth weight after adjustment for the non-genetic effects in that model,

d = the percentage of variation controlled by that effect,

e = ordinary least squares estimate,
f = the percentage difference in weight between males and females,
g = the regression coefficient,
na = not applicable, and
NS = not significant, (P>0.05).

NOTE: All effects were highly significant (P<0.001) except for (sex x dam age) in Models 2 and 4 and date of birth in Model 3, which were significant at P<0.01. All interactions, except for those included in Table 4.2.5.1, were not significant (P>0.05), and all regressions of birth weight on date of birth and dam winter weight were homogeneous.

4.2.6 Birth Weight Discussion

The effect of herd was highly significant (P<0.001) in Model 1. This was the only birth weight model where it was possible to test for the significance of herd. Herd accounted for 11.9% of the total variation and the significant (herd x sex) interaction accounted for a further 3.2% of the variation. The occurrence of this interaction could have arisen from sire differences as the effect of herd and sire on birth weight was completely confounded in this model. However, this was unlikely as each herd had six sires represented in the data set. Asher and Adam (1985) found the effect of herd to be significant after adjusting fawn birth weights from the 1981 fawning season for date of birth, sex and dam liveweight. The effect of different areas on the birth weight of Red deer fawns has been noted in the wild population of Red deer on the Isle of Rhum in Scotland (Guinness et al., 1978a) although other workers also studying the Rhum population and mainland Red deer found no differences in birth weights between areas and assumed that foetal growth rates must be similar in both populations (Mitchell and Lincoln, 1973).

In farmed Red deer in New Zealand it would appear that the effect of herd on the birth weight of Red deer was highly significant and that adjusted birth weights should be compared on a within herd basis only unless the relative genetic merit of the herds are known, for example, through sire referencing and providing the management of the dams is comparable from pre-rut until birth.

The effect of year was significant (P<0.05) in only one of the four models. In this case, Model 1, year accounted for 5.2% of the total variation in birth weight. There were no significant interactions involving year among the fixed effects and all the regressions of birth weight on date of birth or dam pre- or post-fawning winter weight were homogeneous for year. Blaxter *et al.* (1974) with farmed Red deer in Scotland found a difference of 0.68 ± 0.37 in the birth weights of fawns born in 1972 and 1973. However, their data set was very small with only 5 fawns born in 1972 (all from 2 year old dams) and 47 in 1973 (from both 2 and 3 year old dams). While not a direct comparison, there was little difference between the average birth weights of farmed Red deer from the 1980 (Asher *et al.*, 1981) and 1981 (Asher and Adam, 1985) fawning seasons from the same area in New Zealand. In 1980 the birth weight of males was 9.4 kg and females 8.8 kg and in 1981 males were 9.4 kg and females 8.9 kg. Moore (1984) commented that the birth weights of Red deer fawns have increased from 6.6 kg (male) and 6.0 kg (female) in 1973 to 9.5 kg (male) and 8.8 kg (female) in 1982 at the Invermay Agriculture Centre, New Zealand. These increases were largely related to changes in management practices.

While the effect of year on birth weight requires further investigation, a tentative conclusion is that birth weights within a farmed herd show little variation from year to year. The differences in findings between the wild Red deer of Scotland (Mitchell, 1971; Guinness *et al.*, 1978a; Clutton-Brock *et al.*, 1982; Albon *et al.*, 1983, 1987) and the farmed Red deer of New Zealand may be due to differences in the degree of annual climatic variations, as most areas of New Zealand have a more temperate and even climate than that of Scotland. However, it is likely that significant year effects could occur during climatically abnormal years.

In all four models the sex of the fawn had a highly significant (P<0.001) effect on its birth weight, with stag fawns being 0.8 to 1.2 kg (8 to 13%) heavier than hind fawns. The sex of the fawn accounted for between 8 to 21% of the total variation in birth weight across models and was the most important non-genetic effect in three of the four models. The variation between models in the effect of sex on birth weight (refer to Table 4.2.5.1) may have been partially caused by the low number of records in some models and the presence of the (sex x dam age) interaction in Models 2 and 4.

The least squares means for sex ranged from 9.24 to 10.43 kg for males and 8.64 to 9.64 kg for females. These results are similar to that found by Asher *et al.* (1981) for farmed Red deer in New Zealand in the 1980 fawning season (males = 9.4 kg, females = 8.8 kg), with males being 8 to 10% heavier. Asher and Adam (1985) reported a weight difference of 6.4% in favour of males (males = 9.4 kg, females = 8.9 kg) for the 1981 fawning season in farmed Red deer. Kelly and Whateley (1975) also found that male fawns were heavier at birth, with the average weight of males being 6.4 kg and that of females 6.0 kg but this difference was not significant. These fawns were born to 90 captured feral hinds in New Zealand. Similar effects have been noted in farmed Scottish deer (Blaxter *et al.*, 1974; Hamilton and Blaxter, 1980). Birth weight differences between the sexes, with males being approximately 0.5 kg heavier than females, have also been found in wild Red deer populations of Scotland (Mitchell, 1971; Mitchell and Lincoln, 1973; Guinness *et al.*, 1978a; Clutton-Brock *et al.*, 1981; Clutton-Brock *et al.*, 1982; Clutton-Brock, 1985) although the average birth weights of the wild Red deer were lower, on average 6 to 7 kg, than the results presented here.

The effect of dam age was highly significant (P<0.001) in all models. The number of dam age classes varied between models, with Models 1, 2 and 4 having the 3 and 4 year old dams combined into one dam age class. In Model 1, the least squares estimate for the 3&4 year old class was not significantly different from zero, whereas in Models 2 and 4 it was the 5 year old class that was not significantly different from zero. In Model 3, both dam age groups (2&3&4 and 5 year old) were significantly different from zero. Dam age accounted for 9 to 17% of the total variation in fawn birth weight. In general, younger dams (2, 3 or 4 year old), produced fawns that were approximately 8% lighter than older dams (5 year old). However, in Models 2 and 4, the 2 year old dams produced the heaviest fawns (5.6% heavier than 5 year old dams), and the 3&4 year old dams produced the lightest fawns (8.6% lighter than 5 year old dams). It is possible, especially as Models 2, 3 and 4, were based on data from only one herd, that the first fawning hinds were preferentially fed during pregnancy. This is a common practice as 2 year old hinds have not yet reached their mature weight (Mitchell, 1973; Mitchell and Lincoln, 1973; Blaxter *et al.*, 1974; Guinness *et al.*, 1978b; Hamilton and Blaxter, 1980; Fennessy, 1986b, 1987) and deer farmers are unwilling to restrict the growth rate of the first fawning dams. Fennessy (1982a) commented that since most of the growth of

the foetus occurs in the last one third of pregnancy, the level of nutrition of the hind in late pregnancy affects foetal growth and consequently, birth weight. In contrast, Adam and Asher (1986) stated that they did not restrict feed intake and believed that the intake of the Red deer hinds did not change markedly to within three weeks of fawning. Such management effects are likely to be reflected in dam pre-rut liveweight which has also been shown to have an effect on fawn birth weight (Blaxter and Hamilton, 1980; Fennessy, 1982a; Adam and Asher, 1986). This point will be expanded later in the discussion.

Other studies have also shown an effect of dam age on birth weight. Blaxter *et al.* (1974) with farmed Red deer in Scotland during the 1973 fawning season found that 3 year old dams produced fawns weighing 1.02 ± 0.33 kg (n=6) more than 2 year old dams (first-fawners, n=41). There were no dams older than 3 years of age in this study. Guinness *et al.* (1978a) with wild Red deer on the Isle of Rhum, Scotland from 1971 to 1976, found that mean fawn birth weight increased with mother's age from first breeding at 3 years of age to a peak in dams of 9 to 10 years of age and then subsequently declined. In a New Zealand study comparable to the one presented here, with data collected from four farms, Asher and Adam (1985) found a small effect of dam age. Two year old dams (n=3) produced fawns with an adjusted mean birth weight of 9.16 kg, with older dams (n = 174) producing fawns of 9.11 kg birth weight. Thus, 2 year old dams produced fawns which were approximately the same weight as those from older dams. However, only one of the four farms in this study had 2 year old dams and these represented only 3.2% of all hinds in the study. Therefore, considerable bias in the results may have occurred. In the study of Asher and Adam (1985) when birth weight had been previously adjusted for dam pre-rut liveweight the effect of dam age was not significant, which was in agreement with the study of Blaxter and Hamilton (1980). These findings were in contrast to the results presented here.

The (sex x dam age) interaction accounted for approximately 10% of the total variation in Models 2 and 4 and may have been caused by the skewed distribution of dam ages between years and sexes, particularly as 7 of the 10 offspring from 2 year old dams were male. Asher and Adam (1985) did not report any significant interactions between fixed effects for birth weight.

In Models 2 and 4 where dam pre-fawning winter weight was fitted, and in Model 3 where dam post-fawning winter weight was fitted, both dam age and dam liveweight were significant regardless of the order of fit of these two variables. In Model 4, where both dam liveweights were fitted, only the first of the two was significant (P<0.005) regardless of their order of fit. However, dam pre-fawning winter weight, which included the 15-month weights for 2 year old dams, controlled more of the total variation in birth weight, than did dam post-fawning winter weight. Therefore, the results presented here indicated that should birth weight be adjusted for dam liveweight, then the dam pre-fawning winter weight should be used in preference to the dam post-fawning winter weight.

Dam pre-fawning winter weight was highly significant (P<0.001) in Models 2 and 4 controlling approximately 16% of the total variation in birth weight. The regression coefficient of 0.062 kg birth weight per kg of dam pre-fawning winter weight is similar to the regression coefficient for dam post-fawning winter weight in Model 3 of 0.068 kg birth weight per kg of dam post-fawning winter weight. Dam post-fawning winter weight accounted for 20% of the total variation in birth weight using Model 3.

These results were similar to the findings of other studies where the effect of dam liveweight, taken immediately prior to the rut, on birth weight have been examined. The data from farmed Red deer in Scotland used by Blaxter and Hamilton (1980) suggested that younger (and smaller) hinds produced smaller fawns, however it was apparent that there was no effect of age of hind (2,3,4,5,6,7 years) on the weight of her fawn at birth which could not be explained by her body weight. They calculated that an increase of 20 kg in hind body weight at the time of the rut would increase birth weight by 1.05 kg. This gives a regression coefficient of 0.053 kg birth weight per kg dam liveweight. Asher and Adam (1985), with farmed Red deer in New Zealand, found that dam liveweight had a highly significant (P<0.001) effect on birth weight with a regression coefficient of 0.036 ± 0.007 (mean ± S.E.) kg birth weight per kg of dam liveweight. Fennessy (1982a) and Adam and Asher (1986) also reported that birth weight was positively associated with dam liveweight.

The date of birth of the fawn was not significant (P>0.05) in three of the four models. In Model 3, where date of birth was significant (P<0.01), an increase in birth weight of 0.028 kg for each day later the fawn was born from 1 November

was calculated. Date of birth accounted for 4.2% of the total variation in this model, which was a considerably smaller amount than was controlled by each of the other significant non-genetic effects. Blaxter *et al.* (1974) found that the later a fawn was born the heavier it was; fawn birth weight increased by 0.33 kg if it was born a month late, that is, an increase of 0.011 kg per day. The significance of this effect was not indicated. Adam and Asher (1986) commented that birth weight was positively associated with birth date for Red deer. In contrast, Asher and Adam (1985) reported that there was a small, non-significant, effect of 0.003 ± 0.005 (mean $\pm$ S.E.) kg birth weight for each day later a fawn was born. Guinness *et al.* (1978a) studying wild Red deer on the Isle of Rhum, Scotland, also found no significant relationship between birth weight and date of birth. It is possible that an apparent effect of date of birth is caused by differences in dam liveweight prior to fawning as has been discussed earlier. In conclusion, it appears that for Red deer, the date of birth has only a small, and usually non-significant, effect on birth weight. This is probably due to their relatively short peak of fawning, which is four to six weeks long (Asher and Adam, 1985). The relative importance of the non-genetic effects for birth weight in Red deer are similar to those for birth weight in beef cattle as reviewed in Section 2.2.1.

In conclusion, herd, sex of fawn, age of dam and dam winter weight all had marked effects on birth weight, whereas year within herds and date of birth had only a small, if not insignificant, effect. It should be noted that should dam liveweights be used to adjust fawn birth weights then both the environmental variation and the genetic variation are decreased. If sufficient genetic variance is removed the genetic ranking of the fawns may be altered. This, in turn, will reduce the effectiveness of selection by increasing the error of predicting genetic merit. Therefore, birth weights within a herd need to be adjusted for sex and dam age if selection on predicted genetic merit is to be undertaken. On the available evidence, dam age should contain at least three age classes; 2 year old (first fawners), 3 and 4 year old, and older dams. There is need for further investigation into the effects of year, date of birth, dam age, particularly with older dam age groups, and the relationship between the effects of dam age and dam liveweight on birth weight.

4.3 MARCH WEIGHT

4.3.1 Model 5

The non-genetic effects of herd, year, sex, age of dam, and age at March weighing (age at mwt) were fitted to March weight. From the original database of 2874 March weights, 1318 observations were chosen that met the following criteria:

(i)   59 days (2 months) < age at mwt < 151 days (5 months),

(ii)   number of records in any given herd-year combination > 9,

(iii)   dam age grouped into four classes: 2, 3, 4 and 5+ years, and

(iv)   each herd required a minimum of 2 dams in each dam age class.

The number of observations by herd, year, sex and dam age are given in Table 4.3.1.1. A detailed presentation of the data set is given in Appendix 2, Table 9.2.1.

TABLE 4.3.1.1: Number of records in each class of non-genetic effect in Model 5. (N = 1318)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	70	1982	30	male	644	2 year	280
2	47	1983	202	female	674	3 year	263
3	111	1984	597			4 year	302
4	171	1985	489			5+ year	473
5	102						
6	205						
7	178						
8	135						
9	193						
10	42						
11	64						

A linear model with March weight as the dependent variable and herd, year, sex, age of dam, and all first order interactions as the independent variables was fitted. Age at mwt was also fitted as a covariate in this model.

When all first-order interactions among the fixed effects were included in the model, the following were not significant: (herd x sex)(P=0.09), (year x sex)(P=0.16) and (sex x dam age)(P=0.79). The (year x dam age) interaction although significant (P=0.007), controlled only a small amount of variation (0.7% reduction in R^2). This interaction could have arisen through the unbalanced nature of the data set with regard to the numbers in each of the dam age classes. Due to this possible reason and, as animals are usually compared within years, this interaction was removed from Model 5. However, should hind productivity indices be calculated, as for breeding cows in Beefplan through Breeding Value (maternal ability) (Packard and Morris, 1986), then this interaction will require further investigation as it suggests that the adjustment factors for dam age vary among years.

The (herd x year) interaction, which was highly significant (P<0.001) and controlled 2.6% variation (reduction in R^2), was excluded from Model 5 as animals within a herd are usually compared on a contemporary basis making it unnecessary to adjust for this interaction.

The regression of March weight on age at mwt was homogeneous between years (P=0.45) and sexes (P=0.47). Although significant heterogeneity existed between herds (P<0.001) and between dam ages (P=0.01) they were considered to be homogeneous due to the small amount of variation each controlled, 1.5 and 0.4% respectively. The significance of these regressions suggests the need for within herd adjustment for age at mwt.

The ANOVA based on the model resulting from the above discussion is given in Table 4.3.1.2 with the percentage of variation each of the non-genetic effects controlled. The least squares estimates and means are presented in Tables 4.3.1.3 and 4.3.1.4.

TABLE 4.3.1.2: Analysis of variance for March weight and the percentage of variation controlled (%VC) by each non-genetic effect using Model 5.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	10	1043.5	***	15.1
Year	3	431.7	***	1.9
Sex	1	6747.7	***	9.7
Dam age	3	2543.3	***	11.0
Age at mwt	1	12098.2	***	17.5
(herd x dam age)	30	52.2	***	2.3
Error	1269	23.3		42.5
Total	1317			100.0

$R^2 = 57.5\%$

The results shown in Table 4.3.1.3 indicated that males were 10.6% heavier than females at the March weighing, given that all other non-genetic effects were equal. Overall, these results indicated that fawns from 2, 3 and 4 year old dams were 9.3, 4.5 and 1.3% lighter, respectively, at the March weighing than fawns from 5+ year old dams, given that all other non-genetic effects were equal. However, due to the presence of the (herd x dam age) interaction the magnitude and direction of this difference varied between herds.

TABLE 4.3.1.3: Ordinary least squares estimates (LSE) and means (LSM) for sex, dam age, and (herd x dam age) interaction and the regression coefficient for age at March weighing (age at mwt), with their respective standard errors (S.E.) for Model 5. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	2.229	0.139	46.69	0.34
	female	-2.229	0.139	42.23	0.33
Dam age	2 year	-2.632	0.344	41.83	0.47
	3 year	-0.125	0.323	44.34	0.44
	4 year	1.086	0.302	45.56	0.41
	5+ year	1.671	0.329	46.14	0.46
Age at mwt(kg/day)		0.256	0.012		

(herd x dam age) interaction

Herd 1	2 year	2.988	1.014
	3 year	0.487	1.170
	4 year	-1.228	0.948
	5+ year	-2.247	0.889
Herd 2	2 year	-5.099	1.804
	3 year	1.034	1.192
	4 year	2.048	1.137
	5+ year	2.067	1.794
Herd 3	2 year	-1.084	0.921
	3 year	0.298	0.794
	4 year	-0.536	0.720
	5+ year	1.323	0.875
Herd 4	2 year	0.633	0.658
	3 year	-0.677	0.661
	4 year	-1.362	0.701
	5+ year	1.406	0.687
Herd 5	2 year	3.787	1.316
	3 year	-2.289	1.456
	4 year	-1.843	0.963
	5+ year	0.345	0.824

TABLE 4.3.1.3 (continued)

EFFECT		LSE	S.E.	LSM	S.E.
Herd 6	2 year	-0.939	0.607		
	3 year	-0.014	0.727		
	4 year	0.765	0.715		
	5+ year	0.188	0.588		
Herd 7	2 year	-1.330	0.682		
	3 year	0.932	0.681		
	4 year	-0.056	0.708		
	5+ year	0.454	0.611		
Herd 8	2 year	-1.571	0.782		
	3 year	0.533	0.775		
	4 year	-0.080	0.795		
	5+ year	1.117	0.687		
Herd 9	2 year	-0.570	0.813		
	3 year	1.219	0.736		
	4 year	-0.424	0.734		
	5+ year	-0.225	0.578		
Herd 10	2 year	1.090	1.441		
	3 year	-2.386	1.327		
	4 year	3.694	1.610		
	5+ year	-2.397	1.076		
Herd 11	2 year	2.095	1.173		
	3 year	0.863	1.196		
	4 year	-0.977	0.942		
	5+ year	-1.980	1.736		

TABLE 4.3.1.4: Combined ordinary least squares estimates of dam age and (herd x dam age) interaction for Model 5.

HERD NUMBER	DAM AGE			
	2 year	3 year	4 year	5+ year
1	0.356	0.362	-0.142	-0.576
2	-7.731	0.909	3.134	3.688
3	-1.548	0.173	0.549	2.994
4	-1.999	-0.802	-0.277	3.078
5	1.155	-2.414	-0.757	2.016
6	-3.571	-0.139	1.851	1.860
7	-3.962	0.807	1.029	2.126
8	-4.203	0.408	1.006	2.788
9	-3.202	1.094	0.662	1.446
10	-1.542	-2.511	4.779	-0.726
11	-0.537	0.737	0.108	-0.309

The results of Model 5 indicated that herd, year, sex of fawn, age of dam, and age at mwt caused significant differences in March weight. The significant (herd x dam age) interaction indicated that adjustment factors for dam age should be calculated on a within rather than across herd basis.

4.3.2 Model 6

4.3.2.1 Model 6A

This model was fitted to test the usefulness of dam pre-fawning winter weight as an adjustment factor for March weight. The non-genetic effects of herd, year, sex, age of dam, age at mwt, and dam pre-fawning winter weight were fitted to March weight. From the original database of 2874 March weights, 154 observations were chosen that met the following criteria:

(i)   59 days < age at mwt < 151 days,

(ii)   each record required a dam pre-fawning winter weight,

(iii)   number of records in any given herd-year combination > 9,

(iv)   herd-year combinations required dams in both dam age classes, and

(v)   dam age grouped into two classes: 2 and 3+ years.

The pre-fawning winter weight for the 2 year old dams corresponded to their 15-month weight. The number of observations by herd, year, sex, and dam age are given in Table 4.3.2.1.1. A detailed presentation of the data set is given in Appendix 2, Table 9.2.2.

TABLE 4.3.2.1.1: Number of records in each class of non-genetic effect in Model 6A. (N = 154)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	59	1984	17	male	88	2 year	32
2	21	1985	137	female	66	3+ year	122
3	74						

A linear model with March weight as the dependent variable and herd, year, sex, age of dam, and all first order interactions as the independent variables was fitted. Age at mwt and dam pre-fawning winter weight were also fitted as covariates in the model.

The order of fitting the independent variables affected the significance of dam age. When dam age was fitted before dam pre-fawning winter weight it was significant (P<0.001), but when it was fitted after dam pre-fawning winter weight it became non-significant (P=0.36). Dam age was therefore removed from Model 6A.

When the first-order interactions among the fixed effects were included in the model, (herd x sex)(P=0.18) and (year x sex)(P=0.36) were not significant. Due to the unbalanced nature of the data set, the (herd x year) interaction could not be tested for significance.

The regression of March weight on age at mwt was homogeneous between herds (P=0.85), years (P=0.23) and sexes (P=0.99). The regression of March weight on dam pre-fawning winter weight was homogeneous between years (P=0.07) and sexes (P=0.89) but not between herds (P=0.004). The heterogeneity between herds for the regression of March weight on dam pre-fawning winter weight may have occurred because of the relatively small number of records in each dam age sub-class and the skewed distribution of dam age within each herd (as shown in Appendix 2, Table 9.2.2). Furthermore, 2 year old dams have not yet reached mature body weight and are therefore lighter than 3 year old and older dams. Another possible explanation is that it is the policy of some breeders to preferentially feed the first-fawning hinds compared to the mixed-age hinds.

The ANOVA based on the model resulting from the above discussion is given in Table 4.3.2.1.2 with the percentage of variation each of the non-genetic effects controlled. The least squares estimates and means are presented in Table 4.3.2.1.3.

TABLE 4.3.2.1.2: Analysis of variance for March weight and the percentage of variation controlled (%VC) by each of the non-genetic effects using Model 6A.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	2	335.8	***	8.6
Year	1	221.3	***	2.8
Sex	1	998.5	***	12.8
Age at mwt	1	2548.7	***	32.7
Dam pre-fawning weight	1	749.8	***	9.6
Dam weight within herds	2	94.2	**	2.4
Error	145	16.7		31.3
Total	153			100.0

$R^2 = 68.9\%$

The results shown in Table 4.3.2.1.3 indicated that males were 12.2% heavier than females at the March weighing, given that all other non-genetic effects were equal.

TABLE 4.3.2.1.3: Ordinary least squares estimates (LSE) and means (LSM) for sex and the regression coefficients for age at March weighing (age at mwt), dam pre-fawning winter weight, and dam pre-fawning winter weight within herds, with their respective standard errors (S.E.) for Model 6A.
(units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	2.420	0.339	44.50	0.74
	female	-2.420	0.339	39.66	0.82
Age at mwt(kg/day)		0.360	0.036		
Dam weight(kg/kg dam wt)		0.156	0.040		
Dam weight within herds(kg/kg dam wt)					
	Herd 1	0.072	0.049		
	Herd 2	-0.218	0.068		
	Herd 3	0.146	0.049		

The results of Model 6A indicated that herd, year, sex, age at mwt and dam pre-fawning winter weight caused significant differences in March weight. The heterogeneous nature of dam pre-fawning winter weight between herds suggests that should dam pre-fawning winter weight (including 2 year old dams) be used as an adjustment factor for March weight, it will either need to be calculated on a within herd basis or herd management will need to be standardized for hinds of all liveweights, that is, for each age group.

4.3.2.2 Model 6B

This model was the same as Model 6A except only 3 year and older dams were included in the data set. This was undertaken to examine whether the inclusion of 2 year old dams, and therefore their 15-month weights, was altering the significance of the other effects in the model and to determine the degree of change in the regression coefficient for dam pre-fawning winter weight.

The non-genetic effects of herd, sex, dam age, age at mwt, and dam pre-fawning winter weight were fitted to March weight. From the original database of 2874 March weights, 210 observations were chosen that met the following criteria:

  (i)   59 days < age at mwt < 151 days,
  (ii)   each record required a dam pre-fawning winter weight,
  (iii) number of records in any given herd-year combination > 9,
  (iv)   dam age grouped into two classes: 3 and 4+ years, and
  (v)   herd-year combinations required dams in both dam age classes.

These criteria reduced the potential data set down to a very small size which only included data from one year. The number of observations by herd, year, sex and dam age are given in Table 4.3.2.2.1. A detailed presentation of the data set is given in Appendix 2, Table 9.2.3.

TABLE 4.3.2.2.1: Number of records in each class of non-genetic effect in Model 6B. (N = 210)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	15	1985	210	male	112	3 year	39
2	35			female	98	4+ year	171
3	42						
4	20						
5	53						
6	45						

A linear model with March weight as the dependent variable and herd, sex, age of dam, and all first order interactions as the independent variables was fitted. Age at mwt and dam pre-fawning winter weight were also fitted as covariates in this model.

Regardless of the order of fit of the independent variables dam age and dam pre-fawning winter weight, dam age was not significant (P>0.19). Therefore dam age was removed from Model 6B.

When the first order interaction among the fixed effects, (herd x sex), was included in the model it was found to be non-significant (P=0.06) and was therefore excluded from Model 6B.

The regression of March weight on age at mwt was homogeneous between herds (P=0.06) and sexes (P=0.30). The regression of March weight on dam pre-fawning winter weight was homogeneous between herds (P=0.19) and sexes (P=0.81).

The ANOVA based on the model resulting from the above discussion is given in Table 4.3.2.2.2, with the percentage of variation each non-genetic effect controlled. The least squares estimates and means are presented in Table 4.3.2.2.3.

TABLE 4.3.2.2.2: Analysis of variance for March weight and the percentage of variation controlled (%VC) by each non-genetic effect using Model 6B.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	5	617.6	***	25.8
Sex	1	1289.7	***	10.8
Age at mwt	1	2466.2	***	20.6
Dam pre-fawning weight	1	481.0	***	4.0
Error	201	23.0		38.8
Total	209			100.0

$R^2 = 61.2\%$

The results shown in Table 4.3.2.2.3 indicated that males were 10.6% heavier than females at the March weighing, given that all other non-genetic effects were equal.

TABLE 4.3.2.2.3: Ordinary least squares estimates (LSE) and means (LSM) for sex and the regression coefficients for age at March weighing (age at mwt) and dam pre-fawning winter weight, with their respective standard errors (S.E.) for Model 6B. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	2.305	0.337	48.03	0.48
	female	-2.305	0.337	43.42	0.52
Age at mwt(kg/day)		0.310	0.031		
Dam weight(kg/kg dam weight)					
		0.177	0.039		

The results of Model 6B indicated that herd, sex, age at mwt, and dam pre-fawning winter weight caused significant differences in March weight. The homogeneity of dam pre-fawning winter weight of 3 year old dams and older dams across herds suggests that a single adjustment factor would be applicable to all herds. The effect of year could not be tested in this model due to insufficient data.

There was insufficient data to run a model similar to Model 6B on immature dams alone. While there is no direct comparison some inferences can be made from the previous two models. First, if dam pre-fawning winter weight is fitted before dam age, dam age becomes non-significant (P>0.05) in all cases. Therefore it appears that a single adjustment factor, that is, dam pre-fawning winter weight, would be appropriate in accounting for environmental effects due to dam age. Secondly, the regression coefficients for March weight on dam pre-fawning winter weight were very similar in Models 6A and 6B, that is, 0.156

and 0.177 kg of March weight per kg of dam weight, respectively. This indicated that the 15-month weight is an indicator of mature weight and that it is appropriate to use the 15-month weight of a 2 year old dam as a dam pre-fawning winter weight adjustment factor.

However, the above conclusions are based on very small data sets especially the number of 2 year old dams (as shown by Appendix 2, Tables 9.2.2 and 9.2.3) therefore, the results should be treated with caution.

4.3.3 Model 7

This model was fitted to test the usefulness of dam post-fawning winter weight as an adjustment factor for March weight. The non-genetic effects of herd, year, sex, dam age, age at mwt, and dam post-fawning winter weight were fitted to March weight. From the original data set of 2874 March weights, 579 observations were chosen that met the following criteria:

    (i)   59 days < age at mwt < 151 days,

    (ii)   each record required a dam post-fawning winter weight,

    (iii)   number of records in any given herd-year combination > 9,

    (iv)   dam age grouped into two classes: 2 and 3+ years, and

    (v)   herd-year combinations required dams in both dam age classes.

The number of observations by herd, year, sex and dam age are given in Table 4.3.3.1. A detailed presentation of the data set is given in Appendix 2, Table 9.2.4.

TABLE 4.3.3.1: Number of records in each class of non-genetic effect in Model 7. (N = 579)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	16	1984	274	male	293	2 year	147
2	99	1985	305	female	286	3+ year	432
3	47						
4	28						
5	96						
6	129						
7	115						
8	49						

A linear model with March weight as the dependent variable and herd, year, sex, age of dam, and all first order interactions as the independent variables was fitted. Age at mwt and dam post-fawning winter weight were also fitted as covariates in this model.

Year was not significant (P=0.34) when fitted after herd but became significant (P=0.002) when fitted first in Model 7. Removing year from Model 7 caused a small, 0.019%, reduction in R^2. Therefore, year was not included in Model 7. Dam age was highly significant (P<0.003) regardless of whether it was fitted before or after dam post-fawning winter weight.

When the first-order interactions among the fixed effects were included in the model, (herd x sex)(P=0.09) and (sex x dam age)(P=0.38) were non-significant and were therefore excluded from Model 7.

The regression of March weight on age at mwt was homogeneous between herds (P=0.14), sexes (P=0.09) and dam ages (P=0.91). The regression of March weight on dam post-fawning winter weight was homogeneous between sexes (P=0.06) and dam ages (P=0.22) and although heterogeneous between herds (P=0.02) it was considered to be homogeneous because of the small amount of variation controlled (1.1% reduction in R^2).

The ANOVA based on the model resulting from the above discussion is given in Table 4.3.3.2, with the percentage of variation each non-genetic effect controlled. The least squares estimates and means are presented in Tables 4.3.3.3 and 4.3.3.4.

TABLE 4.3.3.2: Analysis of variance for March weight and the percentage of variation controlled (%VC) by each non-genetic effect using Model 7.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	7	215.5	***	5.6
Sex	1	3390.1	***	12.7
Dam age	1	3552.8	***	13.3
Age at mwt	1	6629.9	***	24.8
Dam post-fawning weight	1	1479.7	***	5.5
(herd x dam age)	7	75.0	***	2.0
Error	560	17.2		36.1
Total	578			100.0

$R^2 = 63.9\%$

The results shown in Table 4.3.3.3 indicated that males were 10.6% heavier than females at the March weighing, given that all other non-genetic effects were equal. Generally, 2 year old dams reared fawns that were 2.5% lighter than 3 year old and older dams at the March weighing, given that all other non-genetic effects were equal. However, the direction and magnitude of the dam age effect varied between herds, as shown in Table 4.3.3.4, indicating the need for estimation of dam age adjustment factors on a within herd basis.

TABLE 4.3.3.3: Ordinary least squares estimates (LSE) and means (LSM) for sex, dam age, and (herd x dam age) interaction and the regression coefficients for age at March weighing (age at mwt) and dam post-fawning winter weight, with their respective standard errors (S.E.) for Model 7. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	2.251	0.175	47.13	0.31
	female	-2.251	0.175	42.63	0.31
Dam age	2 year	-0.564	0.269	44.31	0.44
	3+ year	0.564	0.269	45.44	0.28
Age at mwt(kg/day)		0.335	0.017		
Dam weight(kg/kg dam weight)					
		0.179	0.021		

(herd x dam age) interaction

		LSE	S.E.		
Herd 1	2 year	2.207	0.944		
	3+ year	-1.156	0.537		
Herd 2	2 year	-0.817	0.669		
	3+ year	0.885	0.921		
Herd 3	2 year	0.625	0.462		
	3+ year	-1.726	0.450		
Herd 4	2 year	-0.972	0.548		
	3+ year	0.954	0.585		
Herd 5	2 year	-2.207	0.944		
	3+ year	1.156	0.537		
Herd 6	2 year	0.817	0.669		
	3+ year	-0.885	0.921		
Herd 7	2 year	-0.625	0.462		
	3+ year	1.726	0.450		
Herd 8	2 year	0.972	0.548		
	3+ year	-0.954	0.585		

TABLE 4.3.3.4: Combined ordinary least squares estimates of dam age and (herd x dam age) interaction for Model 7.

HERD NUMBER	DAM AGE	
	2 year	3+ year
1	1.643	-0.592
2	-1.381	1.449
3	0.061	-1.162
4	-1.536	1.518
5	-2.771	1.720
6	0.253	-0.321
7	-1.189	2.290
8	0.408	-0.390

The results of Model 7 indicated that herd, sex of fawn, age of dam, age at mwt, and dam post-fawning winter weight caused significant differences in March weight. The presence of the (herd x dam age) interaction suggests that either dam age adjustment factors be calculated on a within rather than across herd basis or that the management of dam age groups be standardized across herds.

4.3.4 Model 8

4.3.4.1 Model 8A

This model was fitted to test the possible usefulness of concurrently adjusting March weight for both dam pre- and post-fawning winter weights. The non-genetic effects of herd, sex, dam age, age at mwt, dam pre-fawning winter weight, and dam post-fawning winter weight were fitted to March weight. From the original database of 2874 March weights, 115 observations were chosen that met the following criteria:

(i)   59 days < age at mwt < 151 days,

(ii)   each record required both a dam pre- and post-fawning winter weight,

(iii) number of records in any given herd-year combination > 9,

(iv) dam age grouped into two classes: 2 and 3+ years, and

(v) herd-year combinations required dams in both dam age classes.

The pre-fawning winter weight of 2 year old dams corresponded to their 15-month weight. The number of observations by herd, year, sex, and dam age are given in Table 4.3.4.1.1. A detailed presentation of the data set is given in Appendix 2, Table 9.2.5.

TABLE 4.3.4.1.1: Number of records in each class of non-genetic effect in Model 8A. (N = 115)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	41	1985	115	male	64	2 year	28
2	74			female	51	3+ year	87

A linear model with March weight as the dependent variable and herd, sex, age of dam, and all first order interactions as the independent variables was fitted. Age at mwt, dam pre-fawning winter weight, and dam post-fawning winter weight were also fitted as covariates in this model.

The order of fit of the two dam weights was important. The dam weight fitted first in the model was always significant (P<0.05) and the second was always non-significant (P>0.05). Dam pre-fawning winter weight controlled a higher percentage of variation (0.6% reduction in R^2) than did dam post-fawning winter weight (0.2% reduction in R^2). More importantly, when dam age was fitted after dam pre-fawning winter weight but without dam post-fawning winter weight in the model, dam age became non-significant (P>0.05). However, when dam age was fitted after post-fawning winter weight but without dam pre-fawning winter weight in the model, dam age remained significant (P<0.05). Therefore dam post-fawning winter weight and dam age were excluded from Model 8A.

When the first order interaction among the fixed effects, (herd x sex) was included in the model it was found to be non-significant (P=0.07) and was therefore excluded from Model 8A.

The regression of March weight on age at mwt was homogeneous between herds (P=0.76) and sexes (P=0.91). The regression of March weight on dam pre-fawning winter weight was homogeneous between herds (P=0.98) and sexes (P=0.94).

The ANOVA based on the model resulting from the above discussion is given in Table 4.3.4.1.2, with the percentage of variation each non-genetic effect controlled. The least squares estimates and means are presented in Table 4.3.4.1.3.

TABLE 4.3.4.1.2: Analysis of variance for March weight and the percentage of variation controlled (%VC) by each non-genetic effect using Model 8A.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	1	503.6	***	8.4
Sex	1	891.4	***	14.9
Age at mwt	1	2051.3	***	34.3
Dam pre-fawning weight	1	988.5	***	16.5
Error	110	14.1		25.9
Total	114			100.0

$R^2 = 74.1\%$

The results shown in Table 4.3.4.1.3 indicated that males were 11.0% heavier than females at the March weighing, given that all other non-genetic effects were equal.

TABLE 4.3.4.1.3: Ordinary least squares estimates (LSE) and means (LSM) for sex and the regression coefficients for age at March weighing (age at mwt) and dam pre-fawning winter weight, with their respective standard errors (S.E.) for Model 8A. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	2.380	0.361	47.89	0.48
	female	-2.380	0.361	43.13	0.55
Age at mwt(kg/day)		0.344	0.037		
Dam weight(kg/kg dam weight)					
		0.304	0.036		

The results of Model 8A indicated that herd, sex, age at mwt, and dam pre-fawning winter weight, including 2 year old dams, caused significant differences in fawn March weight.

These results are consistent with the findings of Models 6A, 6B and 7. Dam pre-fawning winter weight accounted for more variation in dam age than does dam post-fawning winter weight when 2 year old dams were included.

To minimize the number of environmental corrections these results indicated that a single adjustment for dam pre-fawning winter weight could be used rather than adjustments for: both dam pre- and post-fawning winter weight; or dam post-fawning winter weight alone. If the fawn's March weight is adjusted for dam post-fawning winter weight but not dam pre-fawning winter weight then a further adjustment for the age of the dam is required.

The above conclusions are based on a very small data set covering only one fawning (as shown in Appendix 2, Table 9.2.5) therefore, the results should be treated with caution.

4.3.4.2 Model 8B

This model was the same as Model 8A except only 3 year and older dams were included in the data set. This was undertaken to examine whether the inclusion of 2 year old dams, and therefore their 15-month weights, was altering the significance of the other effects in the model and to determine the degree of change in the regression coefficient for dam winter weight.

The non-genetic effects of herd, sex, dam age, age at mwt, dam pre-fawning winter weight, and dam post-fawning winter weight were fitted to March weight. From the original database of 2874 March weights, 132 observations were chosen that met the following criteria:

(i)   59 days < age at mwt < 151 days,

(ii)   each record required both a dam pre- and post-fawning winter weight,

(iii)   number of records in any given herd-year combination > 9,

(iv)   dam age grouped into two classes: 3 and 4+ years, and

(v)   herd-year combinations required dams in both dam age classes.

The number of records meeting the criteria increased from Model 8A as the herd-year combinations were no longer required to have 2 year old and older dams. The number of observations by herd, year, sex, and dam age are given in Table 4.3.4.2.1. A detailed presentation of the data set is given in Appendix 2, Table 9.2.6.

TABLE 4.3.4.2.1: Number of records in each class of non-genetic effect in Model 8B. (N = 132)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	34	1985	132	male	67	3 year	20
2	53			female	65	4+ year	112
3	45						

A linear model with March weight as the dependent variable and herd, sex, dam age, and all first order interactions as the independent variables was fitted. Age at mwt, dam pre-fawning winter weight, and dam post-fawning winter weight were also fitted as covariates in this model.

Dam age was not significant (P>0.05) regardless of the order of fit of the independent variables dam age and dam pre- and post-fawning winter weight. That is, regardless of whether dam age was fitted before or after the dam winter weights. This result was consistent with the findings of Model 6B. Therefore, dam age was excluded from Model 8B.

The order of fit of the two dam weights was important. The dam weight fitted first in the model was always significant (P<0.05) and the second was always non-significant (P>0.05). Dam pre-fawning winter weight controlled a higher percentage of variation (1.30% reduction in R^2) than did dam post-fawning winter weight (0.01% reduction in R^2). Thus, when both weights were included in the model, dam post-fawning winter weight accounted for little variation in March weight whereas, dam pre-fawning winter weight accounts for just over one percent of the variance. Therefore, dam post-fawning winter weight was excluded from Model 8B.

When the first order interaction among the fixed effects, (herd x sex), was included in the model, it was found to be significant (P=0.04) and controlled more than 2% of the variation. The (herd x sex) interaction therefore remained in Model 8B.

The regression of March weight on age at mwt was homogeneous between herds (P=0.12) and sexes (P=0.39). The regression of March weight on dam pre-fawning winter weight was also homogeneous between herds (P=0.07) and sexes (P=0.96).

The ANOVA based on the model resulting from the above discussion is given in Table 4.3.4.2.2, with the percentage of variation each non-genetic effect controlled. The least squares estimates and means are presented in Tables 4.3.4.2.3 and 4.3.4.2.4.

TABLE 4.3.4.2.2: Analysis of variance for March weight and the percentage of variation controlled (%VC) by each non-genetic effect using Model 8B.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	2	150.7	**	5.1
Sex	1	1193.9	***	20.0
Age at mwt	1	1305.0	***	21.9
Dam pre-fawning weight	1	281.4	***	4.7
(herd x sex)	2	68.8	*	2.3
Error	124	22.1		46.0
Total	131			100.0

$R^2 = 54.0\%$

The results shown in Table 4.3.4.2.3 indicated that males were 11.1% heavier than females at the March weighing, given that all other non-genetic effects were equal. However, the magnitude of the difference varied between herds, as shown in Table 4.3.4.2.4.

TABLE 4.3.4.2.3: Ordinary least squares estimates (LSE) and means (LSM) for sex and (herd x sex) interaction, and the
regression coefficients for age at March weighing (age at mwt) and dam pre-fawning winter weight, with their respective standard errors (S.E.) for Model 8B. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	2.460	0.438	49.33	0.59
	female	-2.460	0.438	44.41	0.63
Age at mwt(kg/day)		0.286	0.036		
Dam weight(kg/kg dam weight)					
		0.187	0.054		
(herd x sex) interaction					
Herd 1	male	1.592	0.647		
	female	-0.547	0.569		
Herd 2	male	-1.045	0.593		
	female	-1.592	0.647		
Herd 3	male	0.547	0.569		
	female	1.045	0.593		

TABLE 4.3.4.2.4: Combined ordinary least squares estimates of sex and (herd x sex) interaction for Model 8B.

SEX	HERD NUMBER		
	1	2	3
Male	4.052	1.415	3.007
Female	-3.007	-4.052	-1.415

The results of Model 8B indicated that herd, sex, age at mwt, and dam pre-fawning winter weight caused significant differences in March weight. The presence of the (herd x sex) interaction suggests that adjustment factors for sex of fawn may need to be calculated on a within rather than across herd basis. However, none of the previous analyses have shown this interaction to be of consequence. The effect of year could not be examined due to insufficient data.

The results of Model 8B were expected given the results of Model 8A. That is, only one of the two dam winter weights was required to adjust March weight, and that dam pre-fawning winter weight accounted for more variation in March weight than dam post-fawning winter weight, even when 2 year old dams were excluded. However, dam pre-fawning winter weight accounted for less variation in Model 8B than 8A (4.7% and 16.5%, respectively). The regression coefficient of March weight on dam pre-fawning winter weight was lower in Model 8B than 8A (0.187 kg and 0.304 kg March weight per kg of dam weight, respectively). This result was contrary to that of Models 6A and 6B. While this may be a function of the small size of the data sets, it is also possible that the effect of dam winter weight on March weight is much greater for 2 year old dams than older dams. This suggests that a dam age adjustment factor is required in conjunction with any dam weight adjustment factor if 2 year old dams are to be included.

4.3.5 Summary of Models for March Weight

The results of the six models for March weight are summarized in Table 4.3.5.1.

TABLE 4.3.5.1: Analysis of variance summary for March weight using Models 5, 6A, 6B, 7, 8A and 8B.

EFFECT	MODEL 5	6A	6B	7	8A	8B
N^a	1318	154	210	579	115	132
R^{2b}	57.5	68.9	61.2	63.9	74.1	54.0
S.D.^{c}	4.82	4.08	4.80	4.14	3.76	4.71
HERD						
% VC^d	15.1	8.6	25.8	5.6	8.4	5.1
YEAR						
% VC	1.9	2.8	na	NS	na	na
SEX						
LSE^e male	2.229	2.420	2.305	2.251	2.380	2.460
LSE female	-2.229	-2.420	-2.305	-2.251	-2.380	-2.460
% M > F^f	10.6	12.2	10.6	10.6	11.0	11.1
% VC	9.7	12.8	10.8	12.7	14.9	20.0
DAM AGE						
LSE 2 year	-2.632	NS	NS	-0.564	NS	NS
LSE 3 year	-0.125			0.564		
LSE 4 year	1.086					
LSE 5+ year	1.671					
% VC	11.0			13.3		
AGE AT MWT						
β^g(kg/day)	0.256	0.360	0.310	0.335	0.344	0.286
% VC	17.5	32.7	20.6	24.8	34.3	21.9
DAM PRE-FAWNING WINTER WEIGHT						
β(kg/kg dam wt)	na	0.156	0.177	na	0.304	0.187
% VC		9.6	4.0		16.5	4.7
DAM POST-FAWNING WINTER WEIGHT						
β(kg/kg dam wt)	na	na	na	0.179	NS	NS
% VC				5.5		
(HERD X DAM AGE)						
% VC	2.3	na	na	2.0	na	na
(HERD X SEX)						
% VC	NS	NS	NS	NS	NS	2.3
(DAM WINTER WEIGHT WITHIN HERDS)						
% VC	na	2.4	NS	NS	NS	NS

TABLE 4.3.5.1 (continued)

where:
a = the total number of records in the data set,
b = the coefficient of determination,
c = the standard deviation of March weight after adjustment for the non-genetic
    effects in that model,
d = the percentage of variation controlled by that effect,
e = ordinary least squares estimate,
f = the percentage difference in weight between males and females,
g = the regression coefficient,
na = not applicable, and
NS = not significant.

NOTE: All non-genetic effects were highly significant (P<0.001) except for herd (Model 7) and dam weight within herds (Model 6A) which were significant at P<0.01 and the (herd x sex) interaction (Model 8B) which was significant at P<0.05.

4.3.6 March Weight Discussion

In all cases the effect of herd was highly significant (P<0.001), except Model 8B (P<0.01), which was primarily a reflection of different management practices across herds but may also have included genetic differences between herds. This indicated that adjusted March liveweights should be compared only on a within herd basis unless the relative genetic merit of the herds is known, for example, through the use of sire referencing. The presence of significant interactions between the fixed effects, (herd x dam age) in Model 5 and (herd x sex) in Model 8B, plus the heterogeneous nature of the regression of dam post-fawning winter weight on March weight between herds in Model 6A, indicated that adjustment factors for non-genetic effects should be calculated on a within herd basis.

The effect of year was highly significant (P<0.001) in two out of the three models that contained year, even though only a small number of years were able to be compared. In the case of Model 7, year was not significant unless fitted before herd and even then year only controlled a very small amount of variation (0.02%). However, Blaxter and Hamilton (1980) found that year had a significant effect on growth from birth to weaning in farmed Red deer in Scotland. The significance of year suggests that March liveweights from two

different years should not be directly compared unless adjusted for year through BLUP analyses as was discussed for beef cattle in Section 2.2.2.5. It is also possible that interactions involving year will arise through changes in climatic and management conditions, however in most cases this could not be thoroughly tested due to insufficient data. In practical terms, year effects can largely be ignored as selection usually takes place within a particular age group.

In all cases the sex of the fawn had a highly significant (P<0.001) effect on its March liveweight, with stag fawns being approximately 4.5 to 4.8 kg (11 - 12%) heavier than hind fawns. There was very little difference between the six models presented even though the size of the data sets varied tremendously. The difference of approximately 4.7 kg liveweight between the sexes was higher than the 2.7 kg liveweight difference documented by Asher and Adam (1985), but was very similar to the 5 kg (10 - 12%) difference reported by Fennessy (1986b) and the 3.9 kg difference derived from Adam and Moir (1987) in Scottish farmed Red deer.

Dam age was significant (P<0.001) in all cases except where dam pre-fawning winter weight was included in the model. This suggested that dam pre-fawning winter weight, regardless of whether or not 2 year old dams were included (refer to Models 6 and 8), accounted for most of the variation due to dam age. However, the size of the data sets used to show this result were extremely small. It would therefore be useful to examine this relationship further with larger data sets. The dam pre- and post-fawning winter weights are taken at the same time of the year, usually in June - July, the only difference being that they are one year apart. The high correlation between years for adjusted dam winter weight from $2^1/2$ years of age onwards (Chapter 6, Table 6.2.2) suggested that there should be little difference between the effect of fitting either of the dam weights although the results of the analyses presented in this study showed otherwise.

In Model 5, dam age accounted for 11% of the variation in March weight with 2 year old dams rearing fawns that were 9.3% lighter than mature dams (5 years of age and older), a difference of 4.3 kg in March weight. In Model 7, dam age accounted for 13.3% of the variation in March weight with 2 year old dams rearing fawns that were 2.5% lighter than older dams (3 years of age and older), a difference of 1.1 kg. This was lower than the 5.1 kg difference between 2 year old and older dams reported by Asher and Adam (1985) however, their data set

was very small with only three 2 year old dams and 173 older dams. The presence of a significant (herd x dam age) interaction in both Models 5 and 7 indicated that the age groups were being treated differently in different herds, thus 2 year old dams did not always rear fawns that were lighter than older dams. The effect of dam age was most pronounced when 2 year old dams were included. In Models 6B and 8B where only 3 year old and older dams were included, dam age was not significant regardless of the order of fit of the independent variables. The effect of the (herd x dam age) interaction could be overcome by including dam weight in the model rather than dam age.

The extent of the effect of dam age on March weight is masked by the size of the data sets. It was only when N > 1000 (Model 5) that dam age could be separated into four age classes; 2, 3, 4 and 5+ years. In the other models, and in other unpublished work (Fennessy, pers. comm.), it has only been possible to distinguish two dam age classes, 2 and 3+ years, yet it is known that Red deer hinds do not reach mature weight until approximately 5 years of age (Mitchell, 1973; Mitchell and Lincoln, 1973; Mitchell and Brown, 1974; Wegge, 1973; Guinness *et al.*, 1978b; Hamilton and Blaxter, 1980; Fennessy, 1986b; Fennessy, 1987). Blaxter *et al.* (1974) noted that the 1970 born deer farmed at the Rowett Institute in Scotland reached mature weight at 3 years of age whereas the wild deer took 4 to 6 years to reach the same mature weight. Mature hind weight may be reached even later in some populations, for example, Dzieciolowski (1970) showed that Red deer hinds in Poland do not reach mature liveweight until 8 years of age. As dam liveweight significantly influences the March weight of the fawn, and as dam liveweight is so closely associated with dam age until maturity, it is logical to assume that dam age will influence the March weight of the fawn until mature liveweight is reached. This effect was only shown by Model 5. The uncertainty of when farmed Red deer hinds reach mature weight, in terms of developing age of dam adjustment factors for March weight, may be overcome by using dam liveweight as an adjustment factor.

Dam pre-fawning winter weight was highly significant (P<0.001) in all models it was fitted in. In Model 8B, where both dam pre- and post-fawning winter weights were fitted, dam pre-fawning winter weight controlled a greater percentage of variation in March weight than did post-fawning winter weight. Dam pre-fawning winter weight controlled between 5% (Model 8B) and 17% (Model 8A) variation in March weight. Dam post-fawning winter weight was

only significant (P<0.001) when it was the only dam weight included in the model. In this case (Model 7), dam post-fawning winter weight controlled approximately 6% variation but dam age was also highly significant and controlled a greater amount of variation, 13.3%. Blaxter and Hamilton (1980) found that the rate of growth between birth and weaning increased with the weight of the dam at the time of the rut. This was significant in 1976 (a good year) but not in 1978 (a poor year). Regression equations showed that a difference of 20 kg in the body weight of dams would increase the growth rate of the fawns by 22 to 35 grams a day, that is, by 10.7 to 12.8% for stag fawns and by 9.9 to 14.2% for hind fawns. Therefore, it appears that should dam winter weight be used as an adjustment factor for March weight, then dam pre-fawning winter weight should be used regardless of the maturity of the dam.

Age at mwt was highly significant (P<0.001) in all models with a fawn gaining approximately 315 grams per day of age up to March weighing. There was very little difference between the six models presented even though the size of the data sets varied tremendously. This was very similar to the 318 and 287 grams per day for male and female farmed Red deer fawns, respectively, reported by Kelly and Drew (1976), the 310 ± 17 grams per day (mean ± S.E.) reported by Asher and Adam (1985) and the 378 (1985, n=181) and 311 (1986, n=193) grams per day calculated by Fennessy (unpublished data) from a single herd. Moore (1984) calculated growth rates of male fawns from birth to weaning of 300, 230 and 400 grams per day in 1972, 1973 and 1982, respectively at the Invermay Agriculture Centre, New Zealand. Youngson (1970) obtained a growth rate of 203 grams per day with hand-reared Red deer hinds between 4 and 20 weeks of age on the Isle of Rhum, Scotland. Adam and Moir (1987) presented an overall mean liveweight gain of 367 grams per day from birth to 14 weeks of age in Scottish farmed Red deer which was similar to the estimate of 300 to 400 grams per day presented by Loudon et al. (1984). Adam and Moir (1987) also noted that birth date did not significantly influence liveweight gain during any 2-week interval except from 4 to 6 weeks after birth. At this stage fawn liveweight gain tended to increase significantly with earlier calving date (P<0.01). Thus, earlier born fawns (those older than average at weaning) were always heavier than late-born fawns. Fennessy (unpublished data) found that age at weaning controlled a large amount of variation, fitting weaning age added 37.7% to the coefficient of determination in 1985 and 36.5% in 1986. Blaxter and Hamilton (1980) also noted that date of birth (and hence duration of the

suckling period) was the main determinant of weaning weight in farmed Scottish Red deer.

In conclusion, herd, year, sex of fawn, age of dam, age at March weighing and dam pre-fawning winter weight all have marked effects on March weight accounting for 54 to 74% of the total variation in March weight. While dam pre-fawning winter weight provided an adequate adjustment for dam age in Models 6A and 6B, the difference in the regression coefficients in Models 8A and 8B, caused by the exclusion of 2 year old dams, indicated that dam pre-fawning winter weight may not be an appropriate adjustment for dam age. More importantly, dam liveweights, when fitted as covariates, include both genetic and environmental components. Using dam liveweights as correction factors for March weight will remove a portion of the genetic variance. Even though this effect is likely to be small, using dam winter weight as an adjustment factor may affect the genetic ranking of the fawns, which in turn, will reduce the effectiveness of selection. This is important for March weight as this is the first opportunity for within herd selection. A further consideration is the relative difficulty of recording dam liveweight compared to dam age. Dam age is readily assessed from the year of birth of the hind, whereas dam winter weight will need to be annually recorded.

The relative importance of the non-genetic effects in this study were similar to the published reports for weaning weight in beef cattle, as reviewed in Section 2.2.2. However, dam liveweight may have a greater effect on fawn March liveweight in Red deer than in beef cattle. This effect may also control a greater proportion of the variance usually attributed to age of dam in Red deer than in beef cattle. Even with Red deer it appears that if March weight is to be adjusted for dam pre-fawning winter weight a further adjustment for age of dam is also required if 2 year old dams (first fawners) are included. Therefore, there may be little advantage in using dam liveweight as an adjustment factor for March weight in preference to using age of dam adjustment factors as is commonly practiced in the beef industry. This aspect requires further research to determine the most appropriate adjustment factor for Red deer.

Therefore, March weights within a herd need to be adjusted for the following non-genetic effects if selection on predicted genetic merit is to be undertaken: year, unless comparison is on a within year basis only; sex; age of dam,

particularly 2 year old dams versus older dams; and, most importantly, age at the March weighing.

4.4 15-MONTH WEIGHT

4.4.1 Model 9

The non-genetic effects of herd, sex, age of dam, and age at the 15-month weighing (age at wt) were fitted to 15-month weight. From the original database of 1255 15-month weights, 304 records were chosen that met the following criteria:

(i)   364 days (12 months) < age at wt < 501 days (17 months),

(ii)   15-month weights which were recorded in 1986,

(iii)   number of records in any given herd > 9,

(iv)   dam age grouped into two classes: 2 and 3+ years, and

(v)   herds must have at least 2 records of each sex.

The number of observations by herd, sex, and dam age are given in Table 4.4.1.1. A detailed presentation of the data set is given in Appendix 3, Table 9.3.1.

TABLE 4.4.1.1: Number of records in each class of non-genetic effect in Model 9. (N = 304)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	12	1986	304	male	136	2 year	80
2	58			female	168	3+ year	224
3	124						
4	37						
5	45						
6	15						
7	13						

A linear model with 15-month weight as the dependent variable and herd, sex, and age of dam and all first order interactions as the independent variables was fitted. Age at wt was also fitted as a covariate in this model.

The order of fitting the independent variables affected the significance of dam age. When dam age was fitted before age at wt it was significant (P=0.02) and age at wt was non- significant (P=0.07). However, when dam age was fitted after age at wt it became non-significant (P=0.052) and age at wt became significant (P=0.002). Removing dam age from Model 9 caused a small, 0.29%, reduction in R^2. Therefore dam age was not included in Model 9.

Although age at wt was significant, it was removed from Model 9 because of the small amount of variation controlled (0.8% reduction in R^2). The regression of 15-month weight on age at wt was homogeneous between sexes (P=0.69) and herds (P=0.07).

When the first order interaction among the fixed effects, (herd x sex), was included in the model, it was found to be significant (P<0.05) and controlled greater than 2% of the variation in 15-month weight. Therefore, the (herd x sex) interaction remained in Model 9.

The ANOVA based on the model resulting from the above discussion is given in Table 4.4.1.2, with the percentage of variation each of the non-genetic effects controlled. The least squares estimates and means are presented in Tables 4.4.1.3 and 4.4.1.4.

TABLE 4.4.1.2: Analysis of variance for 15-month weight and the percentage of variation controlled (%VC) by each of the non-genetic effects using Model 9.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	6	803.4	***	6.3
Sex	1	53792.5	***	70.4
(herd x sex)	6	528.9	***	4.1
Error	290	50.5		19.2
Total	303			100.0

$R^2 = 80.8\%$

The results shown in Table 4.4.1.3 indicated that for the same age at wt, male Red deer were 30.3% heavier than female Red deer at the 15-month weighing, given that all other non-genetic effects were equal. However, the presence of the (herd x sex) interaction shows that the magnitude of this difference varied between herds (as shown in Table 4.4.1.4). This indicates that adjustment factors for the effect of sex on 15-month weight should be calculated on a within rather across herd basis.

TABLE 4.4.1.3: Ordinary least squares estimates (LSE) and means (LSM) for sex and (herd x sex) interaction with their respective standard errors (S.E.) for Model 9. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	12.388	0.564	106.43	0.79
	female	-12.388	0.564	81.65	0.81
(herd x sex) interaction					
Herd 1	male	0.440	1.847		
	female	7.327	0.984		
Herd 2	male	0.661	0.781		
	female	-2.776	1.178		
Herd 3	male	-0.051	1.068		
	female	-2.094	1.654		
Herd 4	male	-3.507	1.764		
	female	-0.440	1.847		
Herd 5	male	-7.327	0.984		
	female	-0.661	0.781		
Herd 6	male	2.776	1.178		
	female	0.051	1.068		
Herd 7	male	2.094	1.654		
	female	3.507	1.764		

TABLE 4.4.1.4: Combined ordinary least squares estimates of sex and (herd x sex) for Model 9.

HERD NUMBER	SEX	
	MALE	FEMALE
Herd 1	12.829	-5.061
Herd 2	13.049	-15.164
Herd 3	12.337	-14.482
Herd 4	8.881	-12.829
Herd 5	5.061	-13.049
Herd 6	15.164	-12.337
Herd 7	14.482	-8.881

These results indicated that age of dam and age at wt, provided the weight is recorded between 12 and 17 months of age, had little effect on the 15-month weight of farmed Red deer.

As there was only appropriate data from one year for analysis it was not possible to estimate the effect of year. In beef cattle studies, year has been shown to have a significant effect on yearling to 18-month weight (Baker *et al.*, 1974; Pabst *et al.*, 1977; Nicoll and Rae, 1978). Therefore, it is likely that the year the weight was recorded would be a significant effect for 15-month weight in Red deer. Thus, records should not be directly compared across years unless year effects have been adjusted for.

4.4.2 Model 10

This model was fitted to test the usefulness of dam post-fawning winter weight as an adjustment factor for 15-month weight. The non-genetic effects of herd, sex, age of dam, dam post-fawning winter weight, and age at the 15-month weighing (age at wt) were fitted to 15-month weight. From the original data set of 1255 15-month weights, 174 were chosen that met the following criteria:

    (i)   364 days < age at wt < 501 days,

(ii)   15-month weights which were recorded in 1986,

(iii)   each record required a dam post-fawning winter weight,

(iv)   number of records in any given herd > 9,

(v)   dam age grouped into two classes: 2 and 3+ years, and

(vi)   each herd required at least two records of each sex.

The number of observations by herd, year, sex and dam age are given in Table 4.4.2.1. A detailed presentation of the data set is given in Appendix 3, Table 9.3.2.

TABLE 4.4.2.1: Number of records in each class of non-genetic effect in Model 10. (N = 174)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	12	1986	174	male	77	2 year	46
2	91			female	97	3+ year	128
3	37						
4	34						

A linear model with 15-month weight as the dependent variable and herd, sex, age of dam, and all fist order interactions as the independent variables was fitted. Age at wt and dam post-fawning winter weight were also fitted as covariates in this model.

The order of fit affected the significance of dam age. Dam age was significant if fitted before dam post-fawning winter weight (P=0.005) but became non-significant when fitted after dam post-fawning winter weight (P=0.08). When dam age was removed from the model, a small, 0.14%, reduction in variation occurred. Therefore, dam age was not included in Model 10.

When the first order interaction among the fixed effects, (herd x sex), was fitted it was not significant (P=0.06), and was therefore excluded from Model 10.

The regression of 15-month weight on age at wt was homogeneous between herds (P=0.14) and sexes (P=0.21). The regression of 15-month weight on dam post-fawning winter weight was homogeneous between herds (P=1.00) and sexes (P=0.28).

The ANOVA based on the model resulting from the above discussion is given in Table 4.4.2.2, with the percentage of variation controlled by each of non-genetic effects. The least squares estimates and means are presented in Table 4.4.2.3.

TABLE 4.4.2.2: Analysis of variance for 15-month weight and the percentage of variation controlled (%VC) be each of the non-genetic effects using Model 10.

SOURCE OF VARIATION	D.F.	MEAN SQUARE	SIGN.	%VC
Herd	3	790.3	***	6.9
Sex	1	23203.1	***	67.9
Age at wt	1	980.9	***	2.9
Dam winter weight	1	881.7	***	2.6
Error	167	40.2		19.7
Total	173			100.0

$R^2 = 80.3\%$

The results shown in Table 4.4.2.3 indicated that for the same age at wt, male Red deer were 28.3% heavier than female Red deer at the 15-month weighing, given that all other non-genetic effects were equal.

TABLE 4.4.2.3: Ordinary least squares estimates (LSE) and means (LSM) for sex and the regression coefficients for age at the 15-month weighing (age at wt) and dam post-fawning winter weight, with their respective standard errors (S.E.) for Model 10. (units = kg)

EFFECT		LSE	S.E.	LSM	S.E.
Sex	male	11.737	0.495	106.27	1.08
	female	-11.737	0.495	82.80	0.97
Age at wt (kg/day)		0.185	0.048		
Dam winter weight (kg/kg dam wt)					
	0.?39	0.051			

These results indicated that herd, sex of yearling, age at wt, and dam post-fawning winter weight caused significant differences in the 15-month weight. However, age at wt and dam post-fawning winter weight controlled only a small amount of the variation in 15-month weight.

4.4.3 Summary of Models for 15-month Weight

Due to insufficient data it was not possible to test the effect of dam pre-fawning winter weight on 15-month weight.

The results of the two models for 15-month weight are summarized in Table 4.4.3.1.

TABLE 4.4.3.1: Analysis of variance summary for 15-month weight using Models 9 and 10.

EFFECT	MODEL 9	MODEL 10
N^a	304	174
R^{2b}	80.8	80.3
S.D.^{c}	7.11	6.34
HERD % VC^d	6.3	6.9
SEX LSE^e male LSE female % M > F^f % VC	12.388 -12.388 30.3 70.4	11.737 -11.737 28.3 67.9
DAM AGE % VC	NS	NS
AGE AT 15-MONTH WEIGHING β^g (kg/kg day) % VC	NS	0.185 2.9
DAM POST-FAWNING WINTER WEIGHT β (kg/kg dam wt) % VC	na	0.239 2.6
(HERD X SEX) % VC	4.1	NS

where:
a = the total number of records in the data set,
b = the coefficient of determination,
c = the standard deviation of 15-month weight after adjustment for the non-genetic effects in that model,
d = the percentage of variation controlled by that effect,
e = ordinary least squares estimate,
f = the percentage difference in weight between males and females,
g = the regression coefficient,
na = not applicable, and
NS = not significant, (P>0.05).

NOTE: All effects were highly significant (P<0.001).

4.4.4 15-month Weight Discussion

In both models the effect of herd was highly significant (P<0.001), which indicated that 15-month weights should be compared on a within herd basis, unless the relative genetic merit of the herds is known. The effect of herd controlled approximately 6.5% variation in both models.

The effect of year could not be calculated due to insufficient data.

In both models the effect of sex was highly significant (P<0.001), with sex accounting for approximately 70% of the total variation in 15-month weight. In both models, males were approximately 24 kg (30%) heavier than females at the 15-month weighing. Adam and Asher (1986) noted that both average daily gain from weaning to 15-months of age and liveweight at 15-months of age will be lower for females than males. Males tend to grow faster and attain mature weight later than females. Adam and Moir (1985) also noted that stags have a greater liveweight gain per day between 6 and 11 months of age than hinds. Suttie et al. (1987) found that intakes and growth rates between the sexes up to about 6 months of age were similar but after that time stags grew faster. They hypothesized that changes in the growth rate between the sexes occurs when young male deer begin to secrete measurable amounts of testosterone and thus begin to develop secondary sexual characters such as rapid rate of gain. In their study 15-month old stags were 34 kg (41%) heavier than hinds of the same age. Dzieciolowski (1970) and Mitchell et al. (1986) noted that male Red deer took a year or two longer to reach maturity than did females.

The presence of the significant (P<0.001) (herd x sex) interaction in Model 9 indicated that adjustment factors for non-genetic effects should be calculated on a within rather than across herd basis. This effect may have been caused by management differences between herds, with some herds preferentially feeding female yearlings so that they achieve a high liveweight at puberty, or through sire effects being confounded within herds. Although this interaction was not significant (P>0.05) in Model 10, this may have been a function of the lower number of herds in this model.

While dam age (2 year old versus older dams), was significant (P<0.05) in both models, it only accounted for a small amount of variation (<1%), in 15-month

weight. This suggested that it may be unnecessary to use dam age as an adjustment factor for 15-month weight.

Age at the 15-month weighing was also significant ($P<0.05$) in both models, but it was only in Model 10 that it controlled sufficient variation (2.9%) to consider it as an adjustment factor. In this case, the regression coefficient was 185 grams per day which was between the 144 grams per day reported by Youngson (1970) for hand-reared Red deer hinds on the Isle of Rhum, Scotland, and the 210 grams per day reported by Suttie *et al.* (1983) for Scottish Red deer stags between 5 and 15-months of age on an unrestricted diet. Further study is needed to determine the importance of age at the 15-month weighing on 15-month weight.

When dam post-fawning winter weight was fitted in Model 10, it was significant, controlling 2.6% of the variation. As with age at wt, this is only a very small portion of the total variation accounted for by the model (80.3%).

Due to the lack of appropriate data, the effect of dam pre-fawning winter weight on 15-month weight could not be analysed. It was likely, due to the high phenotypic correlation between mature dam ages for dam winter weight (Chapter 6, Table 6.2.2), that similar results to Model 10 would be expected.

Although dam post-fawning winter weight had a significant effect on 15-month weight, it is not recommended to use such a covariate as an adjustment factor for non-genetic effects due to the removal of some genetic variation which is included in the dam winter weight. Furthermore, it controlled only 2.6% of the variation in 15-month weight.

In comparison with studies on the importance of non-genetic effects in beef cattle, as reviewed in Section 2.2.3, it appeared that age at weighing had a greater influence on the yearling weight of beef cattle than on the 15-month weight of Red deer. However, by 18-months of age Nicoll and Rae (1978) found that although age at weighing was highly significant in beef cattle this effect did not control as much variation as it had for weaning weight and that herd and year effects had become relatively more important. Koch and Clarke (1955a) concluded that adjustment for age at weighing was of no practical

importance for the 18-month weight of Hereford heifers in their study. Thus, the importance of adjusting for age at weighing by 15-months of age in Red deer may vary across herds.

The large influence of sex appears to be similar in beef cattle and Red deer.

In contrast to the results of this study for Red deer, age of dam effects have been shown to be significant and of practical importance for the 18-month weight of beef cattle (Nicoll and Rae, 1978). In the study of Nicoll and Rae (1978) the magnitude of the age of dam effect on 18-month weight was similar to the effect on weaning weight. Other beef cattle studies have shown that the effect of age of dam decreases with the age of the offspring (Koch and Clarke, 1955a; Pabst *et al.*, 1977) but that it may still be of importance by 18-months of age.

The effect of herd on yearling to 18-month weight in beef cattle has been shown to be an important source of variation (Section 2.2.3.6), as found in this study for Red deer.

In this study a significant (herd x sex) interaction occurred in Model 9, which accounted for 4.1% of the variation in 15-month weight. The presence of this interaction was documented in the beef cattle study of Baker *et al.* (1974). Further interactions among the non-genetic effects for beef cattle have been reviewed in Section 2.2.3.7. The presence of these interactions indicated that there may be a need to calculate adjustment factors on a within herd and year basis, and possibly, on a within sex basis for 12- to 18-month weight. Further study is required to determine the importance of the (herd x sex) interaction for Red deer.

In conclusion, the non-genetic effects of herd and sex accounted for most of the controllable variation, around 76%, in 15-month weight. Overall, both models had a coefficient of determination of approximately 80%. Thus, most of the important non-genetic effects at the March weighing are no longer important by the 15-month weighing. It would appear that provided selection were carried out on a within herd and sex basis, prior adjustment of the records of yearling Red deer for non-genetic effects would be unnecessary.

CHAPTER 5
HERITABILITIES

5.1 INTRODUCTION

The heritability of traits are extremely important in prediction of rates of response from various types of selection and these predictions are necessary when comparing alternative breeding plans.

The practical animal breeder is mainly concerned with heritability defined, in the narrow sense, as the ratio of additive genetic variance to the total or phenotypic variance. The additive genetic variance is the component of total variance thought of as arising from the average effects of the genes. It reflects the variation that is predictably transmitted from parent to offspring and considered responsible for the resemblance between relatives under mass mating regimes. The estimation of the amount of additive genetic variance depends on the measurement of the degree of resemblance between relatives.

The sets of relatives most commonly used for estimating heritability in animal breeding and those used in this study are: half-sib, utilizing ANOVA techniques to estimate variance components; and dam-offspring, utilizing regression and correlation methods of estimation.

For some purposes (mostly concerned with the rate of response of the trait to selection) it is convenient to classify heritabilities of 0.4 and above as high; 0.2 to 0.4 as intermediate and those below 0.2 as low (Turner and Young, 1969).

Heritability estimates can be used to:

    (i)   predict the breeding value of an individual,

    (ii)   predict the rate of genetic gain which can be achieved by selection,

    (iii)   determine the most appropriate type of selection i.e. individual or family, and

(iv)   construct selection indices.

The purpose of this chapter was to provide estimates of the heritability of birth weight, March weight and 15-month weight of farmed Red deer in New Zealand.

5.2 BIRTH WEIGHT

A paternal half-sib estimate of the heritability of birth weight was derived using Henderson's Method 3. From the original database of 311 birth weights, 265 observations were chosen that met the following criteria:

(i)   number of records in any given herd-year combination > 9,

(ii)   herds were represented in at least two years,

(iii)   dam age grouped into three classes: 2, 3 and 4+ years,

(iv)   number of records per sire in any given herd-year combination > 2, and

(v)   in any given year the number of herds > 1.

The number of observations by herd, birth year, sex and dam age are given in Table 5.2.1. There were no dams older than 6 years of age. A detailed presentation of the data set is given in Appendix 4, Table 9.4.1.

TABLE 5.2.1: Number of records in each class of non-genetic effect for the paternal half-sib estimation of the heritability of birth weight.
(N = 265, sires = 14)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	45	1983	64	male	146	2 year	48
2	119	1984	152	female	119	3 year	84
3	101	1985	49			4+ year	133

A mixed model with herd, year, sex, and dam age as the fixed effects, date of birth as a covariate, and sire nested within herd as the random effect was fitted to birth weight.

Year and date of birth were not significant (P=0.16 and 0.62, respectively) and were removed from the model.

When the first order interactions among the remaining fixed effects were included in the model, the following were not significant: (herd x dam age)(P=0.60) and (sex x dam age)(P=0.53). These interactions were therefore excluded from the model. The (herd x sex) interaction was significant (P=0.02) and accounted for 2.3% of the total variation in birth weight. This interaction therefore remained in the model.

The interactions involving the random effect, sire nested within herd, (sire x sex)(P=0.55) and (sire x dam age)(P=0.49), were not significant and were excluded from the model.

The analysis of the model resulting from the above discussion and the heritability of birth weight is given in Table 5.2.2.

TABLE 5.2.2: Variance components and heritability (h^2) estimate with standard error (S.E.) for birth weight using Henderson's Method 3.

VARIANCE COMPONENT	D.F.	MEAN SQUARE	h^2 (S.E.)
Sire nested within herd	11	4.786	0.67 (0.29)
Error	246	1.128	

$R^2 = 42.0\%, k_1 = 16.1$

Where the Expected Mean Squares (EMS) are:

$EMS_{\text{sire nested within herd}} = \sigma^2_e + k_1\sigma^2_s$, and

$EMS_{\text{error}} = \sigma^2_e$.

There was insufficient data to obtain an estimate of the heritability of birth weight using the offspring-dam regression procedure.

5.3 MARCH WEIGHT

5.3.1 Paternal Half-sib

An estimate of the heritability of March weight was derived using Henderson's Method 3. From the original database of 2627 records with sire identified, 1131 observations were chosen that met the following criteria:

(i)   59 days < age at mwt < 151 days,

(ii)   number of records in any given herd-year combination > 9,

(iii)   herds were represented in at least two years,

(iv)   dam age grouped in four classes: 2, 3, 4 and 5+ years,

(v)   number of records per sire in any given herd-year combination > 2, and

(vi)   in any given year the number of herds > 1.

The number of observations by herd, birth year, sex and dam age are given in Table 5.3.1.1. A detailed presentation of the data set is given in Appendix 4, Table 9.4.2.

TABLE 5.3.1.1: Number of records in each class of non-genetic effect for the paternal half-sib estimation of the heritability of March weight.
(N = 1131, sires = 59)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	69	1983	175	male	571	2 year	240
2	47	1984	546	female	560	3 year	225
3	110	1985	410			4 year	246
4	152					5+ year	420
5	102						
6	197						
7	177						
8	99						
9	178						

A mixed model with herd, year, sex, and dam age as the fixed effects, age at mwt as a covariate, and sire nested within herd as the random effect was fitted to March weight.

When the first order interactions among the fixed effects were included, (year x sex) and (sex x dam age) were found to be non-significant (P>0.05). The remainder, (herd x year), (herd x sex), (herd x dam age) and (year x dam age) were significant (P<0.05) but each controlled less than 1.5% variation in March weight and were therefore excluded from the model. The regression coefficient of mwt on age was homogeneous between years and sexes and was considered homogeneous between herds and dam ages due to the small amount of variation controlled.

The interactions involving the random effect, sire nested within herd, were significant (P<0.05). The (sire x sex) interaction controlled only 1.8% variation and was therefore excluded from the model. The interactions of (sire x year) and (sire x dam age) could not be tested due to an inadequate number of sire connections across years and dam ages, respectively. It was considered unlikely the (sire x dam age) interaction would be significant in a balanced data set and

there was no evidence of this interaction in the beef cattle studies reviewed. Although the regression of mwt on age was heterogeneous between sires and accounted for 4.2% variation, it was assumed to be homogeneous to simplify the analysis.

Though the data set was too unbalanced to test the effect of the (sire x year) interaction there was some evidence of its existence. The within-year within-sire variance of offspring March weight adjusted for the non-genetic effects of sex, age of dam and age at mwt as in Model 5 (Section 4.3.1), is shown in Figure 5.3.1 for each sire with progeny in more than one year. The adjusted variance for each sire within year was plotted against the adjusted variance for the same sire in the adjacent year. From this graph it was apparent that the within-sire variance for adjusted March weight changed between years.

The analysis of the model resulting from the above discussion and the estimate of the heritability of March weight using Henderson's Method 3, is given in Table 5.3.1.2. The heritability estimates of March weight calculated from variance components estimated by Henderson's Method 3 (HM3), MIVQUE (minimum variance quadratic unbiased estimation), ML (maximum likelihood) and REML (restricted maximum likelihood) are presented in Table 5.3.1.3. These analyses examined the effect the method of estimation had on variance component and heritability estimates.

FIGURE 5.3.1: The within sire variance for March weight adjusted for the non-genetic effects using Model 5 in one year plotted against that sire's adjusted March weight variance in the adjacent year.

within sire variance of fawn March weight (1984)
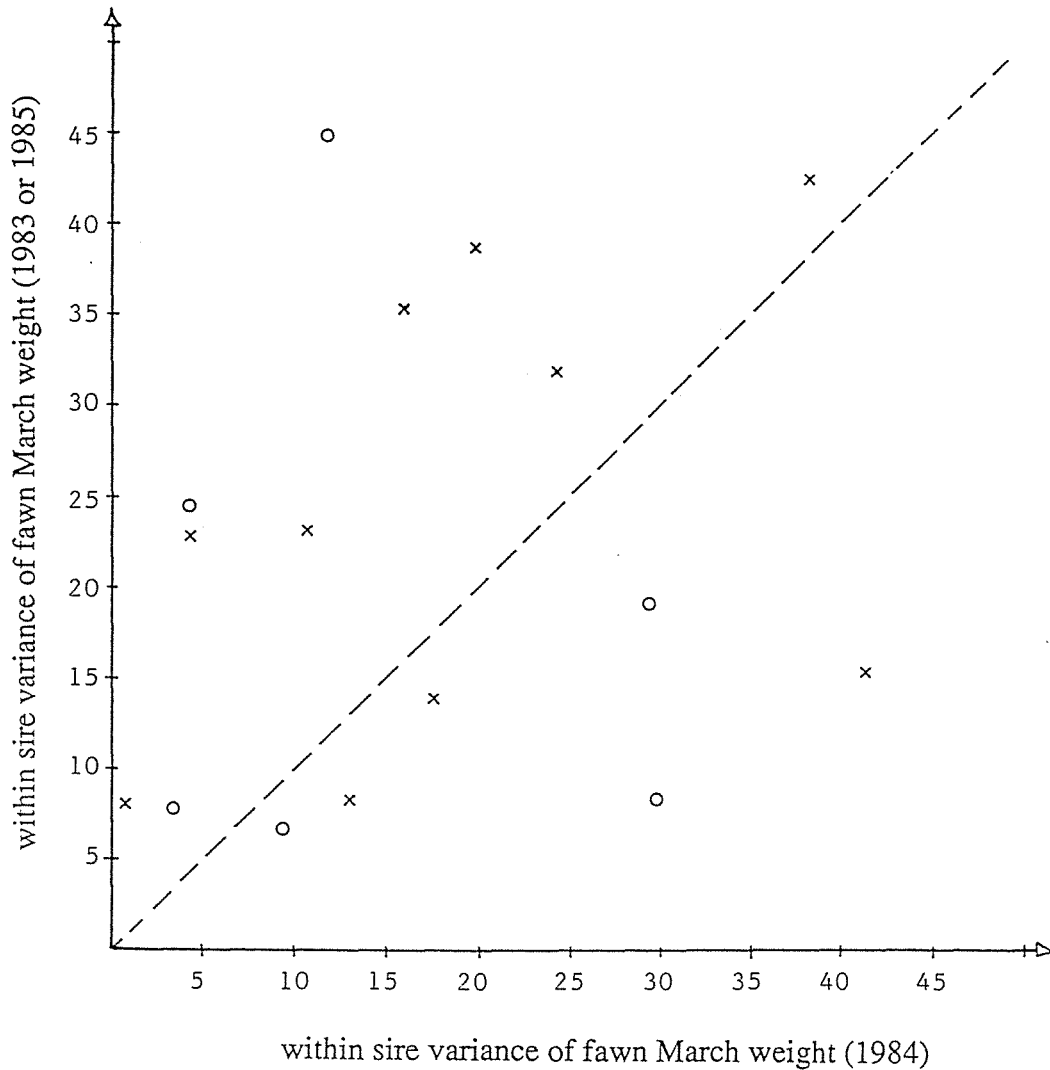
where:

o is the within sire adjusted March weight variance for 1983 versus 1984, and

x is the within sire adjusted March weight variance for 1984 versus 1985.

The broken line represents the plot of points had the within sire adjusted March weight variance been equal for the two adjacent years.

TABLE 5.3.1.2: Variance components and heritability (h^2) estimate with standard error (S.E.) for March weight using Henderson's Method 3.

VARIANCE COMPONENT	D.F.	MEAN SQUARE	h^2 (S.E.)
Sire nested within herd	50	92.110	0.77 (0.15)
Error	1065	18.887	

$R^2 = 64.7\%$, $k_1 = 16.2$

Where the Expected Mean Squares are:

$EMS_{\text{sire nested within herd}} = \sigma^2_e + k_1\sigma^2_s$, and
$EMS_{\text{error}} = \sigma^2_e$.

TABLE 5.3.1.3: Heritability estimates for March weight from paternal half-sib data using Henderson's Method 3 (HM3), Minimum Variance Quadratic Unbiased Estimation (MIVQUE), Maximum Likelihood (ML) and Restricted Maximum Likelihood (REML) methods of variance component estimation.

METHOD OF ESTIMATION	h^2
HM3	0.77
MIVQUE	0.69
ML	0.68
REML	0.85

where:
$h^2 = 4(\sigma^2_{\text{sire}} / \sigma^2_{\text{sire}} + \sigma^2_{\text{error}})$

5.3.2 Offspring-Dam Regression

Estimates of the heritability of March weight were calculated using the offspring-dam regression procedure. Two models were utilized. This was undertaken to investigate the effect removal of the non-genetic effects had on the

heritability estimate. In the first, the dam record was adjusted for herd nested within year and the offspring record was adjusted for herd nested within year and sex effects. From the original database of 87 offspring-dam pairs, 86 were chosen that met the following criterion:

        (i)   number of pairs in any given herd-year combination > 1.

In the second, offspring-dam pairs were adjusted for known non-genetic effects. The dam weight record was adjusted for herd nested within year, dam age and age at mwt. The offspring weight record was adjusted for herd nested within year, sex, dam age and age at mwt. From the original database of 87 pairs, 59 were chosen that met the following criteria:

        (i)   59 days < age at mwt < 161 days,

        (ii)   dam age grouped into two classes: 2 and 3 years, and

        (iii)   number of pairs in any given herd-year combination > 1.

Model 5 (Section 4.3.1) was applied to the data, except that there were only two dam age classes as there were no older dams that met the data set criteria.

The results of the regression analyses are given in Table 5.3.2.1.

TABLE 5.3.2.1: The regression coefficients (β) and March weight heritability (h^2) estimates from the offspring-dam regression with and without adjustment for non-genetic effects with their respective standard errors (S.E.).

	β	h^2	S.E.
Offspring-dam	0.0764	0.15	0.30
Offspring-dam adjusted for non-genetic effects	0.2500	0.50	0.42

These heritability estimates indicated that when there was no adjustment for non-genetic effects the heritability of March weight was low. When non-genetic effects are adjusted for, the heritability of March weight was high. However, both of these estimates had a high standard error, due to the low number of pairs, which indicated that they may not be different.

5.4 15-MONTH WEIGHT

A paternal half-sib estimate of the heritability of 15-month weight was derived using Henderson's Method 3. From the original database of 917 15-month records with sire identified, 342 were chosen that met the following criteria:

(i)   364 days < age at wt < 501 days,

(ii)   1984 birth year records only,

(iii)   each sire required > 2 records, and

(iv)   each herd required > 4 records.

The number of observations by herd, birth year and sex are given in Table 5.4.1. A detailed presentation of the data set is given in Appendix 4, Table 9.4.3.

TABLE 5.4.1: Number of records in each subclass of non-genetic effect for the paternal half-sib estimation of the heritability of 15-month weight. (N = 342, sires = 28)

HERD	n	YEAR	n	SEX	n
1	12	1984	342	male	148
2	13			female	194
3	56				
4	117				
5	7				
6	52				
7	41				
8	14				
9	13				
10	17				

A mixed model with herd and sex as the fixed effects, age at weighing as a covariate, and sire nested within herd as the random effect was fitted to 15-month weight.

As the first order interaction between the fixed effects, (herd x sex), was significant (P<0.05) this interaction was included in the model. The regression of weight on age at weighing was homogeneous between herds and sexes.

The interaction (sire nested within herd x sex) was non-significant (P=55.9%) and the regression coefficient 15-month weight on age at weighing was homogeneous between sires nested within herds.

The variance components of the model resulting from the above discussion and the estimate of the heritability of 15-month weight are given in Table 5.4.2.

TABLE 5.4.2: Variance components and the heritability (h^2) estimate with standard error (S.E.) for 15-month weight using Henderson's Method 3.

VARIANCE COMPONENT	D.F.	MEAN SQUARE	h^2 (S.E.)
Sire nested within herd	18	115.562	0.60 (0.22)
Error	304	40.106	

$R^2 = 85.5\%$, $k_1 = 10.6$

Where the Expected Mean Squares are:

$EMS_{\text{sire nested within herd}} = \sigma^2_e + k_1\sigma^2_s$, and

$EMS_{\text{error}} = \sigma^2_e$.

5.5 DISCUSSION

No heritability estimates for birth weight, March weight or 15-month weight for Red deer were found in the literature examined. However, several studies of wild and farmed Red deer populations have alluded to a genetic relationship between parents and offspring for a number of liveweight traits.

In two studies of wild Red deer populations in Scotland, Mitchell *et al.* (1976) and Mitchell *et al.* (1986) found the correlations between hinds and fawns in condition (as measured by the kidney fat index) and carcass weight were highly significant (r = 0.55 to 0.63, P=0.001). Jaw bone length in fawns was also related to condition and carcass weight in hinds (r = 0.47 to 0.54, P=0.01) but not to their jawbone length. It seemed that the size, weight and condition of a fawn was related to the weight and condition but not the skeletal size of its mother. Due to the large environmental effects exerted on liveweight from birth onwards in the wild, it would seem reasonable for there to be a closer relationship between the size of a fawn and its dam under more controlled farmed conditions.

Clutton-Brock *et al.* (1984) studying wild Red deer on the Isle of Rhum, Scotland, noted that a hind's dominance rank (a function of hind age and body weight (Clutton-Brock *et al.*, 1984; Thouless and Guinness, 1986)) was correlated with the social rank of her mother (r = 0.201, P<0.05) which indicated a possible link between the body size of the mother and that of her offspring. In a later study, Clutton-Brock *et al.* (1986) found that on average, dominant hinds produced offspring that were 0.3 kg heavier at birth than those of subordinates (P<0.01). Hinds' ranks were also significantly correlated with the mean birth weight of their offspring (r = 0.455, P<0.001). The average birth weight of fawns produced by different hinds (expressed as the average deviation from the mean weight of fawns born in each year) was significantly correlated with the average weight of fawns produced by their mothers (r = 0.484, P<0.001) (Clutton-Brock *et al.*, 1986). Albon *et al.* (1987) studying the same population concluded that the mean birth weight of fawns born to different groups of hinds was significantly related to the mean birth weight of the group itself (r = 0.705, P<0.05). However, they noted that 50% of the variance in offspring birth weight was left unaccounted for. As individual differences in birth weight were

correlated with adult weight in the same population (Clutton-Brock *et al.*, 1987) these studies indicated that the liveweight of a parent is one of the determinants of the liveweight of its offspring.

In farmed Red deer populations in Scotland both Blaxter and Hamilton (1980) and Blaxter *et al.* (1981) noted that fawn birth weight is related to the weight of the hind at the time she conceived, a weight which is perhaps the best index of her size. Blaxter *et al.* (1981) further noted that the size of the dam influenced the fawn's growth rate and hence the weaning weight of the fawn. Similar results have been found for farmed Red deer in New Zealand (Asher *et al.*, 1981; Asher and Adam, 1985; Adam and Asher, 1986).

Maternal and direct genetic effects for growth are confounded in the above studies of Red deer. Maternal effects are a source of environmental resemblance between dams and their offspring (Falconer, 1981). Koch and Clark (1955c) concluded that maternal environment had a large influence on birth weight and growth rate from birth to weaning in beef cattle, but only a small influence on weaning to yearling growth rate. Therefore, it is possible that the some of the relationships found in the above studies were largely due to maternal effects.

In a study of the performance of a herd of farmed Red deer in New Zealand, Fennessy (1983) indicated the repeatability of mothering performance of a hind was high, as shown by the weaning weights of her offspring, and that there was a positive relationship between the mothering ability of a dam and that of her female offspring. However, not all of this relationship will be of genetic origin due to the fact that the same fawns which contribute to the dam's ranking are the same animals which subsequently produce fawns of their own. This is important since the heavier hinds at first mating tend to wean heavier fawns as two-year olds.

In the same study, Fennessy (1983) noted considerable differences in the average weaning weight of progeny from different sires, with the same trend seen over two fawnings. That is, the sires with the highest average in the first year of the study also had the highest average the following year. This pattern was also seen in growth rates from 9- to 15-months of age.

A similar effect was seen in nutrition trials with young stags at Invermay Research Station, New Zealand. A 3 kg (7%) difference between the progeny of the two sires at 6-months of age, had increased to 18 kg (20%) at 15-months of age, and to 25 kg (23%) at 24-months of age (Fennessy, 1982). This illustrated the presence of differences between sires in the mean growth rates of their progeny; however, there were also large differences in growth rates among the progeny of the same sire.

The heritability of birth weight was high (0.67 ± 0.29 (± S.E)) when calculated from paternal half-sib data using Henderson's Method 3. This was higher than most paternal half-sib estimates of birth weight heritability for beef cattle as reviewed in Section 2.4.1, Table 2.4.1.

The heritability of March weight was high, 0.77 ± 0.15 (± S.E.) when calculated by Henderson's Method 3. Although the presence of a possible (sire nested within herd x year) interaction could not be tested due to the extremely unbalanced data set, there was some evidence to suggest that it did exist, see Figure 5.3.1. If such an interaction was contributing to the sire variance then the heritability estimate would be inflated. Such an interaction could arise through: a genotype x environment interaction; a large paddock or mob effect where year and paddock were completely confounded which induced a common environmental component (Falconer, 1981); or, by non-random mating. During the time this data was collected it was a relatively common practice for breeders to fawn hinds in their respective single-sire mating groups. Hinds and fawns remained in these groups until weaning. Therefore, it was quite possible that many of the sires represented in the data had their progeny treated in this manner. This management technique could inflate the between sire variance by adding any paddock or mob effect to the sire effect thereby inflating the heritability estimate. Bourdon and Brinks (1982) noted that their estimate of weaning weight heritability could have been biased upwards by a partial confounding of sires and a seasonal effect which was not adequately accounted for by the model. The possible presence of a genotype x environment interaction has not been studied in deer to date but it is well documented in other farmed species (Newman, 1988).

The heritability of March weight estimated by the offspring-dam regression with prior adjustment of the data for non-genetic effects was also high, 0.50 ± 0.42 (± S.E.). Conversely, the heritability of March weight was low when the data was

adjusted for only the herd x year subclass, 0.15 ± 0.30 (± S.E.). These estimates were based on a small number of offspring-dam pairs as reflected in the high standard errors.

The lower March weight heritability estimate when using the regression of offspring on dam method compared to the paternal half-sib variance component method could be caused by a negative environmental correlation between preweaning growth of the female and her subsequent maternal ability (Barlow, 1987). Such correlations have been reviewed by Koch (1972). Direct genetic (non-maternal) and maternal genetic variances and covariances also influence the relative magnitude of parameter estimates. Such effects have been shown by Koch and Clark (1955b) and Koch (1972).

All the estimates of March weight heritability fall within the normal bounds. In most cases the standard error of the heritability estimate was high, reflecting the small number of records contributing to each estimate.

The heritability estimates of March weight presented in this study were higher than the weaning weight estimates for beef cattle as reviewed in Section 2.4.2, Table 2.4.1.

The estimates of the heritability of March weight calculated by four different statistical procedures (Table 5.3.1.4) were similar, though the estimate using REML was slightly higher than the rest. HM3 will underestimate the heritability of the trait if the data arose from populations that have been undergoing selection (Henderson, 1986a,b). Newer methods now exist that are capable of yielding smaller sampling variance and mean square errors. These are ML, REML, and MIVQUE. These methods control bias due to selection (Sorensen and Kennedy, 1984; Henderson, 1986b) although ML estimators may not be free of all forms of selection bias (Sorensen and Kennedy, 1984).

In comparisons of variance components and heritability estimates calculated by different procedures, Knights *et al.* (1984) found little difference between HM3 and REML and Hayes and Cue (1985) concluded that the advantage of REML over HM3 was small. Using sheep field data, Tait (1983) found good agreement between the heritability estimates calculated by HM3, REML and MIVQUE for birth, weaning and 2-tooth weight. In a computer simulation study, Lin and

McAllister (1984) found little difference between HM3, ML and REML procedures when no selection had been applied to the population. However, REML estimates approached actual parameters more closely than the other two methods. When selection had been applied to the population, all estimates of heritability were lower regardless of the procedure used and ML yielded the closest estimates to the actual parameters because the error variance component was biased downwards. This overestimation seems to compensate for the reduction of heritability from selection. In populations where selection has occurred it appears preferential to use REML procedures for calculating the variance components and hence the heritability rather than other procedures such as HM3 (Henderson, 1986a).

The small differences in the heritability estimates of March weight calculated by the different procedures probably reflected that little selection for March weight has been undertaken in the herds in this study.

The heritability of 15-month weight, 0.60 ± 0.22 ($\pm$ S.E.), estimated by Henderson's Method 3, was lower than the heritability of March weight estimated by the same method. Usually the heritability of liveweights increase as the age at which the weight was taken increases, as the magnitude of the environmental effects influencing the weight are reduced. This was not found in this study. The poor accuracy of the heritability determination, as indicated by the high standard errors may have masked this trend.

The heritability of 15-month weight was not able to be estimated by the offspring-dam regression due to lack of appropriate data.

The heritability estimate of 15-month weight was higher than most of the heritability estimates for yearling weight in beef cattle as reviewed in Section 2.4.3, Table 2.4.1.

In conclusion, the heritabilities of birth weight, March weight and 15-month weight were estimated to be high. Such results could be expected given the diverse base of Red deer in New Zealand. As intensive selection is carried out for these traits over future generations the heritability of these liveweights may decrease. In the interim however, selection for March weight and/or 15-month weight will result in rapid positive and permanent genetic gain.

CHAPTER 6
CORRELATIONS

6.1 INTRODUCTION

The development of effective breeding programmes which involve selection on more than one trait requires, among other parameters, the knowledge of genetic and phenotypic correlations between each pair of traits under consideration.

The phenotypic correlation is the observed correlation between traits on the same animal arising from the combined effects of genotype and environment. A genetic correlation is the correlation between an animal's genetic value for one trait and the same animal's genetic value for another trait.

In selecting for two traits, it is necessary to take account that they may be independent of each other, or be either positively or negatively correlated. It is the genetic correlation which decides what change will take place in one trait, in future generations, as a result of selection for the other. A positive genetic correlation between two traits means that selecting for one will bring about on increase in the other. Conversely, a negative genetic correlation implies that selection for one trait will cause some reduction in the other.

Genetic correlations can be used to:

(i)   indicate the changes which are likely in traits other than those under selection (correlated responses),

(ii)   define what counter selection should be applied to diminish or prevent the effect of such changes where they are undesirable,

(iii)   judge if indirect selection on an easily measured trait can be used to obtain genetic gains, instead of direct selection on a trait that is more difficult, or expensive, to measure,

(iv)   increase the intensity of selection where the desired trait is measurable in one sex only but the secondary trait is measurable in both, and

(v)   minimize the age at selection where the secondary trait is highly correlated with the desired trait but measurable at an earlier age.

Phenotypic correlations can be used for similar purposes but do not relate to future generations. The most effective use that can be made of a correlated trait, is in combination with the desired trait as an additional source of information about the breeding values of individuals (Falconer, 1981).

The purpose of this chapter was to provide estimates of genetic and phenotypic correlations for liveweight traits of farmed Red deer in New Zealand, thereby providing essential information for the construction of selection indices and prediction of correlated responses to selection for liveweight at a given age.

6.2 PHENOTYPIC CORRELATIONS

The phenotypic correlations between birth weight, March weight and 15-month weight were calculated. The phenotypic correlations between dam ages for dam winter liveweight were also calculated. Due to insufficient data it was not possible to compute all possible age combinations.

For liveweight traits of the animal before first mating (birth weight, March weight and 15-month weight), observations were chosen that met the following criteria:

(i)   number of records in any given herd-year combination > 9, and for the phenotypic correlation between March weight and 15-month weight only,

(ii)   59 days < age at March weighing < 161 days, and

(iii)   364 days < age at 15-month weighing < 501 days.

For the phenotypic correlations calculated using records adjusted for known non-genetic effects, a model with herd nested within year, sex and age of dam as the fixed effects, and date of birth as a covariate, was fitted to birth weight. The

same model was fitted to March weight except that the covariate, date of birth, was replaced by age at mwt. In all cases the first order interactions were either non-significant (P>0.05) or controlled less than two percent of the total variation. The same methodology as described in Chapters 3 and 4 was used to establish the appropriate model. Birth weight was adjusted for the effects of herd nested within year, sex and dam age. March weight was adjusted for herd nested within year, sex, dam age and age at mwt, except for the correlation between birth weight and March weight where it was further adjusted for the (herd nested within year x dam age) interaction and the regression of March weight on age at mwt for herds nested within year. Fifteen-month weight was adjusted for herd nested within year and sex and also age at the 15-month weighing in the phenotypic correlation between March weight and 15-month weight. Unadjusted phenotypic correlations refer to correlations between pairs of traits that have been adjusted for herd nested within year only.

The phenotypic correlation between March weight and 15-month weight was also calculated without age restrictions on the data set. This was to increase the number of records used in the calculation and to see if the inclusion of late-born fawns, in particular, would alter the magnitude of the correlation.

The phenotypic correlations between birth weight, March weight and 15-month weight are presented in Table 6.2.1.

TABLE 6.2.1: Adjusted and unadjusted phenotypic correlations (rp) between birth weight (bwt), March weight (mwt) and 15-month weight (ylg).

PAIR OF TRAITS	rp unadjusted	adjusted	n	SIGNIFICANCE
No age restrictions				
bwt and mwt	0.45	0.49	310	**
bwt and ylg	0.57	0.34	80	**
mwt and ylg	0.61	0.54	480	**
With age restrictions				
mwt and ylg	0.58	0.51	358	**

where:

n = number of pairs of records, and

** = all correlations were significant at $P < 0.01$.

Phenotypic correlations were calculated between each pair of dam winter weights. Due to insufficient data, not all possible correlations were able to be calculated. All the phenotypic correlations presented in Table 6.2.2 were adjusted for non-genetic effects, where significant. Each original model included herd, year, month the winter weight was taken, sex of the fawn and all first order interactions. All the dams in this study had reared a fawn prior to the weight being taken, except for the ylg age group. In all cases the sex of fawn effect was not significant (P>0.05) and was removed from the model. Herd was significant (P<0.05) for all dam ages, where data from more than one herd was analysed, except the ylg age group. Year was significant (P<0.05) only for the ylg and 6 year old and older dam age groups. The month the weight was taken was only significant for dam age groups 6 years of age and over. The first order interactions among the remaining fixed effects for each dam age pair were not significant (P>0.05).

The phenotypic correlations between pairs of dam winter weights are presented in Table 6.2.2. The phenotypic correlation between the winter weights of mature dams (6 years of age and older) recorded in consecutive years is denoted by the 6+ and 7+ pair of dam ages.

TABLE 6.2.2: Adjusted phenotypic correlations (rp) for dam winter liveweight at various ages.

PAIRS OF DAM AGES (years)	rp	n	SIGNIFICANCE
ylg and 2	0.75	62	**
2 and 3	0.49	35	**
3 and 4	0.86	55	**
3 and 5	0.68	12	*
4 and 5	0.89	35	**
5 and 6	0.97	9	**
7 and 8	0.85	36	**
6+ and 7+	0.85	56	**

where:

ylg   =   15-month weight of the dam,

6+ and 7+ = pairs of consecutive dam ages ranging from 6 years of age and older,

n   =   number of pairs of records,

**   =   significant at $P < 0.01$, and

*   =   significant at $0.01 < P < 0.05$.

6.3 GENETIC CORRELATIONS

The genetic correlations between birth weight and March weight, and March weight and 15-month weight were calculated from the variance and covariance components obtained by equating Henderson's Method 3 mean squares to their expectations. From the original database of 311 birth weight records, 265 observations were chosen that met the following criteria:

(i)   March weight was recorded on the same fawn,

(ii)   number of records in any given herd-year combination > 9,

(iii)   number of records per sire in any given herd-year combination > 2,

(iv)   herds were represented in at least two years, and

(v)   number of sires in any given herd > 2.

From the original database of 1255 15-month weight records, 270 were chosen that met the above criteria and the following age restrictions:

(vi)   the fawn was weaned at the March weighing,

(vii)   59 days < age at March weighing < 161 days, and

(viii) 364 days < age at 15-month weighing < 501 days.

The number of observations by herd, year, sex and dam age are given in Table 6.3.1 for the genetic correlation between birth weight and March weight and Table 6.3.2 for the genetic correlation between March weight and 15-month weight. A detailed presentation of the data set is given in Appendix 4, Table 9.4.1 and Appendix 5, Table 9.5.1 for the above genetic correlations, respectively.

There was insufficient data to calculate the genetic correlation between birth weight and 15-month weight.

TABLE 6.3.1: Number of records in each class of non-genetic effect for the estimation of the paternal half-sib genetic correlation between birth weight and March weight. (N = 265, sires = 14)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	45	1983	64	male	146	2 year	48
2	119	1984	152	female	119	3 year	84
3	101	1985	49			4+ year	133

TABLE 6.3.2: Number of records in each class of non-genetic effect for the estimation of the paternal half-sib genetic correlation between March weight and 15-month weight. (N = 270, sires = 25)

HERD	n	YEAR	n	SEX	n	DAM AGE	n
1	12	1984	270	male	128	2 year	69
2	13			female	142	3 year	55
3	32					4 year	47
4	117					5+ year	99
5	7						
6	36						
7	40						
8	13						

A mixed model with herd, year, sex and dam age as the fixed effects, date of birth as a covariate, and sire nested within herd as the random effect was fitted to birth weight. Date of birth was not significant (P=0.30) and was removed from the model. The first order interactions among the fixed effects were either non-significant or controlled less than two percent of the total variation in birth weight except for the (herd x sex) interaction (P=0.004). This interaction controlled 2.6% of the total variation in birth weight and therefore remained in this model. For further details refer to Chapter 5, Section 5.2.

A mixed model with herd, year, sex and dam age as the fixed effects; age at mwt as a covariate; and sire nested within herd as the random effect was fitted to March weight. All the non-genetic effects were significant (P<0.05) and all the first order interactions were either non-significant (P>0.05) or controlled less that two percent of the total variation in March weight, except for the (herd x sex) interaction (P=0.002). This interaction controlled 2.5% of the total variation in March weight and therefore remained in this model.

For the genetic correlation between March weight and 15-month weight a mixed model was fitted to each of the weights. A mixed model with herd, sex and dam age as the fixed effects, age at mwt as a covariate, and sire nested within herd as

the random effect was fitted to March weight. A mixed model with herd and sex as the fixed effects, age at the 15-month weighing as a covariate, and sire nested within herd as the random effect was fitted to 15-month weight. In both models the first order interactions among the fixed effects were non-significant (P>0.05) or controlled less than two percent of the total variation in the respective liveweight.

The genetic correlations calculated from the models discussed above are presented in Table 6.3.3 along with the genetic correlation between March weight and 15-month weight when no age restrictions were applied to the data set. The age restrictions were relaxed to increase the size of the data set and to observe the change in the genetic correlation with particular regard to the inclusion of late-born fawns.

TABLE 6.3.3: Genetic correlation (r_G) between birth weight (bwt) and March weight (mwt) and between March weight and 15-month weight (ylg) with their respective standard errors (S.E.) using Henderson's Method 3.

PAIR OF TRAITS	r_G	S.E.	k	n
adjusted for non-genetic effects, no age restrictions				
bwt and mwt	0.93	0.24	9.5	265
mwt and ylg	0.52	0.49	9.9	308
adjusted for non-genetic effects, with age restrictions				
mwt and ylg	0.32	0.44	9.5	270

All estimates were within the range of ± 1. The genetic correlation between birth weight and March weight was strongly positive, the genetic correlation between March weight and 15-month weight with no age restriction was moderately to strongly positive, and the genetic correlation between March weight and 15-month weight with restricted ages was moderately positive. These estimates had high standard errors which was a reflection of the small size of the data sets, in particular the low number of offspring for many of the sires

represented in the genetic correlation between March weight and 15-month weight as shown in Appendix 5, Table 9.5.1. These results indicate that selection for increased liveweight at a given age will increase liveweight at all other ages.

6.4 DISCUSSION

The phenotypic correlations between birth weight, March weight and 15-month weight were all moderately positive, regardless of whether the records were adjusted for known sources of non-genetic variation or merely adjusted for herd nested within year. In general, the phenotypic correlation between records adjusted for non-genetic variation were lower than those which had been adjusted for herd nested within year only. The exception to this was the phenotypic correlation between birth weight and March weight where the unadjusted phenotypic correlation was lower than the adjusted phenotypic correlation (0.45 and 0.49, respectively). The phenotypic correlation between March weight and 15-month weight was calculated with and without age restrictions on the data set. While the correlations were slightly higher with no age restrictions there was little difference between the estimates. These moderately positive phenotypic correlations indicated that animals were relatively consistent in their liveweight ranking from birth to 15-months of age.

No phenotypic correlation estimates between liveweight traits for Red deer were found in the literature examined. However, several studies with both wild and farmed Red deer populations have alluded to relationships between liveweight traits on the same animal.

Clutton-Brock *et al.* (1987), studying wild Red deer on the Isle of Rhum, Scotland, stated that individual differences in birth weight are correlated with adult weight in the same population. Albon *et al.* (1987), working with the same population, also noted the close relationship between birth weight and adult size and suggested that an individuals birth weight may influence its subsequent growth trajectory, exerting a stronger effect on its adult size than resource availability during its first year of life.

A study of farmed Red deer in Scotland showed that for any level of feeding the effect of weight at weaning persisted to 15-months, more so at higher levels of feeding, but that the effect was not large (Blaxter *et al.*, 1981). Loudon and Milne (1985) concluded that weaning weight was an important determinant of weight at 16-months of age.

Asher *et al.* (1981) and Adam and Asher (1986), studying records from farmed Red deer in New Zealand, found that March weight was positively related to birth weight. Fennessy (1983), with data from one herd, noted that the heavier fawns at weaning tended to have slightly faster growth rates subsequently. Fennessy (1983) concluded that growth rate was quite a repeatable character, that is, a stag with a high growth rate from 9 - 15 months of age tended to have a high growth rate from 21 - 27 months of age.

The phenotypic correlations between dam ages for dam winter liveweight were generally highly positive. The exception was between 2 and 3 year old dams which was only moderately positive. In all cases the correlations were significant at $P<0.01$ except between 3 and 5 year old dams which was significant at $P<0.05$. These results indicated that once a dam has reached mature liveweight at approximately 4 to 5 years of age, this weight remained relatively stable. Should mature dam liveweight be required either as a correction factor or as a trait in a selection index, then this weight need not be taken every year due to its high repeatability. The highly positive phenotypic correlation between 15-month weight and 2 year old dam winter weight indicated that 15-month weight is a good indicator of later dam winter weights, but the medium phenotypic correlation between 2 and 3 year old dam winter weights indicated that this relationship may change. Therefore, these results indicate that dam winter liveweight should be recorded annually until at least 4 years of age. Due to insufficient data it was not possible to calculate all the possible weight combinations and further work is required to establish the true repeatability of dam winter liveweight.

The genetic correlation between birth weight and March weight was strongly positive (0.93 ± 0.24) ($\pm$ S.E.) indicating that selection for March weight will cause an increase in birth weight in ensuing generations. The age restricted genetic correlation between March weight and 15-month weight was moderately positive (0.32 ± 0.44), while the genetic correlation between these traits with no

age restrictions was higher (0.52 ± 0.49). The increase in the phenotypic and genetic correlations when no age restrictions were applied to the data set could either be due to the increased number of records included in the analysis, or because of the smaller time lapse between weighings in some cases. Very late born fawns were previously excluded from the data set, as were animals that had their 15-month weight recorded before they reached 12-months of age. The inclusion of these animals could have elongated the scatter of points which may have increased the correlation. Several studies on Red deer populations have shown that very late born fawns tend to be smaller than average the following year and are less likely to survive their first winter of life (Blaxter *et al.*, 1974; Clutton-Brock *et al.*, 1982; Clutton-Brock *et al.*, 1987). Feeding trials with Red deer have shown that there is little compensatory growth in their second summer of life (Blaxter *et al.*, 1981; Loudon and Milne, 1985; Milne and Sibbald, 1986). While some trials have shown that considerable compensatory growth can occur, the winter-restricted animals failed to compensate fully over the following summer and were skeletally smaller than the fully-fed deer (Suttie, 1980; Suttie *et al.*, 1983; Adam and Moir, 1985). Reports from the Invermay Agriculture Centre in New Zealand indicated that some compensatory growth in smaller fawns can occur during the winter if they are preferentially fed (Fennessy, 1982a; Pearse, 1987).

Comparisons of the results of this study with estimates from studies with beef cattle show that the adjusted phenotypic correlation between birth weight and March weight (which is equivalent to weaning weight in beef cattle) of 0.49 is similar to those reviewed in Section 2.5.1.1, Table 2.5.1.1.

The adjusted phenotypic correlation between birth weight and 15-month weight in this study was 0.34. The range of phenotypic correlation estimates between birth weight and yearling weight in beef cattle was 0.35 to 0.60 (Section 2.5.1.2, Table 2.5.1.1). Thus, the estimate from this study is slightly lower than that typically found in beef cattle studies.

The age restricted, adjusted phenotypic correlation between March weight and 15-month weight of 0.51 is within the range of estimates taken at a similar age in beef cattle reviewed in Section 2.5.1.3, Table 2.5.1.1.

Overall, the estimates of the phenotypic correlations between liveweight traits of Red deer presented in this study are slightly lower, though similar, to the published estimates for the equivalent pairs of traits in beef cattle.

No genetic correlation estimates for Red deer were found in the literature examined. The genetic correlation between birth weight and March weight of 0.93 is higher than most of the estimates reviewed for beef cattle in Section 2.5.2.1, Table 2.5.1.1 for the equivalent pair of traits. The genetic correlation between age restricted March weight and 15-month weight was estimated to be 0.32 in this study. This is lower than most of the estimates reviewed for beef cattle in Section 2.5.2.3, Table 2.5.1.1.

A number of long term selection experiments in beef cattle have shown correlated responses in birth weight and mature liveweight to selection for weaning weight and/or yearling weight (see, for example, Koch *et al.*, 1974a,b; Koch *et al.*, 1982; Morris and Baker, 1982; Baker and Morris, 1984; Frahm *et al.*, 1985a,b; Parnell *et al.*, 1986). Thus, selection for high or low weights, or weight gain at any particular age, is expected to result in concomitant changes in weight at all other ages.

The results of this study indicated that March weight and 15-month weight of Red deer can be genetically increased by selection and strongly imply that selection for March weight or 15-month weight will result in improved growth rate at all stages of growth. The medium to high genetic correlation between March weight and 15-month weight will allow breeders to use March weight as an early culling procedure even if the primary selection objective is 15-month weight.

In selection programmes to increase growth performance, some attention should be given to minimizing the correlated response of increased birth weight and possibly increased mature weight. As has been suggested by Baker and Morris (1984), dam weights, like birth weights, should perhaps be optimized rather than maximized. This could be achieved by avoiding direct selection for birth weight and/or mature liveweight and possibly giving negative attention to these traits in a selection objective sufficient to partially offset correlated response to March weight or 15-month weight.

CHAPTER 7
SELECTION INDICES

7.1 INTRODUCTION

The value of an animal is almost always affected by several traits. Therefore the breeder has to consider different characteristics when choosing the most valuable animals as parents for the next generation. An efficient method of selection, when two or more traits are to be improved, is that of the selection index (Turner and Young, 1969).

7.2 DEFINITION OF THE BREEDING OBJECTIVE

The overall breeding objective was defined to be maximization of gross returns per animal per year. This assumes that costs of production are the same for all animals within the herd and that genetic responses in production per animal will result in increased net income per hectare (or per unit of feed intake). While it is desirable to have an objective of increasing overall profit per farm, such an objective requires that all costs and returns associated with change in the level of expression of each trait of economic importance be taken into account. These costs have not been adequately defined for Red deer and are not well defined in other species, particularly in the area of feed consumption.

The identification of the role of the breed in the industry is a good starting point for the definition of the breeding objective in terms of the traits to be included. Red deer are used predominantly in a purebred role for the production of venison and velvet antler. Massey (1987) interviewed a number of Red deer sire breeders. These sire breeders indicated that the following traits were of importance to them: weaning to 15-month liveweight gain; 15-month weight and early maturity balanced against ultimate body size; large, lean progeny; venison production per hectare; and, good temperament in both breeding hinds and stags. One indicated that heavier breeding hinds (130-135 kg liveweight) were desirable. Pearse (1987) also indicated that from an industry point-of-view leanness, tenderness and taste of venison were important. Fennessy (1982b, 1985, 1987) and Dratch and Fennessy (1985) advocated a biological objective of

improved efficiency, basically in terms of kg product produced per breeding hind or per kg of feed intake. There has been little or no published work on an economic objective for farmed Red deer. Dratch and Fennessy (1985) concluded that efficiency should be measured in bioeconomic terms as the value of a herd's products divided by the cost of producing them. This is equivalent to the formula of return on investment utilized by Dickerson (1970) and discussed by Harris (1970).

Farm income from deer is derived from the value of meat on the carcass, velvet antler and the sale of surplus animals. From the previous discussion it appears that the breeding objective for a herd of Red deer breeding hinds should include the following traits: reproduction, venison production, velvet production and feed consumption. In practice, there may be difficulties with the inclusion of some traits due to lack of reliable information about them.

The list of traits to be considered for inclusion in the breeding objective can differ considerably between different sectors of an industry due to conflicting goals (Barlow, 1987). In the development of the breeding objective, it is usually assumed that increased output from genetic gain can be sold with no reduction in price per unit (Ponzoni, 1982). As venison production is below that of world demand at the present time, and is expected to remain so for at least the short-term (Yerex and Spiers, 1987), it is likely that the above assumption will hold not only for the individual producer but also for the entire industry. The market outlook for velvet antler is less clear cut, but it is possible that world demand will fall, which could be accompanied by a fall in returns to the individual producer.

Financial returns to the Red deer farmer arise mainly through the sale of venison and velvet antler. As many farms produce venison as the sole income source, except for the sale of surplus stock, two breeding objectives will be considered. The first objective is solely concerned with increasing carcass weight per animal at approximately 15-months of age. That is,

$$H_1 = a_1 CWT_{15}$$

where; H_1 is objective one, a_1 is the relative economic value of venison from 15-month old deer and CWT_{15} is the breeding value of 15-month carcass weight. The second is concerned with increasing both carcass weight and velvet antler weight. That is,

$$H_2 = a_2CWT_{27} + a_3VWT$$

where; H_2 is objective two, a_2 and a_3 are the relative economic values of venison from 27-month old deer and velvet antler weight, respectively, CWT_{27} is the breeding value of 27-month carcass weight and VWT is the breeding value of 2 year old velvet antler weight.

Birth weight can also be considered a trait of economic importance. It has been documented in cattle that increases in birth weight are often associated with increases in calving difficulty which leads to lower calf survival and hence a lower weaning percentage (Baker and Morris, 1984). This has a negative effect on herd profitability as the breeding female has been maintained for a year for no financial return. Therefore, the effect of holding birth weight constant was also considered.

7.3 SELECTION INDEX PARAMETERS

7.3.1 Relative Economic Values

Relative economic values were assessed from average returns for the products in the 1987/88 production season. The relative economic value for venison from Red deer at either 15- or 27-months of age was estimated to be $5.25 per kg and the relative economic value for velvet antler $120.00 per kg. No allowance was made for changes in return per kg for venison leanness grades and in velvet antler for variation in grade due to colour, shape and size differences. In the case of velvet antler this information is difficult to obtain as the grading system varies from year to year.

Further research is required to establish the relative economic importance of quality grades in Red deer products and to determine the relative economic value of reproduction, which has not been considered here.

7.3.2 Phenotypic and Genetic Parameters

For the two selection objectives defined in Section 7.2 a series of full, reduced and restricted selection indices were calculated using SELIND (Cunningham, 1970).

The estimates of heritability, phenotypic and genetic correlations and phenotypic standard deviations needed for the construction of the indices are presented in Tables 7.3.1 and 7.3.2. Where possible parameters were obtained from the results of this study. Velvet antler parameters were obtained from the review of literature (Sections 2.4.4 and 2.5.1.4). Where no estimates were available the parameters used were estimates derived from beef cattle studies.

TABLE 7.3.1: Genetic and phenotypic parameters used in the construction of the selection indices for the 15-month venison production objective.

TRAITS	PHENOTYPIC S.D. (kg)	HERITABILITIES		AND CORRELATIONS[a]	
		bwt	mwt	ylg	cwt_{15}
bwt	1.07	**0.67**	0.93	0.3^{*}	
mwt	4.82		**0.67**		0.3^{*}
ylg	7.11		0.51	**0.60**	0.8^{*}
cwt_{15}	5.00^{*}				$\mathbf{0.6^{*}}$

where:

 a = genetic correlations above the diagonal, phenotypic correlations below the diagonal and heritabilities on the diagonal,

 * = substitute from beef cattle estimates in the absence of estimates for Red deer,

 bwt = birth weight,

 mwt = March weight,

 ylg = 15-month weight, and

 cwt_{15} = carcass weight at 15-months of age.

TABLE 7.3.2: Genetic and phenotypic parameters used in the construction of the selection indices for the 27-month venison and velvet antler production objective.

TRAITS	PHENOTYPIC S.D. (kg)	HERITABILITIES AND CORRELATIONS[a]
		mwt	ylg	cwt_{27}	vwt
mwt	4.82	**0.67**		0.25^*	0.35^*
ylg	7.11	0.51	**0.60**	0.7^*	0.45^*
cwt_{27}	6.00^*			$\mathbf{0.6^*}$	
vwt	0.35^b	0.39	0.53		**0.35**

where:

a = genetic correlations above the diagonal, phenotypic correlations below the diagonal and heritabilities on the diagonal,

b = Fennessy (pers. comm.),

* = substitute from beef cattle estimates or other species in the absence of estimates for Red deer,

mwt = March weight,

ylg = 15-month weight,

cwt_{27} = carcass weight at 27-months of age, and

vwt = 2 year old velvet antler weight.

7.4 RESULTS

The selection indices for the venison objective constructed from the parameters in Table 7.3.1 are given in Table 7.4.1. The selection indices for the venison and velvet antler objective constructed from parameters given in Table 7.3.2 are given in Table 7.4.2.

TABLE 7.4.1: Selection index solutions for the objective of 15-month venison production, $H_1 = a_1 CWT_{15}$, based on the parameter estimates presented in Table 7.3.1.

TRAIT	1	INDEX NUMBER 2	3	4
b-values				
bwt	*	$*^R$	1.65	0.04^R
mwt	-0.40	-0.90	-0.56	-0.91
ylg	1.91	1.99	1.88	1.99
r_{HI}	0.63	0.62	0.63	0.62
σ_I	12.71	12.53	12.80	12.53
Genetic gain (kg/10 years)				
bwt	0.27	0.00	0.40	0.00
mwt	1.30	-0.02	1.78	-0.02
ylg	10.21	10.18	10.21	10.18
cwt_{15}	5.70	5.61	5.74	5.61

where:

r_{HI} is the correlation between the index and the aggregate genotype.

σ_I is the standard deviation of the index which gives the value of overall gain, in economic units, achieved by one standard deviation of selection on the index per generation.

Genetic gain per ten years, calculated assuming a selection differential of one standard deviation, and divided by the generation interval (4.25 years) and multiplied by 10.

R indicates that this trait has been restricted to zero genetic gain.

* indicates that the trait is included in the objective but has not been recorded.

The explanation of the trait abbreviations are given in Table 7.3.1.

Table 7.4.1 showed the greatest economic gain was made by index 3, $12.80, as this index gave the greatest genetic gain in carcass weight (5.74 kg/10 years). Positive genetic gain was also made in birth weight (0.40 kg). There was little difference between indices 1 and 3 in the predicted genetic gain of carcass weight. Therefore, not recording birth weight appeared to have little effect on the expected genetic gain of carcass weight at 15-months of age.

Comparison of indices 1 and 2 showed that restricting birth weight to zero genetic gain reduced the efficiency (percentage change of σ_I) of the index by 1.5%, with a cost of 18 cents per generation per standard deviation of selection on the index. The reduction in efficiency was slightly greater, 3.5%, between indices 3 and 4, when birth weight was recorded.

Restricting birth weight induced a small negative genetic gain in March weight. This may not be desirable, as many breeders sell fawns at weaning, commonly on a $ per kg basis, for finishing on specialized units.

TABLE 7.4.2: Selection index solutions for the objective of 27-month venison and velvet antler production, $H_2 = a_2 CWT_{27} + a_3 VWT$, based on the parameter estimates presented in Table 7.3.2.

TRAIT	INDEX	NUMBER		
	5	6	5	6
	b-values		Genetic gain	
mwt	-0.15	0.27	2.01	2.39
ylg	2.20	2.99	7.29	8.88
cwt$_{27}$			4.55	5.26
vwt	35.60	*	0.23	0.15
r_{HI}	0.59	0.53		
σ_I	24.27	21.92		

where:

r_{HI} is the correlation between the index and the aggregate genotype.
σ_I is the standard deviation of the index which gives the value of overall gain, in economic units, achieved by one standard deviation of selection on the index per generation.
Genetic gain per ten years, calculated assuming a selection differential of one standard deviation, and divided by the generation interval (4.75 years) and multiplied by 10.
* indicates that the trait is included in the objective but has not been recorded.
The explanation of the trait abbreviations are given in Table 7.3.2.

Table 7.4.2 showed that not recording 2 year old velvet antler weight decreased the efficiency of the index by 10%, with a cost of $2.35 per generation.

Indices 5 and 6 are based on 15-month liveweight as a predictor of 27-month carcass weight. In practice, 27-month weight could also be included in the indices. No parameters were available for 27-month weight at this time. However, it is expected that the correlations between 15-month liveweight and carcass weight would be similar to those between 27-month weight and carcass weight.

Comparison of Tables 7.4.1 and 7.4.2 for genetic gain in carcass weight shows that genetic gain has not been as great for this trait in indices 5 and 6 as in indices 1 to 4. This has occurred because of the greater generation interval, 4.25 versus 4.75 years, that would be expected if measurements were not taken until the males were two years of age. Thus sires could not be selected and used until a year later than could occur for the venison production objective.

The efficiency of index 6 may be improved by the inclusion of spiker antler weight as a predictor of 2 year old velvet antler weight. A study by Moore *et al.* (1988) using data from 97 Red deer stags, calculated the phenotypic correlation between spiker antler weight and adult velvet antler weight to be 0.39. Also, spiker antler weight controlled 27.6% of the variation in 2 year old velvet antler weight. These results suggested that spiker antler weight may be a useful indicator of 2 year old velvet antler weight and could be used as a selection criterion. This would allow selection a year earlier than currently considered possible for velvet antler weight, and hence decrease the generation interval.

7.5 DISCUSSION

The parameters used to construct indices 1 to 5 resulted in an unreasonable negative weighting for March weight. This was most likely due to the high correlation estimates as pointed out by James (1982). Selection index theory is based on the assumption that all covariances are known. In practice, estimates of variances and covariances must be used and these are subject to sampling errors. To reduce sampling errors, genetic parameter estimates should be calculated from very large data sets. As the parameters used for the construction of the indices in this study were estimated from a small data set, sampling errors in the parameters may have affected the selection index solutions.

No selection indices for Red deer were found in the literature examined. However, Butler (1983) suggested that an index with 40 to 50 times the weight of 27-month liveweight deviation for velvet antler weight deviation may be appropriate. The equivalent weighting in the study is approximately 23 to 1. This is a reflection of the relatively greater return for venison that now exists.

Selection for 15-month carcass weight using an index constructed of birth weight, March weight and 15-month weight is expected to return $12.80 per generation per standard deviation of selection. Restricting birth weight to zero genetic gain decreased the return to $12.53 per generation, regardless of whether or not birth weight was recorded. These results imply that there is little economic loss in restricting birth weight and that there is only a small advantage in recording actual birth weights. The small loss in economic gain from not recording actual birth weights is likely to be outweighed by the practical implications of taking birth weights, particularly as recording birth weights has been thought to contribute to lower fawn survival rates on some farms.

Economic response per generation was greater for the venison and velvet indices, reflecting the high value and potential for selection for velvet antler weight. This was, however, heavily dependent upon the relative economic value for velvet antler weight. Including 2 year old velvet antler weight in the index but not recording it, greatly reduced the efficiency of index selection and economic response. A reliable predictor of velvet antler weight is required so that selection for these traits can be completed by 15-months of age.

Further work is required to establish the parameters necessary to construct selection indices incorporating other traits of interest in Red deer, for example, reproduction and velvet antler quality traits. Velvet antler is harvested annually from 1 or 2 years of age, this information could be used to improve the prediction of genetic merit for velvet antler weight, particularly for female relatives. The usefulness of such an approach requires investigation.

Further study is required for the development of selection indices, especially given the unreasonable index weighting factor that occurred in 5 of the 6 indices for March weight in this study. Until these problems are rectified it may be propitious to use direct rather than indirect selection for liveweight and velvet antler traits of Red deer.

CHAPTER 8
CONCLUSIONS

Birth weight was significantly influenced by the following non-genetic effects: herd, sex of fawn, age of dam and dam winter weight. Year within herds and date of birth effects had only small, usually non-significant, influences. Sex was the single most important effect, accounting for between 8 and 21% of the total variation in birth weight. Dam age and dam winter weight were the next most important effects, with each accounting for between 9 and 20% of the total variation. As most selection is conducted on a within herd and year basis, it is recommended that birth weight records be adjusted for sex and age of dam effects. Adjustment for dam winter weight could also be undertaken but this would remove some genetic variation and may cause errors in the prediction of genetic merit of the fawns and/or their dams. However, the amount of genetic variation removed is likely to be small.

March weight was significantly influenced by the following non-genetic effects: herd, year, sex of fawn, age of dam and age at the March weighing. Age at March weighing, which was fitted as a covariate, was the most important effect, accounting for between 17.5 and 34.3% of the total variation in March weight. Sex was the next most important effect, accounting for between 9.7 and 20.0% of the total variation. Dam winter weight could be used as an adjustment factor in place of dam age as there was little difference between the total amount of variation each controlled, between 4.0 and 16.5%. However, adjusting fawn March weight for dam winter weight would remove both environmental and genetic variation, this may reduce the accuracy of selection by causing errors in the prediction of an individual's genetic merit. Also, dam winter weight would need to be recorded annually, whereas age of dam is readily available. Adjustment of March weight for age of dam was therefore considered preferable to adjustment for dam winter weight. If selection for March weight is to be undertaken within contemporary groups, then adjustment for the effects of age at March weighing, sex of fawn and age of dam (particularly 2 year old versus older dams) is recommended.

Fifteen-month weight was significantly influenced by the non-genetic effects of herd, sex, age at weighing and dam winter weight. Sex of animal controlled the largest proportion of variation in 15-month weight, approximately 70%. Although the effects of age at weighing and dam winter weight were significant (P<0.001) with each controlling approximately 2.5% of the total variation in 15-month weight, they appeared to be of little practical importance. Provided selection at 15-months of age is conducted on a within herd and sex basis, it is concluded that prior adjustment of the weight records of Red deer for non-genetic effects is unnecessary.

The estimates of the heritabilities of birth, March and 15-month weights of Red deer were high indicating that selection for these traits will result in rapid genetic gain. All estimates were accompanied by high standard error estimates, these were largely a reflection of the small number of records in some subclasses and the unbalanced nature of the data sets.

The phenotypic correlation estimates between birth, March and 15-month weights were consistently positive and of moderate to strong magnitude. The phenotypic correlation estimates between dam winter weight in adjacent years were strongly positive. The genetic correlation estimates between birth, March and 15-month weights were consistently positive and of moderate to strong magnitude. The results of this study indicated that selection for March and/or 15-month weight should result in improved growth rate at all stages of growth. The moderate to high genetic correlation between March and 15-month weight will allow breeders to use March weight as an early indicator of 15-month weight. The strong positive genetic correlation between birth and March weight, and the expected, though not estimated, positive genetic correlation between birth and 15-month weight, implied that selection for higher March and/or 15-month weight will lead to higher birth weights. This will be undesirable if a concurrent increase in fawning difficulty and fawn mortality arises from selection on later weights.

The high heritability estimates for birth, March and 15-month weights and the moderate to strong positive genetic correlations estimated between these traits could be a result of the diverse and relatively unselected population base of farmed Red deer in New Zealand. As intensive selection is carried out for these traits over future generations, the heritability of these liveweights may decrease.

The selection indices presented in this study demonstrated potential genetic and economic gains that can be made for venison and/or velvet antler production. Economic response per generation was greater for the venison and velvet antler objective, reflecting the high value and potential for selection for velvet antler weight. A reliable predictor of 2 year old velvet antler weight is required in order that selection for this trait can be undertaken by 15-months of age. This would improve genetic gain per year by decreasing the generation interval and would also decrease the time the breeder takes to obtain economic gain from selection. Due to the strong positive correlations between liveweights in the parameter sets used to construct the selection indices, negative index weighting factors were obtained for March weight. These were considered unreasonable and indicated the need for further investigation. In the interim, it may be preferable to select animals solely on the basis of their 15-month weight if the objective is to increase venison production, until more reliable selection indices can be developed.

When larger and more balanced data sets become available, further research is required on the influence of non-genetic effects for liveweight traits. Particular emphasis is required on the presence and importance of interactions which can occur between the non-genetic effects. This will provide valuable information for the formulation of adjustment factors and the importance of developing these within herd and/or year.

The heritability estimates from this study may have been inflated due to the inherent nature of the data set. The heritability of liveweight traits require further monitoring with a more balanced data set that has a larger number of records spanning a greater number of years. Estimates of the heritability of mature liveweight and the correlations between mature liveweight and earlier weights would also be useful in determining the importance of indirect selection for mature weight through earlier liveweight traits.

The phenotypic and genetic correlations between liveweight also require updating with a more balanced and larger data set. Genetic correlation estimates between birth and 15-month weight, and between the birth, March and 15-month weights and later liveweight traits are also required for use in developing appropriate breeding programmes and selection index formulation.

Further development of appropriate selection indices for Red deer will be required when the above mentioned parameters become available. Consideration must also be given to the reasons for the negative index weighting factors found in this study for March weight.

Phenotypic and genetic parameters are required for the other strains of the *Cervus elaphus* species (that is, Wapiti/Canadian Elk, New Zealand-type Wapiti and their crosses with Red deer) as the initial analyses in this study indicated these strains had different variances to Red deer for March weight. Phenotypic and genetic parameters are also required for Fallow deer which belong to a different genus.

APPENDICES

APPENDIX 1

TABLE 9.1.1: Distribution of data used in Model 1.

(N = 257)

HERD NUMBER	DAM AGE CLASS		NUMBER OF RECORDS PER BIRTH YEAR		
		1982	1983	1984	1985
1	2 year		2	3	14
	3 year		12	28	3
	4 year			25	12
	5+ year				21
	Total		**14**	**56**	**50**
2	2 year	5	7	18	
	3 year		18	12	
	4 year	10		18	
	5+ year		25	24	
	Total	**15**	**50**	**72**	

TABLE 9.1.2: Distribution of data used in Model 2.

(N = 54)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR	
		1984	1985
1	2 year	3	7
	3 year		3
	4 year	11	11
	5 year		19
	Total	**14**	**40**

TABLE 9.1.3: Distribution of data used in Model 3.
        (N = 106)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR		
		1983	1984	1985
1	2 year		3	14
	3 year	12	21	3
	4 year		21	12
	5 year			20
	Total	**12**	**45**	**49**

TABLE 9.1.4: Distribution of data used in Model 4.
        (N = 53)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR	
		1984	1985
1	2 year	3	7
	3 year		3
	4 year	11	11
	5 year		18
	Total	**14**	**39**

APPENDIX 2

TABLE 9.2.1: Distribution of data used in Model 5.

(N = 1318)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR			
		1982	1983	1984	1985
	2 year			8	8
	3 year				10
1 4	year			7	12
	5+ year			2	23
	Total			**17**	**53**
	2 year			4	
	3 year		18		
2 4	year		2	19	
	5+ year		2	2	
	Total		**22**	**25**	
	2 year			3	15
	3 year			28	3
3 4	year			27	14
	5+ year				21
	Total			**58**	**53**
	2 year	11	1	29	11
	3 year	2	15	5	23
4 4	year		4	29	2
	5+ year	1	1	8	29
	Total	**14**	**21**	**71**	**65**
	2 year			3	5
	3 year			4	2
5 4	year			20	3
	5+ year			23	42
	Total			**50**	**52**
	2 year			40	29
	3 year			28	3
6 4	year			18	13
	5+ year			47	27
	Total			**133**	**72**

(continued)

TABLE 9.2.1 (continued)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR			
		1982	1983	1984	1985
	2	year		11	9 21
	3	year		20	11 9
7	4	year		8	11 13
	5+	year		10	24 31
	Total		**49**	**55**	**74**
	2	year	5	7	16
	3	year		17	12
8	4	year	11		18
	5+	year		26	23
	Total	**16**	**50**	**69**	
	2	year		8	15 1
	3	year		8	14 10
9	4	year		6	12 13
	5+	year		38	36 32
	Total		**60**	**77**	**56**
	2	year			7
	3	year			9
10	4	year			5
	5+ year			21	
	Total			**42**	
	2	year			13
	3	year			12
11	4	year			35
	5+	year			4
	Total				**64**

TABLE 9.2.2: Distribution of data used in Model 6A.

(N = 154)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR 1984	1985
1	2 year	3	7
	3+ year	14	35
Total	**17**	**42**	
2	2 year		1
	3+ year		20
	Total		**21**
3	2 year		21
	3+ year		53
	Total		**74**

TABLE 9.2.3: Distribution of data used in Model 6B.

(N = 210)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR	
		1984	1985
1	3 year		6
	4+ year		9
	Total		**15**
2	3 year		3
	4+ year		32
	Total		**35**
3	3 year		3
	4+ year		39
	Total		**42**
4	3 year		10
	4+ year		10
	Total		**20**
5	3 year		9
	4+ year		44
	Total		**53**
6	3 year		8
	4+ year		37
	Total		**45**

TABLE 9.2.4: Distribution of data used in Model 7.

(N = 579)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR	
		1984	1985
1	2 year	7	
	3+ year	9	
	Total	**16**	
2	2 year	3	15
	3+ year	44	37
	Total	**47**	**52**
3	2 year		11
	3+ year		36
	Total		**47**
4	2 year		5
	3+ year		23
	Total		**28**
5	2 year	34	
	3+ year	62	
	Total	**96**	
6	2 year	9	21
	3+ year	46	53
	Total	**55**	**74**
7	2 year	15	1
	3+ year	45	54
	Total	**60**	**55**
8	2 year		26
	3+ year		23
	Total		**49**

TABLE 9.2.5: Distribution of data used in Model 8A.
(N = 115)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR	
		1984	1985
1	2 year		7
	3+ year		34
	Total		**41**
2	2 year		21
	3+ year		53
	Total		**74**

TABLE 9.2.6: Distribution of data used in Model 8B.
(N = 132)

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER BIRTH YEAR	
		1984	1985
1	3 year		3
	4+ year		31
	Total		**34**
2	3 year		9
	4+ year		44
	Total		**53**
3	3 year		8
	4+ year		37
	Total		**45**

APPENDIX 3

TABLE 9.3.1: Distribution of data used in Model 9.

(N = 304) [1984 born animals only]

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER SEX MALE	FEMALE
1	2 year	2	3
	3+ year	5	2
	Total	**7**	**5**
2	2 year	9	19
	3+ year	14	16
	Total	**23**	**35**
3	2 year	20	16
	3+ year	39	49
	Total	**59**	**65**
4	2 year	1	4
	3+ year	12	20
	Total	**13**	**24**
5	2 year	4	2
	3+ year	15	24
	Total	**19**	**26**
6	2 year		
	3+ year	8	7
	Total	**8**	**7**
7	2 year		
	3+ year	7	6
	Total	**7**	**6**

TABLE 9.3.2: Distribution of data used in Model 10.

(N = 174) [1984 born animals only]

HERD NUMBER	DAM AGE CLASS	NUMBER OF RECORDS PER SEX	
		MALE	FEMALE
1	2 year	2	3
	3+ year	5	2
	Total	7	5
2	2 year	17	13
	3+ year	29	32
	Total	46	45
3	2 year	1	4
	3+ year	12	20
	Total	13	24
4	2 year	4	2
	3+ year	7	21
	Total	11	23

APPENDIX 4

TABLE 9.4.1: Distribution of data used for the estimation of birth weight heritability and the genetic correlation between birth weight and March weight. (N = 265)

HERD	SIRE NUMBER	NUMBER OF RECORDS PER BIRTH YEAR 1983	1984	1985	TOTAL
Herd 1	1	11	9		20
	2		5		5
	3		10		10
	4	10			10
Herd 2	5			20	20
	6			11	11
	7			11	11
	8	5	16	7	28
	9	9	40		49
Herd 3	10	12	11		23
	11	17	22		39
	12		14		14
	13		5		5
	14		20		20

TABLE 9.4.2: Distribution of data used for the estimation of March weight heritability. (N = 1131)

HERD	SIRE NUMBER	NUMBER OF RECORDS PER BIRTH YEAR			
		1983	1984	1985	TOTAL
Herd 1	1		5	10	15
	2		7	11	18
	3			12	12
	4		5		5
	5			9	9
	6			4	4
	7			6	6
Herd 2	8	12	9		21
	9		5		5
	10		11		11
	11	10			10
Herd 3	12			22	22
	13			11	11
	14			11	11
	57		17	8	25
	58		41		41
Herd 4	15		11	36	47
	16		19		19
	17		7	7	14
	18		3		3
	19			5	5
	20			12	12
	59	21	31		52
Herd 5	21		17		17
	22			14	14
	55		33	38	71
Herd 6	23		16		16
	24		26	27	53
	25		32		32
	26			4	4
	27			8	8
	28			4	4
	56		52	28	80

(continued)

TABLE 9.4.2 (continued)

HERD	SIRE NUMBER	NUMBER OF RECORDS PER BIRTH YEAR			
		1983	1984	1985	TOTAL
Herd 7	29	16			**16**
	30		29		**29**
	31		25		**25**
	32	14			**14**
	33	19			**19**
	34			28	**28**
	35			25	**25**
	36			21	**21**
Herd 8	37	13	12		**25**
	38	17	21		**38**
	39		11		**11**
	40		5		**5**
	41		20		**20**
Herd 9	42		7	31	**38**
	43		6		**6**
	44	10			**10**
	45		4		**4**
	46	9	5		**14**
	47	17	24		**41**
	48		11	11	**22**
	49		15		**15**
	50		4		**4**
	51	6			**6**
	52	11			**11**
	53			3	**3**
	54			4	**4**

TABLE 9.4.3: Distribution of data used for the estimation of 15-month weight heritability. (N = 342)

HERD	SIRE NUMBER	NUMBER OF RECORDS PER BIRTH YEAR 1983	1984	1985
Herd 1	1		3	
	2		5	
	3		4	
Herd 2	4		6	
	5		7	
Herd 3	6		11	
	7		14	
	8		7	
	9		3	
	10		21	
Herd 4	11		13	
	12		24	
	13		31	
	14		49	
Herd 5	15		4	
	16		3	
Herd 6	17		36	
	18		16	
Herd 7	19		7	
	20		5	
	21		3	
	22		17	
	23		9	
Herd 8	24		3	
	25		5	
	26		6	
Herd 9	27		13	
Herd 10	28		17	

APPENDIX 5

TABLE 9.5.1: Distribution of data used for the estimation of the genetic correlation between March weight and 15-month weight. (N = 270)

HERD	SIRE NUMBER	NUMBER OF RECORDS PER BIRTH YEAR 1983	1984	1985
Herd 1	1		3	
	2		5	
	3		4	
Herd 2	4		6	
	5		7	
Herd 3	6		12	
	7		7	
	8		3	
	9		10	
Herd 4	10		13	
	11		24	
	12		31	
	13		49	
Herd 5	14		4	
	15		3	
Herd 6	16		20	
	17		16	
Herd 7	18		7	
	19		5	
	20		3	
	21		16	
	22		9	
Herd 8	23		3	
	24		5	
	25		5	

BIBLIOGRAPHY

Aaron, D.K., Frahm, R.R., Buchanan, D.S. (1986): Direct and correlated responses to selection for increased weaning or yearling weight in Angus cattle. II. Evaluation of response. Journal of Animal Science 62: 66-76.

Adam, C.L. (1985): Recent developments for lowground Red deer farming. In: Rowett Research Institute, Annual Report of Studies in Animal Nutrition and Allied Sciences. 40: 34-50.

Adam, C.L., Moir, C.E. (1985): Effect of winter nutrition of young farmed Red deer on their subsequent growth at pasture. Animal Production 40: 135-141.

Adam, C.L., Moir, C.E. (1987): A note on the effect of birth date on the performance of suckled Red deer calves and their dams on low-ground pasture. Animal Production 44: 330-332.

Adam, J.L., Asher, G.W. (1986): Deer growth and production. In: Proceedings of a Deer Course for Veterinarians 3: 8-16.

Ahunu, B., Makarechian, M. (1986): Influence of birth date, sex of calf, breed group and age of dam on preweaning performance of range beef calves. Canadian Journal of Animal Science 66: 381-388.

Albon, S.D., Guinness, F.E., Clutton-Brock, T.H. (1983): The influence of climatic variation on the birth weights of Red deer (*Cervus elaphus*). Journal of Ecology 200: 295-298.

Albon, S.D., Clutton-Brock, T.H., Guinness, F.E. (1987): Early development and population dynamics in Red deer. II. Density-independent effects and cohort variation. Journal of Animal Ecology 56: 69-81.

Alenda, R., Martin, T.G. (1987): Genetic parameters and consequences of selection for growth traits in a beef herd selected for yearling weight. Journal of Animal Science 64: 366-372.

Anderson, J.H., Wilham, R.L. (1978): Weaning weight correction factors from Angus field data. Journal of Animal Science 47: 124-130.

Asher, G.W., Adam, J.L. (1985): Reproduction of farmed Red and Fallow deer in northern New Zealand. In: Biology of Deer Production. Edited by P.F. Fennessy and K.R. Drew, The Royal Society of New Zealand, Wellington, Bulletin 22, pp.217-224.

Asher, G.W., Adam, J.L., Langridge, M., Howell, L.J. (1981): Calving and fawning performance of Red and Fallow deer in northern North Island regions. Proceedings of the Ruakura Farmers' Conference, Hamilton, 33: 97-99.

Bailey, D.R.C., Lawson, J.E. (1986): Genetic progress through selection for postweaning gain in Angus and Hereford cattle. In: 3rd World Congress on Genetics Applied to Livestock Production, Edited by G.E. Dickerson and R.K. Johnson, University of Nebraska Board of Regents, Nebraska, 12: 210-214.

Baker, R.L. (1980): The role of maternal effects on efficiency of selection in beef cattle - A review. Proceedings of the New Zealand Society of Animal Production 40: 285-303.

Baker, R.L., Morris, C.A. (1984): A review of correlated responses to weight selection in beef cattle under different management and climatic conditions. In: Proceedings of the 2nd World Congress on Sheep and Beef Cattle Breeding, Edited by J.H. Hofmeyr and E.H.H. Meyer, South African Stud Book and Livestock Improvement Association, Pretoria, pp.236-251.

Baker, R.L., Carter, A.H., Cox, E.H., Templer, H.A. (1974): Influence of birth date and dam's age on early growth in beef cattle. Proceedings of the New Zealand Society of Animal Production 34: 115-130.

Barlow, R. (1978): Biological ramifications of selection for preweaning growth in cattle. A review. Animal Breeding Abstracts 46: 469-494.

Barlow, R. (1987): An introduction to breeding objectives for livestock. In: Proceedings of the Sixth Conference of the Australian Association of Animal Breeding and Genetics, Perth, pp.162-169.

Bean, K.G., Seifert, G.W., Aspden, W.J. (1982): Comparison of two methods for correcting weaning weight for dam age. In: Proceedings of the Third Conference of the Australian Association of Animal Breeding and Genetics, Edited by C.P. McPhee, Albion Press Ltd. pp.86-87.

Becker, W.A. (1984): Manual of Quantitative Genetics, Fourth Edition. Academic Enterprises, Pullman, Washington. 188pp.

Bertrand, J.K., Benyshek, L.L. (1987): Variance and covariance estimates for maternally influenced beef growth traits. Journal of Animal Science 64: 728-734.

Blaxter, K.L., Hamilton, W.J. (1980): Reproduction in farmed Red deer 2. Calf growth and mortality. Journal of Agricultural Science 95: 275-284.

Blaxter, K.L., Kay, R.N.B., Sharman, G.A.M., Cunningham, J.M.M., Hamilton, W.J. (1974): Farming the Red deer. Department of Agriculture and Fisheries for Scotland, Edinburgh, Her Majesty's Stationary Office. 92pp.

Blaxter, K.L., Boyne, A.W., Hamilton, W.J. (1981): Reproduction in farmed Red deer 3. Hind growth and mortality. Journal of Agricultural Science 96: 115-128.

Bourdon, R.M., Brinks, J.S. (1982): Genetic, environmental and phenotypic relationships among gestation length, birth weight, growth traits and age at first calving in beef cattle. Journal of Animal Science 55: 543-553.

Brinks, J.S., Clark, R.T., Rice, F.J., Kieffer, N.M. (1961): Adjusting birth weight, weaning weight and preweaning gain for sex of calf in range Hereford cattle. Journal of Animal Science 20: 363-367.

Brinks, J.S., Clark, R.T., Kieffer, N.M., Quesenberry, J.R. (1962): Genetic and environmental factors affecting performance traits of Hereford bulls. Journal of Animal Science 21: 777-780.

Butler, B.M. (1983): Genetic improvement III. The Deer Farmer 16: 15-16.

Carter, A.H. (1971): Effectiveness of growth performance selection in cattle. Proceedings of the New Zealand Society of Animal Production 31: 151-163.

Chapman, H.D., Clyburn, T.M., McCormick, W.C. (1972): Comparison of criteria for selecting introduced beef sires. Journal of Animal Science 35: 321-326.

Clutton-Brock, T.H. (1985): Reproductive success in Red deer. Scientific American 252: 68-74.

Clutton-Brock, T.H., Albon, S.D., Guinness, F.E. (1981): Parental investment in male and female offspring in polygynous mammals. Nature 289: 487-489.

Clutton-Brock, T.H., Guinness, F.E., Albon, S.D. (1982): . Red Deer. Behaviour and Ecology of Two Sexes. The University of Chicago Press, Chicago. 378pp.

Clutton-Brock, T.H., Albon, S.D., Guinness, F.E. (1984): Maternal dominance, breeding success and birth sex ratios in Red deer. Nature 308: 358-360.

Clutton-Brock, T.H., Albon, S.D., Guinness, F.E. (1986): Great expectations: dominance, breeding success and offspring sex ratios in Red deer. Animal Behaviour 34: 460-471.

Clutton-Brock, T.H., Major, M., Albon, S.D., Guinness, F.E. (1987): Early development and population dynamics in Red deer. I. Density-dependent effects on juvenile survival. Journal of Animal Ecology 56: 53-67.

Cundiff, L.V., Willham, R.L., Pratt, C.A. (1966a): Effects of certain factors and their two-way interactions on weaning weight in beef cattle. Journal of Animal Science 25: 972-982.

Cundiff, L.V., Willham, R.L., Pratt, C.A. (1966b): Additive versus multiplicative correction factors for weaning weight in beef cattle. Journal of Animal Science 25: 983-987.

Cunninham, E.P. (1970): SELIND. A Fortran computer program for genetic selection indexes. Users Guide.

Cunningham, E.P., Gjedrem, T. (1970): Genetic control of ewe body weight in selection for higher wool and lamb output. Acta Agriculturae Scandinavica 20: 194-204.

Cunningham, E.P., Henderson, C.R. (1965): Estimation of genetic and phenotypic parameters of weaning traits in beef cattle. Journal of Animal Science 24: 182-187.

Cunningham, E.P., Moen, R.A., Gjedrem, T. (1970): Restriction of selection indexes. Biometrics 26: 67-74.

Dick, A., Dodd, C. (1985): Stags put to the test in Hawkes Bay. The Deer Farmer 24: 23.

Dickerson, G. (1970): Efficiency of animal production - molding the biological components. Journal of Animal Science 30: 849-859.

Dodd, C.J. (1977): Genetic and Environmental Factors Affecting Performance Traits of Straightbred Angus and Friesian-Sired Calves. Thesis, M.Agr.Sc. Massey University.

Dratch, P., Fennessy, P. (1985): Directions in deer breeding... Efficiency. The Deer Farmer 23: 30-33.

Dzieciolowski, R. (1970): Relations between the age and size of Red deer in Poland. Acta Theriologica 15: 253-268.

Eisen, E.J. (1977): Restricted selection index: An approach to selecting for feed efficiency. Journal of Animal Science 44: 958-972.

Elzo, M.A., Quaas, R.L., Pollak, E.J. (1987): Effects of age of dam on weight traits in the Simmental population. Journal of Animal Science 64: 992-1001.

Falconer, D.S. (1981): Introduction to Quantitative Genetics. Second Edition. Longman Incorporated, New York. 340pp.

Fennessy, P.F. (1982a): Growth and nutrition. In: The Farming of Deer. World Trends and Modern Techniques, Edited by D. Yerex, Agricultural Promotion Associates Ltd. Wellington, pp.105-114.

Fennessy, P. (1982b): First understand the basic principles. The Deer Farmer 14: 24a-25.

Fennessy, P. (1983): Selection criteria - what to record. The Deer Farmer 15: 29-34.

Fennessy, P. (1985): Deerplan. The Deer Farmer 26: 37-39.

Fennessy, P. (1986a): Recording schemes and Deerplan. Proceedings of a Deer Course for Veterinarians 3: 121-131.

Fennessy, P. (1986b): Genetic selection. Improving your deer herd. In: Deer Farming - into the Nineties. Edited by P. Owen, Owen Art and Publishing, Brisbane, pp.141-147.

Fennessy, P. (1987): Genetic selection and recording. Proceedings of a Deer Course for Veterinarians 4: 81-93.

Fennessy, P., Dratch, P. (1984): Directions in deer breeding: Themes. The Deer Farmer 22: 34-37.

Fennessy, P., Dratch, P. (1985): Directions in deer breeding: Progeny testing. The Deer Farmer 26: 50-51.

Fennessy, P., Dratch, P. (1986): Farms of the future. The Deer Farmer 30: 34-36.

Fitzhugh, H.A.Jr. (1976): Analysis of growth curves and strategies for altering their shape. Journal of Animal Science 42: 1036-1051.

Frahm, R.R., Nichols, C.G., Buchanan, D.S. (1985a): Selection for increased weaning or yearling weight in Hereford cattle. I. Measurement of selection applied. Journal of Animal Science 60: 1373-1384.

Frahm, R.R., Nichols, C.G., Buchanan, D.S. (1985b): Selection for increased weaning or yearling weight in Hereford cattle. II. Direct and correlated responses. Journal of Animal Science 60: 1385-1395.

Gilmour, A. (1985): REG - A Generalised Linear Models Program. Miscellaneous Bulletin 1 (2nd Edition), Division of Agricultural Services, New South Wales Department of Agriculture.

Gregory, K.E., Blunn, C.T., Baker, M.L. (1950): A study of some of the factors influencing the birth and weaning weights of beef calves. Journal of Animal Science 9: 338-346.

Guinness, F.E., Albon, S.D., Clutton-Brock, T.H. (1978a): Factors affecting reproduction in Red deer *(Cervus elaphus)* hinds on Rhum. Journal of Reproduction and Fertility 54: 325-334.

Guinness, F.E., Clutton-Brock, T.H., Albon, S.D. (1978b): Factors affecting calf mortality in Red deer *(Cervus elaphus)*. Journal of Animal Ecology 47: 817-832.

Hamilton, W.J., Blaxter, K.L. (1980): Reproduction in farmed Red deer 1. Hind and stag fertility. Journal of Agricultural Science 95: 261-273.

Harris, D.L. (1970): Breeding for efficiency in livestock production: Defining the economic objectives. Journal of Animal Science 30: 860-865.

Hartley, H.O., Rao, J.N.K., LaMotte, L. (1978): A simple synthesis-based method of variance component estimation. Biometrics 34: 233-242.

Harwin, G.O., Brinks, J.S., Stonaker, H.H. (1966): Genetic and environmental interactions affecting weaning weights of Hereford calves. Journal of Animal Science 25: 779-782.

Hayes, J.F., Cue, R.I. (1985): A comparison of achieved responses to selection using multitrait selection indices constructed from parameter estimates obtained by three methods of estimation. Zeitschrift fur Tierzuchtung und Zuchtungsbiologie 102: 321- 330.

Hazel, L.N. (1946): The covariance analysis of multiple classification with unequal subclass numbers. Biometrics Bulletin 2: 21-25.

Hemmerle, W.J., Hartley, H.O. (1973): Computing maximum likelihood estimates for the mixed A.O.V. model using the W transformation. Technometrics 15: 819-831.

Henderson, C.R. (1953): Estimation of variance and covariance components. Biometrics 9: 226-252.

Henderson, C.R. (1986a): Estimation of parameters and breeding values for multi-trait selection. In: 3rd World Congress on Genetics Applied to Livestock Production, Edited by G.E. Dickerson and R.K. Johnson, University of Nebraska Board of Regents, Nebraska, 12: 353-355.

Henderson, C.R. (1986b): Recent developments in variance and covariance estimation. Journal of Animal Science 63: 208-216.

Huxley, J.S. (1931): The relative size of antlers in deer. In: Proceedings of the Zoological Society of London, pp.819-864.

Hyvarinen, H., Kay, R.N.B., Hamilton, W.J. (1977): Variation in the weight, specific gravity and composition of the antlers of Red deer (Cervus elaphus L.). British Journal of Nutrition 38: 301-311.

Itulya, S.B., Ray, D.E., Roubicek, C.B., Benson, C.R. (1987): Genetic parameters, maternal ability and related selection criteria for unsupplemented Hereford range cows. Journal of Animal Science 64: 1630-1637.

James, J.W. (1982): Construction, uses, and problems of multitrait selection indices. In: 2nd World Congress on Genetics Applied to Livestock Production, Editorial Garsi, Madrid, 5: pp.130-139.

Jeffery, H.B., Berg, R.T. (1972): An evaluation of several measurements of beef cow size as related to progeny performance. Canadian Journal of Animal Science 52: 23-37.

Jeffery, H.B., Berg, R.T., Hardin, R.T. (1971): Factors affecting preweaning performance in beef cattle. Canadian Journal of Animal Science 51: 561-577.

Jensen, J., Andersen, B.B. (1984): Performance testing of future A.I. bulls for growth rate, feed efficiency and muscularity. Genetic parameters, adjustment for systematic environmental factors, selection indices. Livestock Production Science 11: 475-490.

Kelly, R.W., Drew, K.R. (1976): The behaviour and growth of deer on improved pastures. In: Deer Farming in New Zealand. Progress and Prospects: Edited by K.R. Drew and M.F. McDonald, New Zealand Society of Animal Production, Occasional Publication No.5, pp.20-25.

Kelly, R.W., Whateley, J.A. (1975): Observations on the calving of Red deer (Cervus elaphus) run in confined areas. Applied Animal Ethology 1: 293-300.

Kempthorne, O. (1957): In: An Introduction to Genetic Statistics, John Wiley & Sons Inc, Canada, pp.246-247.

Kempthorne, O., Nordskog, A.W. (1959): Restricted selection indices. Biometrics 15: 10-19.

Knights, S.A., Baker, R.L., Gianola, D., Gibb, J.B. (1984): Estimates of heritabilities and of genetic and phenotypic correlations among growth and reproductive traits in yearling Angus bulls. Journal of Animal Science 58: 887-893.

Koch, R.M. (1972): The role of maternal effects in animal breeding: VI. Maternal effects in beef cattle. Journal of Animal Science 35: 1316-1323.

Koch, R.A., Clark, R.T. (1955a): Influence of sex, season of birth and age of dam on economic traits in range beef cattle. Journal of Animal Science 14: 386-397.

Koch, R.M., Clark, R.T. (1955b): Genetic and environmental relationships among economic characters in beef cattle. II. Correlations between offspring and dam and offspring and sire. Journal of Animal Science 14: 786-791.

Koch, R.M., Clark, R.T. (1955c): Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment. Journal of Animal Science 14: 979-996.

Koch, R.M., Gregory, K.E., Ingalls, J.E., Arthaud, R.L. (1959): Evaluating the influence of sex on birth weight and preweaning gain in beef cattle. Journal of Animal Science 18: 738-744.

Koch, R.M., Cundiff, L.V., Gregory, K.E., Dickerson, G.E. (1973): Genetic and phenotypic relations associated with preweaning and postweaning growth of Hereford bulls and heifers. Journal of Animal Science 36: 235-239.

Koch, R.M., Gregory, K.E., Cundiff, L.V. (1974a): Selection in beef cattle. I. Selection applied and generation interval. Journal of Animal Science 39: 449-458.

Koch, R.M., Gregory, K.E., Cundiff, L.V. (1974b): Selection in beef cattle. II. Selection response. Journal of Animal Science 39: 459-470.

Koch, R.M., Gregory, K.E., Cundiff, L.V. (1982): Critical analysis of selection methods and experiments in beef cattle and consequences upon selection programs applied. In: 2nd World Congress on Genetics Applied to Livestock Production, Editorial Garsi, Madrid, 5: 514-526.

Koger, M., Reynolds, W.L., Meade, J.H., Kirk, W.G., Peacock, F.M., Kidder, R.W. (1962): Environment, sex and age of dam effects. Journal of Animal Science 21: 973 (Abstract).

Langvatn, R., Albon, S.D. (1986): Geographic clines in body weight of Norwegian Red deer: a novel explanation of Bergmann's rule?. Holarctic Ecology 9: 285-293.

Lasley, J.F., Day, B.N., Comfort, J.E. (1961): Some genetic aspects of gestation length, and birth and weaning weights in Hereford cattle. Journal of Animal Science 20: 737-741.

Leighton, E.A., Willham, R.L., Berger, P.J. (1982): Factors influencing weaning weight in Hereford cattle and adjustment factors to correct records for these effects. Journal of Animal Science 54: 957-963.

Lin, C.Y., McAllister, A.J. (1984): Monte Carlo comparison of four methods for estimation of genetic parameters in the univariate case. Journal of Dairy Science 67: 2389-2398.

Loudon, A.S.I., Milne, J.A. (1985): Nutrition and growth of young Red deer. In: Biology of Deer Production. Edited by P.F. Fennessy and K.R. Drew, The Royal Society of New Zealand, Wellington, Bulletin 22, pp.423-427.

Loudon, A.S.I., Darroch, A.D., Milne, J.A. (1984): The lactation performance of Red deer on hill and improved species pastures. Journal of Agricultural Science 102: 149-158.

Luesakul-Reodecha, C., Martin, T.G., Nelson, L.A. (1986): Effects of long-term selection for 365-day weight on maternal performance of beef cows. In: 3rd World Congress on Genetics Applied to Livestock Production, Edited by G.E. Dickerson and R.K. Johnson, University of Nebraska Board of Regents, Nebraska, 12: 205-209.

Lush, J.L., Shrode, R.R. (1950): Changes in milk production with age and milking frequency. Journal of Dairy Science 33: 338-357.

MAFCorp. (1988): Analysis of the 1987 farming statistics. Policy Services, Ministry of Agriculture and Fisheries, Wellington.

Magee, W.T., Brinks, J., Nelson, R.H., Branaman, G.A. (1961): Some factors affecting weaning weight and score of beef calves. Quarterly Bulletin, Michigan State University Agricultural Experiment Station 43: 556-562.

Marlowe, T.J., Mast, C.C., Schalles, R.R. (1965): Some nongenetic influences on calf performance. Journal of Animal Science 24: 494-501.

Massey, W. (1987): What's up in breeder land? The Deer Farmer 37: 15-20.

Mendoza, B.G., Slanger, W.D. (1985): Restricted selection indexes: Genetic responses involving maternal effect for weaning weight and other growth traits in beef cattle. Journal of Animal Science 60: 413-426.

Milne, J.A., Sibbald, A.M. (1986): The effects of live weight at weaning, date of weaning and winter nutrition on the subsequent performance of Red deer. Animal Production 42: 474 (Abstract).

Minyard, J.A., Dinkel, C.A. (1965): Weaning weight of beef calves as affected by age and sex of calf and age of dam. Journal of Animal Science 24: 1067-1071.

Mitchell, B. (1971): The weights of new-born to one-day-old Red deer calves in Scottish moorland habitats. Journal of Zoology 164: 250-254.

Mitchell, B. (1973): The reproductive performance of wild Scottish Red deer, Cervus elaphus. Journal of Reproduction and Fertility (Supplement 19): 271-285.

Mitchell, B., Brown, D. (1974): The effects of age and body size on fertility in female Red deer (Cervus elaphus L.). In: International Congress of Game Biologists, 1974, Edited by I. Kjerner and P. Bjurholm, National Swedish Environment Protection Board, Stockholm, 11: 89-98.

Mitchell, B., Lincoln, G.A. (1973): Conception dates in relation to age and condition in two populations of Red deer in Scotland. Journal of Zoology 171: 141-152.

Mitchell, B., McCowan, D., Nicholson, I.A. (1976): Annual cycles of body weight and condition in Scottish Red deer, Cervus elaphus. Journal of Zoology 180: 107-127.

Mitchell, B., McCowan, D., Parish, T. (1986): Performance and population dynamics in relation to management of Red deer Cervus elaphus at Glenfeshie, Inverness-shire, Scotland. Biological Conservation 37: 237-267.

Moore, G.H. (1984): Better weaning weights, earlier fawning. The Deer Farmer 21: 31.

Moore, G.H. (1987): Twinning and triplets in Red deer. The Deer Farmer 40: 34-35.

Moore, G.H., Littlejohn, R.P., Cowie, G.M. (1988): Liveweights, growth rates and antler measurements of farmed Red deer stags and their usefulness as predictors of performance. New Zealand Journal of Agricultural Research 31(3): In press.

Morley, F.H.W. (1955): Selection for economic characters in Australian Merino sheep. V. Further estimates of phenotypic and genetic parameters. Australian Journal of Agricultural Research 6: 77-90.

Morris, C.A., Baker, R.L. (1982): Cow weights and other correlated responses to yearling or 18-month weight selection. In: 2nd World Congress on Genetics Applied to Livestock Production, Editorial Garsi, Madrid, 8: 294-299.

Morris, C.A., Wilton, J.W. (1976): Influence of body size on the biological efficiency of cows: A review. Canadian Journal of Animal Science 56: 613-647.

Mrode, R.A. (1988): Selection experiments in beef cattle. Part 2: A review of responses and correlated responses. Animal Breeding Abstracts 56: 155-167.

Neville, W.E.Jr. (1962): Influence of dam's milk production and other factors on 120- and 240-day weight of Hereford calves. Journal of Animal Science 21: 315-320.

Newman, S-A.N. (1988): Genetic and Environmental Variation and Genotype x Environment Interactions in New Zealand Romney Sheep: Thesis, Ph.D., Massey University.

Nicoll, G.B. (1975): A Study of Adjustment Factors for the Weaning Weights of Hereford and Angus Calves. Thesis, M.Ag.Sc. Massey University.

Nicoll, G.B., Rae, A.L. (1977): Adjustment factors for Hereford and Angus cattle weights. I. Weight at weaning. New Zealand Journal of Agricultural Research 20: 269-278.

Nicoll, G.B., Rae, A.L. (1978): Adjustment factors for Hereford and Angus cattle weights. II. Weight at eighteen months. New Zealand Journal of Agricultural Research 21: 563-570.

Pabst, W., Kilkenny, J.B., Langholz, H.J. (1977): Genetic and environmental factors influencing calf performance in pedigree beef cattle in Britain. 1. The influence of environmental effects on birth, 200-day and 400-day weights. Animal Production 24: 29-39.

Packard, P.M., Morris, C.A. (1986): Beef cattle. Beefplan. Combined performance and pedigree recording. Aglink FPP 432. Information Services, Ministry of Agriculture and Fisheries, Wellington, New Zealand. 4pp.

Parnell, P.F., Barlow, R., Tier, B. (1986): Realised responses to divergent selection for yearling growth rate in Angus cattle. In: 3rd World Congress on Genetics Applied to Livestock Production, Edited by G.E. Dickerson and R.K. Johnson, University of Nebraska Board of Regents, Nebraska, 11: 330-334.

Patterson, H.D., Thompson, R. (1971): Recovery of the inter-block information when block sizes are unequal. Biometrika 58: 545-554.

Pearse, T. (1987): Fundamental deer management. The Deer Farmer 35: 45-48.

Ponzoni, R.W. (1982): Breeding objectives in sheep improvement programmes. In: 2nd World Congress on Genetics Applied to Livestock Production, Editorial Garsi, Madrid, 5: 619-634.

Preston, T.R., Willis, M.B. (1970): Intensive Beef Production (Second Edition). Pergamon Press Ltd. Oxford, 567pp.

Reimer, D., Kaluba, E.M., Nolan, J.C.Jr., Campbell, C.M. (1986): Breeding better beef. 2. Effect of Angus, Hereford, and Santa Gertrudis sires on preweaning performance of calves. Animal Breeding Abstracts 54: 757 (Abstract).

Rhodes, R.F., Scarth, R.D., Cook, M.K. (1970): The effect of certain biological and environmental factors on weaning weight of beef calves. Journal of Animal Science 31: 168 (Abstract).

Richardson, A.T., Martin, T.G., Hunsley, R.E. (1978): Weaning age of Angus heifer calves as a factor influencing calf and cow performance. Journal of Animal Science 47: 6-14.

SAS Institute Inc. (1985): . SAS User's Guide: Statistics, Version 5 Edition, Cary, North Carolina, 956pp.

Schaeffer, L.R., Wilton, J.W. (1974a): Age of dam, sex and environmental interactions affecting preweaning average daily gains of beef cattle. Canadian Journal of Animal Science 54: 183-190.

Schaeffer, L.R., Wilton, J.W. (1974b): Comparison of the effectiveness of multiplicative and additive adjustment factors in preweaning average daily gain of beef cattle. Canadian Journal of Animal Science 54: 519-532.

Schaeffer, L.R., Wilton, J.W. (1981): Estimation of variances and covariances for use in a multiple trait beef sire evaluation model. Canadian Journal of Animal Science 61: 531-538.

Searle, S.R. (1971): Linear Models. John Wiley and Sons, Inc., New York. 532pp.

Searle, S.R., Henderson, C.R. (1960): Judging the effectiveness of age-correction factors. Journal of Dairy Science 43: 966-974.

Sellers, H.I., Willham, R.L., de Baca, R.C. (1970): Effect of certain factors on weaning weight of beef calves. Journal of Animal Science 31: 5-12.

Sewell, H.B., Comfort, J.E., Day, B.N., Lasley, J.F. (1963): Genetic and Environmental Factors Influencing the Weaning Weight of Beef Calves. Research Bulletin 823, University of Missouri, College of Agriculture, Agricultural Experiment Station, Columbia, Missouri. 41pp.

Simm, G., Smith, C., Prescott, J.H.D. (1985): Environmental effects on bull performance test results. Animal Production 41: 177-185.

Simm, G., Smith, C., Prescott, J.H.D. (1986): Selection indices to improve the efficiency of lean meat production in cattle. Animal Production 42: 183-193.

Singh, A.R., Schalles, R.R., Smith, W.H., Kessler, F.B. (1970): Cow weight and preweaning performance of calves. Journal of Animal Science 31: 27-30.

Snedecor, G.W., Cochran, W.G. (1980): Statistical Methods, Seventh Edition. The Iowa State University Press, Ames, Iowa. 507pp.

Sorensen, D.A., Kennedy, B.W. (1984): Estimation of genetic variances from unselected and selected populations. Journal of Animal Science 59: 1213-1223.

Spiers, I.B. (1987): The development of the deer industry. Proceedings of a Deer Course for Veterinarians 4: 1-8.

Srinivasan, G., Martin, T.G. (1970): Environmental effects on preweaning performance of calves. Journal of Animal Science 31: 168 (Abstract).

Suttie, J.M. (1980): Influence of nutrition on growth and sexual maturation of captive Red deer stags. In: Proceedings of the Second International Reindeer/Caribou Symposium, Edited by E. Reimers, E. Gaare and S. Skjenneberg, Norway, pp.341-349.

Suttie, J.M. (1983): Body size: Dominance relationships in Red deer stag calves. Animal Behaviour 31: 610-611.

Suttie, J.M., Mitchell, B. (1983): Jaw length and hind foot length as measures of skeletal development of Red deer (Cervus elaphus). Journal of Zoology 200: 431-434.

Suttie, J.M., Goodall, E.D., Pennie, K., Kay, R.N.B. (1983): Winter food restriction and summer compensation in Red deer stags (Cervus elaphus). British Journal of Nutrition 50: 737-747.

Suttie, J.M., Fennessy, P.F., Veenvliet, B.A., Littlejohn, R.P., Fisher, M.W., Corson, I.D., Labes, R.E. (1987): Energy nutrition of young Red deer (Cervus elaphus) hinds and a comparison with young stags. Proceedings of the New Zealand Society of Animal Production 47: 111-113.

Swiger, L.A. (1961): Genetic and environmental influences on gain of beef cattle during various periods of life. Journal of Animal Science 20: 183-188.

Swiger, L.A., Koch, R.M., Gregory, K.E., Arthaud, V.H., Rowden, W.W., Ingalls, J.E. (1962): Evaluating pre-weaning growth of beef calves. Journal of Animal Science 21: 781-786.

Swiger, L.A., Gregory, K.E., Koch, R.M., Rowden, W.W., Arthaud, V.H., Ingalls, J.E. (1963): Evaluating post-weaning gain of beef calves. Journal of Animal Science 22: 514-520.

Swiger, L.A., Harvey, W.R., Everson, D.O., Gregory, K.E. (1964): The variance of intraclass correlation involving groups with one observation. Biometrics 20: 818-826.

Tait, S.J. (1983): Estimation of Genetic and Phenotypic Parameters in New Zealand Romney Sheep. Thesis, M.Agr.Sc. Massey University.

Tallis, G.M. (1959): Sampling errors of genetic correlation coefficients calculated from analyses of variance and covariance. Australian Journal of Statistics 1: 35-43.

Thomson, I.F. (1968): Report on the Aberdeen-Angus Cattle Weight Recording Scheme 1961 to 1967. The Beef Recording Association (U.K.) Ltd. Technical Report Number 8. 23pp.

Thouless, C.R., Guinness, F.E. (1986): Conflict between Red deer hinds: The winner always wins. Animal Behaviour 34: 1166-1171.

Turner, H.N., Young, S.S.Y. (1969): Quantitative Genetics in Sheep Breeding, MacMillon, Australia. 332pp.

Vesely, J.A., Robison, O.W. (1971): Genetic and maternal effects on preweaning growth and type score in beef calves. Journal of Animal Science 32: 825-831.

Wegge, P. (1973): Reproductive rates of Red deer (Cervus elaphus atlanticus L.) in Norway. International Congress of Game Biologists 11: 79-87.

Wilson, D.E., Berger, P.J., Willham, R.L. (1986): Estimates of beef growth trait variances and heritabilities determined from field records. Journal of Animal Science 63: 386-394.

Woldehawariat, G., Talamantes, M.A., Petty, R.R.Jr., Cartwright, T.C. (1977): A Summary of Genetic and Environmental Statistics for Growth and Conformation Characters of Young Beef Cattle. Second Edition. Technical Report No. 103, The Texas Agricultural Experiment Station, Texas Agricultural and Mechanical University, Department of Animal Science.

Yerex, D. (1982): The Farming of Deer. World Trends and Modern Techniques. Agricultural Promotion Associates Ltd. New Zealand. 176pp.

Yerex, D., Spiers, I. (1987): Modern Deer Farm Management. Ampersand Publishing Associates Ltd. New Zealand. 168pp.

Youngson, R.W. (1970): Rearing Red deer calves in captivity. Journal of Wildlife Management 34: 467-470.

Zhou, S., Wu, S. (1979): A preliminary study of quantitative and character inheritance of antlers. Acta Genetica Sinica 6: 434-440.