DEVELOPMENT OF COMPUTER MODELS OF DIFFERENT SELECTION STRATEGIES ON POULTRY EGG PRODUCTION

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PREFACE

The experimental work described in this dissertation was conducted at the University of Natal, Pietermaritzburg, under the supervision of Dr Carolyn Hancock.

The results have not been submitted in any other form to another university and except where the work of others is acknowledged in the text, the results are of my own investigation.

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I certify that the above statement is correct.

Dr Carolyn Hancock

Supervisor

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AFE	age at first egg
b	weighting factors given to each trait in an index
$\mathbf{h^2}$	heritability
$\mathbf{h^2_b}$	between family heritability
$\mathbf{h^2_{FI}}$	family-index heritability
$\mathbf{h^2_w}$	within family heritability
i	intensity of selection
I	index value
n	number of individuals in a family
P	phenotypic value
$\mathbf{P_f}$	deviation of an individual's phenotypic value from the population mean
r	correlation coefficient, including correlation of breeding values (degree of relatedness between sibs)
R	response to selection
$\mathbf{R_c}$	response to family-index selection
$\mathbf{R_f}$	response to between family selection
$\mathbf{R_w}$	response to within family selection
S	selection differential
t	correlation of phenotypic values of members of the families
$\mathbf{V_A}$	additive genetic variance
$\mathbf{V_P}$	phenotypic variance
$\mathbf{\sigma_p}$	phenotypic standard deviation

ABSTRACT

Poultry have many behavioural, structural and biological features that are ideal for domestication and for meat and egg production (Appleby *et al.*, 1992). Because of the importance of poultry meat and eggs to the human population, breeders and farmers are always looking for ways of improving these traits. Artificial selection is the primary method of trait improvement, and involves selecting individuals with the highest breeding values as parents in each generation. There are a number of different methods of artificial selection, including: individual selection, between family selection, within family selection, family-index selection and index selection.

In order to maintain a good response to selection breeders are constantly striving to improve the effectiveness and accuracy of the different methods of artificial selection for traits of economic importance. One method of achieving this goal is the use of computer models. Computer models can be used to simulate selection strategies and to predict what strategy will be the most appropriate for the improvement of a particular trait. This is important as all traits are influenced by many different genetic and environmental factors (Falconer and Mackay, 1996).

This investigation was designed to compare the effectiveness of five different artificial selection strategies, namely individual selection, between family selection, within family selection, family-index selection and index selection. Five computer models were developed using Microsoft Excel 2000 and these models were then used to compare the efficiencies of the five selection strategies for four different traits. The selection techniques were applied to an artificially, randomly generated population of 500 chickens. The four traits were egg weight with a heritability of 0.51, egg production with a heritability of 0.22, age at first egg with a heritability of 0.41 and body weight with a heritability of 0.55. Firstly, each of these traits were selected for independently using the first four selection methods and secondly the traits were selected for two at a time using index selection.

The most significant results obtained from the single trait simulations were that for all traits family-index selection produced the best response to selection in the initial generations and between family selection produced the best response in the later generations. The traits with a higher heritability (egg weight and body weight) responded better to individual selection than they did to within family selection and between family selection in the initial generations. However, within family selection and between family selection proved to be more effective for traits with a low heritability such as egg production. Individual selection and family-index selection resulted in a very rapid decline in the standard deviation of all the traits. Between family selection resulted in the slowest drop in the standard deviation of all the traits, which is why this technique produced the best responses to selection in the later generations. The impact of the correlations between the economically important traits were evident from the results of index selection. For example, egg production is negatively correlated with egg weight making it difficult to gain a correlated response in both these traits simultaneously. Furthermore, egg production is negatively correlated with age at first egg implying that early maturing birds will lay more eggs, however, these eggs will be lighter.

The majority of the results obtained were to be expected. Family-index selection takes all the information about an individual's breeding value into account resulting in this method of selection consistently identifying the most desirable individuals being selected. It is therefore the preferred method of selection under all circumstances. It is, however, often not economically and practically efficient to incorporate this technique and the use of another method of selection usually proves to be more beneficial. Individual selection proved to be most effective when applied to traits with high heritabilities, due to the fact that this method selects individuals based on their own phenotypic values. For traits with a high heritability, an individual with a good phenotypic value will have a good breeding value. Between family selection and within family selection proved better for traits with lower heritabilities. For traits with a low heritability the phenotypic value of an individual is a poor indicator of its breeding value. Information from a number of relatives may thus improve the accuracy of prediction of the breeding value by accounting for the influence of environmental effects.

The use of computer models to simulate the selection techniques proved very successful in illustrating the effectiveness of the different selection techniques under various genetic and environmental conditions. The models may also prove to be very effective from an educational perspective.

CHAPTER 1
LITERATURE REVIEW

1.1 INTRODUCTION

The meat and eggs produced by poultry are of great importance to the ever-growing human population (Flock and Preisinger, 2002). In recent years a good laying hen is expected to lay over 300 eggs in one laying season, the equivalent of almost 20 kilograms of egg mass. This type of production, in addition to the meat produced by poultry, provides humans with a vital source of protein (Flock and Preisinger, 2002). The majority of this, in fact more than 90 percent, is produced by chickens, otherwise known as domestic fowl, with turkeys, geese and ducks making minor contributions (Crawford, 1995). The importance of poultry farming is therefore paramount and farmers and scientists need to continue to improve their understanding of these species as well as their genetics and breeding.

One tool that has facilitated the improvement of poultry to suit human needs is artificial selection. Selection involves the choice of the most desirable individuals to be used as parents. An advantage of artificial selection is that it is a safer and more natural way of altering the genes of animals when compared to molecular genetic technologies such as cloning and transgenesis. The disadvantage is that it is time consuming and needs to be applied to an entire population over a number of generations. The ultimate result of selection is an alteration, in a desired direction, of the frequencies of the genes that contribute towards the trait or traits of interest (Falconer and Mackay, 1996).

In poultry there is a distinct separation into strains that are meat producers and strains that are egg producers. Even though both types originated from the same species (*Gallus domesticus*), they are now vastly different. Egg laying strains have mature body weights of between 1.5kg

and 1.8kg, but can lay over 300 eggs a year whereas meat producing strains will have a mature body weight of about 6 – 8 kg but will only lay about 180 eggs in a year. The main reason for these great differences is due to their genetic make-up and many generations of selection (Crawford, 1995).

The success of artificial selection has meant that a lot of attention has been directed towards its improvement. The continual advance in technology, such as in computer capabilities, has proved to be a major contributor to this improvement. Computer modelling is one tool that can and has been used by breeders to improve their selection strategies. As a model is a simple representation of real life processes animal breeders can use them as guidelines to test the effects of different variables and enable them to make accurate predictions (Starfield et al., 1990; Starfield and Bleloch, 1991).

1.2 POULTRY: AN INTRODUCTION

Poultry species have been used for domestic purposes such as the production of meat and eggs since approximately 5400 B.C. (Crawford, 1990). There are a number of behavioural, structural and biological features that help to explain why poultry species have been so successfully domesticated and used for meat and egg production (Appleby et al., 1992).

The following behavioural features have increased the success of poultry domestication. Firstly, poultry form large flocks where males are affiliated to more than one female. This hierarchical structure greatly decreases the injury caused by constant fighting that would take place if more than one male were competing for a female. Secondly matings are promiscuous, meaning that any male may potentially mate with any female. Thirdly, poultry show favourable parent-young interactions such as acceptance of young other than their own, which allows a chick to be reared by a surrogate mother, as well as imprinting by young which means a chick can bond to man and be easily tamed. Lastly, these birds also have limited flight (short flight distances) and show little disturbance due to human activities (Appleby et al., 1992).

Important biological and structural features in poultry include the fact that they are relatively small in size, that they have a rapid rate of reproduction and are quick to reach sexual maturity (Appleby *et al.*, 1992). The primary oocytes or the yolks of chicken eggs are also the largest known cells in the animal kingdom weighing about 20 grams. In addition, the pectoral muscles of flightless birds, such as poultry, contain very little myoglobin and are therefore white. This white muscle or white meat is very desirable to man (Appleby *et al.*, 1992).

1.2.1 Taxonomy of poultry

All domestic poultry come from three Orders, the Galliformes, the Anseriformes and the Columbiformes (Appleby *et al.*, 1992). The Galliformes include the turkeys *(Meleagris gallopavo)*, the Japanese quail (*Coturnix coturnix*), the bobwhite quail (*Colinus virginianus*), the guinea fowls (*Numida meleagris*) and the chickens or domestic fowls (*Gallus gallus* or *Gallus domesticus*). The Anseriformes include the domestic duck (*Anus platyrhynchos*), the muscovy duck (*Cairina moschata*) and the geese (*Anser anser*). Domestic pigeons derived from the Rock Dove (*Columba livia*) are members of the Order Columbiformes (Crawford, 1990; Appleby *et al.*, 1992; Crawford, 1995). The chickens or domestic fowl are the major commercial producers and have therefore been widely domesticated and studied.

1.2.2 Origins and domestication

According to archaeological evidence in China, chickens were the first of the poultry species to become domesticated at approximately 5400 B.C. Geese and domestic ducks are thought to have followed in approximately 2500 B.C. The guinea fowl were probably the next in the sequence (1300 B.C.) followed by the turkeys and muscovy ducks (200 B.C. – A.D.700). The most recent poultry species to become domesticated was probably the Japanese quail and this occurred in approximately the 11th century in Japan, China or Korea (Crawford, 1990).

The origins of chickens or domestic fowls are uncertain and they thus have two scientific names: firstly, *Gallus gallus,* which implies that these birds originated, or were domesticated exclusively from the red junglefowl (*Gallus gallus*) and secondly, *Gallus domesticus,* which implies that they were domesticated from more than one of the wild junglefowl species (Appleby *et al.*, 1992; Crawford, 1995).

At present there are numerous (approximately 70) different chicken breeds. Most of these breeds are hybrids of four original breeds of fowl, namely the White Leghorns, the Rhode Island Red, the Light Sussex and the Barred Plymouth Rock (Appleby *et al.*, 1992).

1.3 EGG PRODUCTION IN CHICKENS

Egg production in chickens is a complex trait. Not only are there various ways of measuring egg production but there are also a number of genes and environmental factors that contribute towards the expression of this trait (Fairfull and Gowe, 1990). The aim of the following section is to discuss egg production in chickens and possible complications thereof.

1.3.1 Historical background of egg production in chickens

Genetic studies of egg production in poultry stocks began at the start of the 20th century. This trait has therefore been studied for just over one hundred years (Fairfull and Gowe, 1990; Gowe and Fairfull, 1995).

Much of the early work on egg production was Mendelian in nature (Fairfull and Gowe, 1990). This implies that the trait shows qualitative inheritance where only one gene determines the expression of the trait (Snustad and Simmons, 2003). However, as the measurement of this trait was continuous in nature, it became evident that egg production in chickens is a quantitative trait

with many genes and many environmental factors that contribute towards its expression (Fairfull and Gowe, 1990; Snustad and Simmons, 2003).

The initial evidence of the quantitative inheritance of egg production was produced by Gowell in 1909, at the Maine Agricultural Experiment Station, where he was amongst the first to test the efficiency of mass selection for the improvement of egg production (Fairfull and Gowe, 1990). In 1915, Pearl published a low correlation between the genotype of an individual and the phenotype. Dryden in 1921 was one of the first scientists to actually improve egg production with the use of artificial selection. In the same year Goodale and Sanborn described separate biological traits connected to egg production such as sexual maturity, rate of lay and persistency. In 1936, Munro proposed that egg production did show polygenic inheritance and was the first to estimate genetic variation as a proportion of phenotypic variation, a measure of heritability in the broad sense (Fairfull and Gowe, 1990). It is now widely accepted that egg production in chickens is quantitative, or polygenic in nature and that it needs to be studied using statistical measures (Fairfull and Gowe, 1990).

1.3.2   Egg production and other traits included in breeding programs

Egg production is a confusing trait in that it has a number of different definitions and depending on which definition is used the selection criteria may differ. Hen-housed egg production is one definition, and is the number of eggs that a hen lays after it has been placed in the laying house. Hens that die or lay no eggs are part of the population and are included in egg production calculations (Fairfull and Gowe, 1990). Hen-housed egg production is a combination of three component traits, age at first egg, viability and rate of lay. Hen-day rate of egg production is another definition, and is the number of eggs laid by a hen divided by the number of days the hen was alive. If egg production is measured in this way the effects of age at first egg and viability are greatly reduced (Fairfull and Gowe, 1990). Yet another definition is that of survivor egg production, which includes the production of all hens that survive to the end of a certain test period (usually about one year). This reduces the effects of morbidity (Fairfull and Gowe, 1990).

The rate of egg production or the number of eggs produced deteriorates with the age of the hen. For this reason some laying hens are only kept for one cycle of production (Ledur *et al.*, 2000; Ledur *et al.*, 2002). Due to the variation of egg production with age, egg production is usually broken down into part records, which further complicates the study of this trait. The trait is usually broken down into three or five part records that depend on the age of the hen. The part records may include the early part record (production up to about 40 weeks of age), middle part record (40-55 weeks of age) or the final part record (56-72 weeks of age). The periods assigned to each part record may differ slightly depending on the preferences of the breeder (Fairfull and Gowe, 1990). As improvement in this trait usually occurs in the early part of the laying cycle, it is important to have a good understanding of the early part records when studying egg production in chickens (Ledur *et al.*, 2000). Using part records during selection is advantageous as it reduces the generation interval, which in turn speeds up the response to selection. Provided the early part record is a good indicator of the lifetime production of a bird, which it usually is with correlations ranging between 0.56 and 0.95 (Fairfull and Gowe, 1990), selection can be applied based on early part records as opposed to lifetime records to reduce the generation interval from 72 weeks to approximately 40 weeks (Hicks *et al.*, 1998).

Chicken breeders, when trying to improve egg production, must consider a number of additional traits in their breeding programs (Manson, 1972). These traits include egg weight, body weight (both of which also vary with age and can therefore also be separated out into part records), mortality, sexual maturity (age at first egg), feed consumption, shell strength, shell shape, shell texture and colour, albumin score and blood spot incidence (Manson, 1972). Many of these traits are correlated, positively or negatively, with each other and with egg production and all this information needs to be taken into consideration in breeding programs (Sharma *et al.*, 1998).

a.   Body weight is a trait that cannot be ignored in breeding programs. Smaller birds are preferable as feed costs are lower in comparison to larger birds and feed costs account for approximately 70 percent of the cost of egg production. By decreasing body weight farmers can therefore decrease expenses. However, body size and egg weight are positively correlated and therefore hens that weigh too little will produce small eggs (Spies *et al.*, 2000). Breeders, thus, need to reduce and then maintain body weight at an

optimum size to ensure a high output of sufficiently large eggs (Gowe and Fairfull, 1995).

b. Egg weight, unlike many other traits, shows an increase with age (Ledur *et al.*, 2002). However, if early egg weight is too low then egg weight will be low throughout the lifetime of the hen. Attention therefore needs to be given to early egg weight, which is not only influenced by body weight, but also by nutritional status and photoperiod (Spies *et al.*, 2000).

c. Breeders, traditionally, do not place a great deal of selection pressure on sexual maturity or age at first egg. There is thought to be an optimum age (between 135 and 150days) at which it is best for hens to begin laying eggs. Although it is useful to have an early age of maturity, especially when practising selection for early part records, a bird that starts producing eggs too early would not have had sufficient time to reach an optimum size, and to build up the energy and calcium reserves needed to maintain high levels of egg production (Gowe and Fairfull, 1995).

d. Mortality or viability is another trait that is often included in breeding programs. Breeders will usually select for a general viability but in some cases specific genes that code for resistance to a disease will be selected for according to the prevalence of that disease (Gowe and Fairfull, 1995).

e. Egg quality traits include egg shell quality (shell strength, thickness, texture, shape and colour), albumin quality and the absence of blood or meat spots. Egg quality receives a lot of attention from breeders due to its economic importance (Hartmann *et al.*, 2003).

   • Shell strength is influenced by a combination of genetic, environmental and physiological factors (Gowe and Fairfull, 1995). There are a number of methods, qualitative and quantitative, that are used to assess the strength of an egg shell.

- A number of studies have concluded that sex-linked genes influence shell colour. Little attention is given to shell colour in white egg laying strains, however in brown egg laying strains this trait receives more selection emphasis (Fairfull and Gowe, 1990).

- Albumin quality is an important egg quality trait. Eggs with large amounts of firm albumin are more popular amongst the public. Albumin consists primarily of water and protein. Variation in albumin quality is largely a result of variation in the protein portion implying that albumin quality is a good indicator of protein quality. The best method of measuring this trait is using Haugh units (log of albumin height corrected for egg weight) (Fairfull and Gowe, 1990).

- Blood spots are an indication of lesser quality eggs and breeders attempt to eliminate blood spot incidence. Blood spots have a genetic basis and their incidence usually increases with age (Fairfull and Gowe, 1990).

1.3.3 Genetic factors to be considered in breeding programs

There are three important aspects that need to be taken into consideration when formulating breeding programs, namely the heritability of a trait, the genetic correlation between traits and the relative economic importance of a trait (Gowe and Fairfull, 1995).

1.3.3.1 Heritability

The heritability of a trait is the ratio of additive genetic variance (V_A) to phenotypic variance (V_P) and is presented as:

$$h^2 = \frac{V_A}{V_P}$$

(Lynch and Walsh, 1998; Lynch and Walsh, 2000)

If a trait has a high heritability it means its phenotypic expression will closely resemble its genotypic expression whereas a trait with a low heritability will have a phenotype that is a poor reflection of the genotypic value. The higher the heritability, the more useful selection based on individual values (as opposed to relatives) will be and the easier it will be to gain genetic improvement in that trait (Falconer and Mackay, 1996). This is because only the phenotypic values of individuals can be directly measured but it is their breeding value or additive value that determines their influence on the next generation. It is the heritability that provides a means of estimating the breeding value using the phenotypic value (Gowe and Fairfull, 1995; Falconer and Mackay, 1996). Heritability estimates of various egg production traits are given in table 1.

Table 1.   The heritability of a number of important egg production traits.

Trait	Heritability	Reference
Hen-housed egg production (40 weeks)	0.22	Fairfull and Gowe, 1990
	0.11	Gowe and Fairfull, 1995
Hen-housed egg production (lifetime)	0.15	Fairfull and Gowe, 1990
	0.09	Gowe and Fairfull, 1995
Survivor egg production (40 weeks)	0.27	Fairfull and Gowe, 1990
Survivor egg production (lifetime)	0.24	Gowe and Fairfull, 1995
Hen-day rate of egg production (40 weeks)	0.14	Fairfull and Gowe, 1990
	0.12	Gowe and Fairfull, 1995
Hen-day rate of egg production (lifetime)	0.22	Fairfull and Gowe, 1990
	0.23	Gowe and Fairfull, 1995
Age at first egg (sexual maturity)	0.42	Manson, 1972
	0.41	Gowe and Fairfull, 1995
	0.25	Szydlowski and Szwaczkowski, 2001
Mature body weight	0.56	Manson, 1972
	0.54	Gowe and Fairfull, 1995
	0.32	Szydlowski and Szwaczkowski, 2001
Egg weight	0.59	Francesch et al., 1997
	0.48	Francesch et al., 1997
	0.50	Francesch et al., 1997
	0.49	Manson, 1972
	0.52	Gowe and Fairfull, 1995
Mortality	0.08	Manson, 1972
Feed efficiency	0.16	Manson, 1972
Shell quality	0.37	Gowe and Fairfull, 1995
Albumin score	0.44	Gowe and Fairfull, 1995
Blood spot incidence	0.05	Gowe and Fairfull, 1995

Table 1 indicates the following:

i.   The heritability of egg production varies considerably from 0.1 to 0.4 (Manson, 1972; Fairfull and Gowe, 1990; Gowe and Fairfull, 1995), which may be due to the fact that there is more than one way of defining this trait and that variation occurs with age or part record. For example the heritability of the early part record may differ from that of the lifetime record. The heritability of hen-housed egg production is lower than that of hen-day rate of egg production and survivor egg production and this is due to the effect of viability on hen-housed egg production (Fairfull and Gowe, 1990).

ii.   The heritability of egg weight lies between 0.45 and 0.55, with an average of 0.51. This is a reasonably high heritability indicating that progress can be made fairly quickly if selection is applied to this trait. Like egg production, the heritability varies with age or part record, however this variation is very small (Manson, 1972; Fairfull and Gowe, 1990; Gowe and Fairfull, 1995; Francesch et al, 1997).

iii.   As with egg weight, the heritability of body weight is also high (between 0.5 and 0.59) meaning that rapid progress is possible in this trait. Once again there is a slight variation depending on the age of the bird (Manson, 1972; Fairfull and Gowe, 1990; Gowe and Fairfull, 1995; Francesch et al, 1997).

iv.   Age at first egg also has a high heritability, with the value falling between 0.33 and 0.46; however, even though rapid progress is possible it is not desirable because of the physiological aspects previously mentioned (Manson, 1972; Fairfull and Gowe, 1990; Gowe and Fairfull, 1995; Francesch et al, 1997).

v.   Egg quality has a high economic value as well as a high heritability (0.33-0.39) and good progress is both possible and desirable (Gowe and Fairfull, 1995).

vi.   Traits with low heritabilities are mortality (0.10), feed efficiency (0.16) and blood spot incidence (0.05). These traits will show very slow progress if selection is practiced and

thus environmental factors may rather be altered to improve these traits (Manson, 1972; Fairfull and Gowe, 1990; Gowe and Fairfull, 1995; Francesch *et al*, 1997).

1.3.3.2 Genetic correlations

The genetic correlations between traits need to be considered. The genetic cause of correlations between traits is primarily pleiotropy (the property of a gene whereby it affects two or more traits), although linkage may also result in correlated traits (Falconer and Mackay, 1996). Traits can be negatively or positively correlated with other traits of economic importance and it is necessary to take these correlations into account when planning a breeding strategy (Sharma *et al*., 1998). There may also be genetic correlations between part records and whole or lifetime records for traits such as egg production. Correlations between part records and lifetime records for egg production are generally very high (between 0.56 and 1.00) meaning that an early part record will be a very good predictor of a lifetime record (Fairfull and Gowe, 1990).

1.3.3.3 Economic importance

The economic weight of a trait is also of importance in breeding programs. To optimise levels of genetic and economic improvement, traits are weighted according to their estimated contributions towards any economic profit when using a selection index. Those with the highest economic importance should be given greater consideration (Jiang *et al*., 1998). A small genetic gain in a trait of high economic value is more desirable than a large genetic gain in a trait with little economic value (Gowe and Fairfull, 1995).

In chickens there are a number of economically important traits that have an effect on the rate of egg production or the quality of the eggs produced. It is therefore important to have an idea of the heritability of each trait, correlations between traits and the relative economic importance of these traits before any breeding programs are implemented.

1.3.4 Environmental influences on egg production

All quantitative traits are influenced not only by a number of genes but also by a number of environmental factors. The environmental factors that influence egg production in chickens include nutrition, light, ambient temperature, water and freedom from disease (Fairfull and Gowe, 1990). Farmers need to employ management strategies that maintain these factors at optimum levels.

Commercial chickens are fed a simple, single nutritionally balanced diet. The diet usually varies, with the age of the birds. The diets of young chicks are high in protein and vitamins, whilst diets of growing birds are lower in both protein and vitamins and laying hens are fed diets that are high in calcium. Domestic birds also require a reliable supply of fresh water, as they do not gain as much water from their food as most wild birds would. Chickens can tolerate a wide range of temperatures (-1 to 37 degrees Celsius). In most systems, however, it is optimal to maintain a temperature of approximately 21 degrees Celsius for economic reasons, as it minimises food consumption (Appleby *et al.*, 1992).

Farmers may also manipulate day length or light cycles. The physiology of egg production is controlled hormonally (mainly by melatonin) and is mediated by day length. Artificial control of day length has two primary aims. Firstly, by using a constant but short day length during rearing, it can prevent birds from maturing too early. Birds that mature too early at too low a body weight will produce small eggs throughout their life (Spies *et al.*, 2000). The second aim is to keep birds in a state of breeding condition for an extended period to increase the number of eggs produced. This is achieved by increasing the day length (or light period) sharply once the birds have reached a desired weight (Fairfull and Gowe, 1990; Appleby *et al.*, 1992; Lewis *et al.*, 1999).

If these environmental factors are kept favourable the many genes that contribute towards egg production can act in ways that allow the chickens to fully express their genetic potential (Fairfull and Gowe, 1990). The farmer is then able to identify those birds with the best genetic potential, from their phenotype, and select them for breeding.

1.4 SELECTION STRATEGIES

Artificial selection, which involves selecting the best animals for breeding is one of the most important tools available for improving the biological and economical efficiency of a livestock population. Artificial selection aims to direct and accelerate biological changes in animals in order to meet the needs and desires of the human population (Lynch and Walsh, 2000).

There are a number of different methods available for the identification and selection of the best animals. These depend on the objectives of the breeder and the status of the population and its environment. The major methods of selection are individual or mass selection, family selection, within family selection, family-index or combined selection and multiple trait or index selection (Falconer and Mackay, 1996).

Individual selection, family selection, within family selection and family-index selection are all selection techniques that select for one trait at a time (Lynch and Walsh, 2000). In the case of egg production in chickens the most profitable trait to select for would be the number of eggs produced. The majority of single trait selection experiments for egg numbers have produced positive genetic progress (Fairfull and Gowe, 1990). Egg weight is also a trait that has commonly been used in single trait experiments and the majority of these have also shown positive genetic improvement (Fairfull and Gowe, 1990). However, correlations between traits, especially egg production traits in chickens tend to complicate single trait selection and it then becomes necessary to include more than one trait in the selection strategy, which is where multiple trait selection or index selection comes into use (Falconer and Mackay, 1996). Explanations of these techniques and the circumstances under which they may be appropriately used will be discussed in the following section.

1.4.1 Individual selection

Individual selection, otherwise known as mass selection, is the simplest and most common method in use (Lynch and Walsh, 2000). Individuals are selected based solely on their own phenotypic value. In most situations individual selection produces the most rapid response, especially when selecting for traits with high heritabilities, and should therefore be the method of choice (Rishell, 1997). There are, however, a number of cases where individual selection will not produce the best response. Traits with low heritabilities, where the environmental variance contributes greatly towards differences in phenotypes, will not respond well to individual selection. In addition individual selection may be impractical in many cases due to difficulties in measuring certain traits for example carcass traits in meat producing animals (Falconer and Mackay, 1996; Lynch and Walsh, 2000).

1.4.2 Family-based selection

Under those circumstances where individual or mass selection is impractical or ineffective breeders can incorporate a family-based scheme. Family-based selection makes use of information or measurements from an individual's relatives (Lynch and Walsh, 2000). It is assumed that there is a degree of relatedness between relatives and therefore the phenotypic value of an individual's relative is a source of information about that individuals breeding value. In traits with low heritabilities, where an individual's phenotypic value is a poor predictor of its breeding value it is often more accurate to use information from an individuals relatives to predict its breeding value (Rishell, 1997). An example of where family information needs to be used to predict breeding values is in milk yield in cattle. Milk yield cannot be measured in males so their breeding values need to be estimated using female relatives (Burnside et al., 1992; Falconer and Mackay, 1996). The breeding value of egg production in male chickens needs to be estimated in a similar way (Falconer and Mackay, 1996; Lynch and Walsh, 2000).

Family based designs are based on two components: the first being the difference between family means and the second is the difference between individuals within a family. Family based selection is therefore separated into three main designs. Firstly, between family selection where entire families are selected based on their phenotypic family mean. Secondly, within family selection, where individuals are selected based on deviations of their phenotypic value from the phenotypic mean of their family. Thirdly, family-index selection, where individuals are chosen based on a weighted index of between and within family components (Falconer and Mackay, 1996; Lynch and Walsh, 2000).

1.4.2.1 Between family selection

When using between family selection, whole families are ranked according to the mean phenotypic value of the family. Entire families, with the highest mean phenotypic values, are then selected. The selected families provide the parents for the next generation. The families used can be full sib families or half sib families (Falconer and Mackay, 1996; Tai *et al.*, 1996; Zhao *et al.*, 1997; Lynch and Walsh, 2000).

Traits with low heritabilities, and where individual-specific environmental effects (environmental effects unique to each individual) contribute greatly towards phenotypic variation, will respond better to between family selection than they will to individual selection. This is because environmental deviations of individuals in each family tend to cancel each other out in the family mean. The phenotypic family mean therefore comes closer to being a measure of the genotypic family mean. In addition, the larger the family size the greater the efficiency of family selection (Falconer and Mackay, 1996; Rishell, 1997; Lynch and Walsh, 2000).

One disadvantage of between family selection, however, is that a compromise has to be made between the intensity of selection (proportion of individuals selected out of the entire population) and the level of inbreeding. To keep inbreeding to a minimum many families should be selected, which decreases the selection intensity leading to decrease in the response to selection (Falconer and Mackay, 1996).

1.4.2.2   Within family selection

Within family selection requires the difference between the phenotypic value of an individual and the mean phenotypic value of the family to which it belongs to be calculated. Individuals with the highest deviations from their family means are selected as parents for the next generation. This method is most useful for traits with low heritabilities and when there is a large amount of environmental variation common to members of a family. Selection within families would help to eliminate this large non-genetic variation from the variation acted on by selection (Falconer and Mackay, 1996; Tai *et al.*, 1996; Rishell, 1997; Zhao *et al.*, 1997; Lynch and Walsh, 2000).

1.4.2.3   Family-index selection

When using family-index selection, or combined selection, a weighted index of the between family and the within family component is calculated for each individual, thus each individual will be assigned an index value that is a weighting of its family mean and its family deviation. Individuals with the highest index values are then selected as parents (Falconer and Mackay, 1996; Lynch and Walsh, 2000). The equation used to calculate the index value for an individual is:

$$I = P + \left\{ \frac{r-t}{1-r} \times \frac{n}{1+(n-1)t} \right\} \times P_f$$

Taken from Falconer (1996).

In this equation P is the phenotypic value of the individual, P_f is the deviation of the individual's family mean from the population mean, r is degree of relatedness between sibs, t is the intraclass correlation and n is the family size (Falconer and Mackay, 1996).

Combined selection is the method that should produce the best response. The reason for this is that this method of selection takes all the available information about an individual into account (Falconer and Mackay, 1996). Combined selection is a combination of individual selection and family selection and the advantages of both these methods will therefore apply. The problem with combined selection is that it is usually very costly. Thus although, theoretically, this method is the most efficient; it may not be the most economically or practically efficient selection method, especially in animal breeding where pedigree records (needed for combined selection) may be costly to obtain (Falconer and Mackay, 1996).

1.4.3 Index selection or multiple trait selection

This method of selection is useful in that multiple traits can be combined into an index value in a similar way to family-index selection. Individuals with the highest index values will be selected. For example, in chickens egg production, egg weight and body weight may be included in an index (Falconer and Mackay, 1996).

The problem with index selection is that the index values are difficult to calculate manually for each individual, especially if there are more than two traits in the index. This is because each trait needs to be assigned a weighting factor. The index of an individual can be estimated using the following equation:

$$I = b_1P_1 + b_2P_2 + b_3P_3 \ldots + b_xP_x$$

Taken from Falconer (1996).

The P values are the values of the various traits or measurements included and the b values are the weighting factors for each of the traits.

One difficulty is the determination of the optimum values of each weighting factor. In the determination of these weighting factors a number of parameters are taken into account, such as the genetic and phenotypic variances, correlations and covariances of each trait as well the economic weightings of each trait. Traits of high economic importance usually receive high weighting factors. The calculation of an index value is thus complex and is accomplished by using complicated matrices and regressions. However, there are now advanced computer software packages that are easily capable of making these calculations (Falconer and Mackay, 1996).

The advantage of using index selection is that no economically important traits will be ignored during selection and consequently no trait should experience negative progress unless negative progress for a trait is desired or if the genetic correlations between two traits are very highly negatively correlated. It is, however, difficult to make very rapid progress in any one trait, unless it is given a very high weighting.

1.5 RESPONSE TO SELECTION

The response to selection is usually given on a per cycle basis. A cycle begins with choosing the parents that will be used to form the next generation and ends with the formation of the offspring of those parents (Lynch and Walsh, 2000). The expected response to selection is the difference in population means between these two populations (the offspring and the parents) in other words it is the change in the population mean following selection (Lynch and Walsh, 1998). The response to selection is a measure of how the forces of selection (S) act upon the degree of inheritance (h^2). The response can therefore be represented as:

$$R = h^2.S \quad \text{(Lynch and Walsh, 1998)}$$

The force of selection (S) is otherwise known as the selection differential and is a measure of how much better the selected parents are in comparison to the entire population. It is the difference between the mean phenotypic value of the selected parents and the mean phenotypic value of the entire population. The selection differential is dependant on the standard deviation of the trait in the population (σ_p) as well as the proportion of the population selected as parents or the selection intensity (i) (Lynch and Walsh, 1998). The selection differential can thus be represented as:

$$S = i.\sigma_p \text{ (Lynch and Walsh, 1998)}$$

The response to selection can therefore be presented as:

$$R = i.h^2.\sigma_p \text{ (Lynch and Walsh 1998; Sharma } et\ al.,\ 1998)$$

Under individual selection this is generally the equation that is used to predict the response to selection. The goal of selection is to gain the maximum response (R) and the above equation indicates the parameters that need to be considered and manipulated in order to gain the maximum possible response.

The most rapid responses are illustrated in traits with high heritabilities. This is because traits with high heritabilities have a high proportion of their phenotypic variance made up of additive genetic variance meaning that it is possible to confidently select individuals with good phenotypes because a good phenotype will be a good predictor of a good genotype (Falconer and Mackay, 1996; Lynch and Walsh, 2000).

Traits with high phenotypic standard deviations (σ_p) will also show greater responses. The standard deviation is a measure of the variation in the population and is a property of both the population and trait under selection. In a population each individual has its own unique genetic make up and this is fixed throughout an individual's lifetime (with the exception of mutations). It is the genetic variation within the population (between individuals), however, that provides the variation for selection to work on (Siegel and Dunnington, 1997). Traits with higher standard

deviations will have a wider variety of individuals to choose from. This allows a smaller proportion of individuals to be selected that will be much better than the mean thereby increasing the selection intensity (i). It is therefore important to accurately rank the members of a population so that the parents selected will be those that are going to produce the best offspring (Falconer and Mackay, 1996).

Selection for a certain trait over a number of generations will result in a gradual improvement in the population mean of that trait provided all the above parameters are favourable. It will, however, also result in a decrease in the additive genetic variance in the population, because selection acts on and uses up the variance of a trait. This will slow the response to selection (R = $i.h^2.\sigma_p$), until eventually there will be too little variation left to gain any significant response (Sharma $et\ al.$, 1998; Lynch and Walsh, 2000).

The response to within family and between family selection is predicted in a similar way to individual selection, although the response equations differ in some respects. In the case of between family selection the phenotypic standard deviation is the standard deviation of family means (σ_f) and the heritability is the heritability of family means (h^2_f), giving the following response equation:

$$R_f = i.\,\sigma_f.h^2_f = i.\,\sigma_p.h^2 \times \sqrt{n\,\frac{1+(n-1)r}{[1+(n-1)t]}}$$

Taken from Falconer (1996).

When using within family selection the phenotypic standard deviation is the standard deviation of within family deviations (σ_w). Similarly, the heritability is the heritability of within family deviations (h^2_w) and the response equation is

$$R_w = i.\sigma_w.h^2_w = i.\sigma_p.h^2 \times (1-r) \times \sqrt{\frac{(n-1)}{[n(1-t)]}}$$

Taken from Falconer (1996).

The response equation for family-index selection or combined selection is then as follows:

$$R_c = i.\sigma_p.h^2 \times \sqrt{1 + \frac{(r-t)^2}{(1-t)} \times \frac{(n-1)}{1+(n-1)t}}$$

Taken from Falconer (1996).

For these family-based selection methods the response is now dependant upon a few additional parameters. These include the relationship between family members (r), (for full sibs $r = \frac{1}{2}$ and for half sibs $r = \frac{1}{4}$), the phenotypic correlation between family members (t) and the family size (n). In general the larger the family size the better the response to selection will be under family-based selection methods (Falconer and Mackay, 1996; Lynch and Walsh, 2000).

1.6 COMPUTER MODELS OR SIMULATIONS

The response of a population to different selection methods may be simulated using computer models. The words model and simulation are generally used interchangeably, however they do have slightly different meanings. A model is any representation or abstraction of a system or process (Starfield et al., 1990; Starfield and Bleloch, 1991). A simulation is a model that mimics

reality. It is a functional model of a system, device or process designed with the aid of a computer. A simulation is therefore the equivalent of a model designed on computer (a computer model) (Robinson, 1994). A more detailed definition of a computer model is a representation of relationships amongst variables by means of instruction codes that can be stored electronically and activated when the user requires a result to be evaluated from certain initial conditions (Kennewell, 2000).

Examples of simple everyday models include model airplanes and model ships. Although model airplanes and ships are no substitute for the real things they do provide useful insight into how the objects work and how the various parts making up the objects are interrelated. Computer models or simulations work in a similar way except that they are more complex and abstract and usually involve the use of mathematical formulae (Starfield and Bleloch, 1991).

The following is an example of a simple mathematic model that is used to simulate a real life situation. This equation models the process of converting U.S. dollars (D) to German marks (M).

$$M = kD \quad \text{(Starfield and Bleloch, 1991).}$$

A computer model consists of a number of variables and parameters. A variable is a value that varies as changes are made to the model. In the above equation M and D are variables. Variables may be input values, which are values we feed into the model (D is an input value) or output values, which are values the model returns (M is an output value). Models also contain a parameter or a number of parameters. A parameter is not a variable, it has to be estimated and entered into the model before we can use the model. A model is all about how certain variables change as the user changes other variables and it is the parameters that control this relationship between the variables in a model. In the above equation k is an example of a parameter. A fixed parameter is called a constant (Starfield et al., 1990; Starfield and Bleloch, 1991).

The function of a model is to define problems, organize thoughts, understand data, communicate and test that understanding and make predictions (Starfield et al., 1990; Starfield and Bleloch, 1991). A model also provides a very holistic picture of the object or system, and it allows the

whole system to be studied. However, all models have limits and they can never exactly mimic the real world (they are abstractions of the real world). They should therefore be developed with the intention that they behave as closely as possible to the actual scenario but at the same time should be used with caution (Starfield *et al.*, 1990; Starfield and Bleloch, 1991).

1.6.1 Development of a computer model

Firstly, a decision on what is to be modelled must be made. This requires a lot of research into the object or process being modelled. Secondly, it is important to evaluate the main components of the system and to determine how they interrelate. It is important to know what the input variables are and what the output variables are. The next step is to construct a mathematical model, which will usually be a number of mathematical equations describing the object or process. This mathematical model must then to be converted into a computer model, which requires a degree of knowledge about the computer software concerned. Lastly, values need to be fed into the model to see what results it gives under different conditions. This step is called simulation (Starfield *et al.*, 1990; Starfield and Bleloch, 1991).

1.6.2 Advantages of computer modelling

One of the major advantages of computer models, in general, is that they can easily predict the behaviour of the system under many different conditions, including conditions that are highly unexpected and seldom occur in nature. For instance in a population model of several species, a useful model will be one that could predict what would happen, for example, if a new predator arrived or if the reproduction rate for one of the species changed (Hastings, 1997).

Another advantage is that computer models can be altered. This may be necessary as an original model may produce results that do not compare favourably with what would be expected. If this is the case the model may be altered and rerun until the model best represents what is being modelled (Podlich and Cooper, 1998). This is an advantage because models are never going to

exactly mimic the real world but it is through trial and error that the best possible model can be designed (Starfield *et al.*, 1990; Starfield and Bleloch, 1991).

Furthermore, the use of computer models may allow scientists to gain a better understanding of a system. Models may reveal flaws in the way people understand the system and can be used to correct these flaws. A computer model may even result in new discoveries such as new mechanisms or behaviours in the system that were previously unknown (Starfield *et al.*, 1990; Starfield and Bleloch, 1991).

Some other advantages that computer models have over conventional models is that they are more accurate, they can be easily converted to and from graphic form, they are often cheaper, they can simulate a variety of material, they can output to peripheral equipment that can create actual products or sounds, they don't require physical tools and materials, they can be viewed from a variety of locations and they are easily transported and displayed (Kennewell, 2000).

In the study of quantitative genetics a number of simplifying assumptions are made in order to develop mathematical equations that describe population means and variances. Examples of such assumptions are the Hardy-Weinberg equilibrium assumptions, which include no mutation, no natural selection, no migration in or out of the population, infinitely large populations where all members of the population breed and where each member produces the same number of offspring and random mating. These assumptions are often considered to be vital for formulating workable expressions. However, they are also thought to impose a number of restrictions on quantitative genetic studies. The use of computer models is one way of relaxing these assumptions and therefore relaxing the restrictions imposed by them (Podlich and Cooper, 1998).

1.6.3   Limitations and disadvantages of computer models

Like every other type of model, a computer model is never going to be an exact replica of reality and must therefore be used with caution. Scientists need to be aware of the limitations of the models when drawing conclusions (Starfield *et al.*, 1990; Starfield and Bleloch, 1991).

One limitation is that computer models can be very complicated to design and often a degree in computer programming and mathematical skills is required. However, as technology increases computer programs become more and more user-friendly and many more people are able to make use of computer modelling. Although the solving of equations is precise, the formulation of equations is not, and with complex, badly understood systems the formulating of incorrect equations may lead to the creation of models that give inaccurate results (Kennewell, 2000).

A major problem with most models, especially in the non-physical sciences, is that there is usually insufficient data to run the model properly. Often modellers tend to try and adapt or constrain their models to fit the available data, which may lead to inaccurate models (Starfield *et al.*, 1990; Starfield and Bleloch, 1991).

In addition, it is often difficult to know where the boundaries or limitations of the model lie.   In other words a model will only be useful under certain conditions and these types of models cannot be relied upon when they are stretched to their limits (conditions where they are no longer useful). However, the fact that a model is only useful under certain limits or conditions does not detract from its usefulness within those conditions. In some cases such as the physical sciences these limits are usually clear and are not a problem. However, in other areas, such as many environmental systems, they are not so clear cut (Starfield *et al.*, 1990; Starfield and Bleloch, 1991).

Lastly, in all models a number of assumptions have to be made because it is simply impossible to include all factors in a model. These assumptions will decrease the accuracy of the model to a degree (Hastings, 1997).

1.6.4 Computer models in education

The theory of constructivism suggests that in order for meaningful learning to take place a student cannot simply obtain knowledge by reading it out of a text book or by formal lectures from a teacher. To prevent rote learning without understanding a student has to interact with new information, reorganize it, and relate it to previous knowledge (Mills, 2002). Meaningful learning is promoted when students have to think about and formulate their own ideas about what is being taught. Computer models enable students to develop their own understanding of concepts which may be difficult to grasp. Thus, models may be used, with proper supervision or guidance from a teacher, to enable students to construct their own ideas and knowledge (Kennewell, 2000; Mills, 2002).

There are a number of reasons as to why computer models have proven to be successful for teaching purposes. Firstly, they allow increased accessibility for students to common problems and provide user-friendly packages. Secondly students using computer models are able to accomplish tasks more quickly and more efficiently and thirdly, computer models are useful in helping students improve their understanding of abstract or difficult concepts (Mills, 2002). This is because a computer model has the ability to communicate a difficult subject in an alternate, simple way, due to their ability to calculate and simplify complex equations. In addition computer models can display a number of visual graphics, which can be discussed between pupils or between pupils and teachers. These displays are striking and easy to remember or fun to work with and will therefore leave a lasting impression on a young student (Kennewell, 2000).

Computer models are widely used to help students and scholars in their studies, especially in disciplines that are difficult to grasp, such as mathematics, statistics and introductory genetics (Kennewell, 2000; Mills, 2002; Soderberg, 2003). A good working knowledge of the basic concepts of all these disciplines is necessary for students to obtain an understanding of the applied subdisciplines of quantitative and population genetics (Soderberg, 2003).

Statistics is a subject that is considered difficult to learn by most students. It is, however, a vital tool for most university, or post secondary science students. At the tertiary level statistics is

required to understand, interpret and critically evaluate research data in many different disciplines, such as quantitative genetics. The need to employ effective methods of teaching statistics, especially the difficult or abstract concepts, in a variety of fields and to a variety of age groups is, therefore, ever increasing (Mills, 2002). Computer models have proven to be an effective method in helping students with their statistical analyses. Mills (2002) reported that students who used statistical computer software during their data analysis gained a more thorough understanding of statistical concepts and that computer modelling programs such as Microsoft Excel and Minitab are now invaluable to learners especially at the tertiary level. It has thus been recommended that computer models be used in the statistics classroom, along with other, simpler models, for example a physical model such as a coin or dice (Mills, 2002).

Kennewell (2000) reviews the use of computer models in mathematics and reports that students with unlimited access to computer models have shown consistently positive results. An example of where a computer model has been useful in education is the calculator (Kennewell, 2000).

Genetics is a subject that is also considered difficult to teach and learn. The applied subdisciplines of population genetics and quantitative genetics (which consist of a number of mathematical and statistical formulae) are thus rarely taught at high school level (Podlich and Cooper, 1998; Soderberg, 2003). For example, students generally find population genetic principles such as Hardy-Weinberg equilibrium confusing and boring to study (Soderberg, 2003). However, research has shown that computer simulations, based on models, may improve student understanding and increase their motivation to learn these numerically and cognitively demanding concepts. This is because the use of computer simulations for teaching population genetics improves graphing skills and the interpretation of different graphs (Soderberg, 2003). Computer models also help students to shift their thinking about genetics from an individual level to a population level and have revealed many misconceptions held by students, including some related to dominance, genetic drift, Hardy-Weinberg equilibrium and fixation (Soderberg, 2003). There are a number of computer models that are now widely used in the field of genetics. Examples of these include EVOLVE, which models the effect of natural selection on artificial populations (Soderberg, 2003), and QU-GENE, which is used for quantitative analysis of genetic models (Podlich and Cooper, 1998).

Thus, if population and quantitative genetics are taught with the aid of computer models, students may obtain a deeper understanding of how it is possible to change the mean value of a population over time, which is the aim of all plant and animal breeders. This change in the population mean requires knowledge of, for example, the variance of the population and the heritability of the trait. A useful model would be one that allows these parameters to be manipulated by the student and allows the resultant changes to be monitored.

The use of computer models in education is, however, a controversial topic. Although models are useful in simplifying complicated problems, caution must be taken not to allow students to become totally dependant on models. Teachers argue that by allowing students access to models they will not understand the theory or the working behind the models. Computer models should thus be used along with adequate guidance or supervision from a teacher (Kennewell, 2000).

1.7 USE OF COMPUTER MODELS IN DEVELOPING BREEDING STRATEGIES

The implementation of a breeding strategy is a costly and time consuming process and furthermore the results obtained from the strategy are of great importance to the breeder. It is thus important to implement the best possible breeding strategy that will reduce costs and time but maximise the results. To do this breeders need to predict what the best strategy is going to be and one way of doing this is by simulating a number of possible breeding strategies using computer models. The results that the models produce may not exactly match the results that would be obtained in reality, but they will help to guide the breeder towards making the correct decisions about which strategies to use under which conditions. A large amount of time and money may be saved, simply because the results of the models may have prevented an inefficient method of selection from being used.

1.8 MOTIVATION

The aim of this investigation was to develop computer models to simulate five different selection techniques, namely individual selection, between family selection, within family selection, family-index selection and index selection. The models could then be used to test the relative efficiencies of these selection techniques under different conditions.

These selection methods were tested on a randomly generated chicken population. The efficiencies of each selection technique were compared for four economically important traits, namely egg weight, egg production, body weight and age at first egg (AFE). These traits all had different heritabilities and different genetic and phenotypic variances.

This investigation therefore tested:

- The mean response to selection for each selection technique.
- The effect each selection technique has on the standard deviation.
- The genetic gain in each trait.
- The change in the standard deviation of each trait.
- The efficiency of each technique at different heritabilities.
- The merits of index selection and how two traits will respond when selected for simultaneously.

The computer models were saved on to a compact disk and may be incorporated by breeders when making selection decisions and in breeding programs, or they may be used for educational purposes for teaching students difficult concepts.

CHAPTER 2

MATERIALS AND METHODS

2.1 INTRODUCTION

Microsoft Excel 2000 was used to develop a number of computer models. The computer models that were developed were for individual selection, between family selection, within family selection, family-index selection and multiple trait or index selection. Four traits were used in the investigation; these traits were mature egg weight, mature body weight, lifetime egg production and age at first egg.

2.2 ASSUMPTIONS MADE IN THE DEVELOPMENT OF THE MODELS

One assumption was that the standard deviation used to generate each generation (except the first generation) was the standard deviation that was halfway between the standard deviation of the entire population and the standard deviation of the selected parents. The reason for this assumption was the standard deviation of the selected parents would be too low and furthermore the standard deviation of the entire population would be too high. A realistic estimate of the standard deviation of the next generation would be somewhere between these two values. This assumption was made for all the selection techniques except between family selection. Between family selection involves the selection of entire families. Most families will contain some above average individuals, some average individuals and some below average individuals. A variety of individuals will thus be chosen as parents, and the standard deviation of the selected parents will therefore be a realistic estimate of the standard deviation of the next generation.

Other assumptions include:

- The way in which individuals were allocated to families (explained on page 56). This assumption was made for between family selection, within family selection and family-index selection.

- In each generation it was assumed the selected parents were mated randomly amongst each other.

- It was assumed that the family size was 5 and that the families were half sib families making r = 0.25, although these two parameters can easily be changed if desired.

- Although the population size was fixed at 500 individuals and the family size was fixed at 5 it was assumed that there was no inbreeding during mating for all the selection strategies.

- In each generation it was assumed there were equal numbers of male and female birds.

- The models were also unable to incorporate the effect of the environment and therefore it was assumed that there were no environmental effects.

2.3 THE ORIGINAL POPULATION

A Microsoft Excel File was opened and named (saved as) "Starting population". On the first spreadsheet in this file ("Sheet 1") a table was set up to show the parameters of each trait.

- In cell F1 the column heading "Trait" was entered.

- In cell F2 the name "Mature egg weight" was entered.

- In cell F3 the name "Lifetime egg production" was entered.

- In cell F4 the name "AFE" was entered.

- In cell F5 the name "Mature body weight" was entered.

These were the four traits that were used in this study.

- In cells G1, H1, I1 and J1 the labels "h^2", "Mean", "Standard deviation" and "Economic weights" were entered respectively.

The heritabilities, the means and the standard deviations of these traits were taken from the literature (Fairfull and Gowe, 1990; Sharma *et al.*, 1998), and entered into the spreadsheet as illustrated in figure 2.1.

The economic weights, however, were calculated manually. To work out the economic weight of mature egg weight the value (number of cents) for a one-gram increase in egg weight was calculated in the following way:

It costs approximately 1000 cents for 12 eggs

1000 cents for 12 x 58.4 grams

1000 cents for 700.8 grams

1.427 cents for one gram

1.427 x 289.9 cents in every laying season

The value for a one gram increase in egg mass was therefore 1.472 cents (assuming that eggs cost R10:00 per dozen) and because hens lay on average 289.9 eggs in a laying season the value of a one gram increase in egg mass in one laying season is 413.69 cents. This value was entered into cell J2.

The economic weight of egg production was calculated by determining the value of a one percent increase in egg production in a laying season. A one percent increase would be approximately equal to 2.9 eggs or 169.36 grams (2.9 x 58.4). This equated to an increase of 241.68 cents (1.427 cents x 169.36) per laying season. This value was entered into cell J3.

For age at first egg the economic value was calculated assuming that every day sooner that a bird begins to lay will equal one egg. One day will therefore be worth 83.34 cents (58.4 grams x 1.427 cents). This value was entered into cell J4 as a negative value because the aim is to lower the number of days taken to reach sexual maturity.

A one kilogram increase in body mass was worth approximately 800 cents (assuming that chicken costs R8:00 per kilogram) when the hens were culled and marketed. The body

maintenance costs of a one kilogram increase in body mass, however, almost cancelled out the gain, and the economic value of a one kilogram increase in body mass was therefore zero. A zero was therefore entered into cell J3. The table produced is presented below:
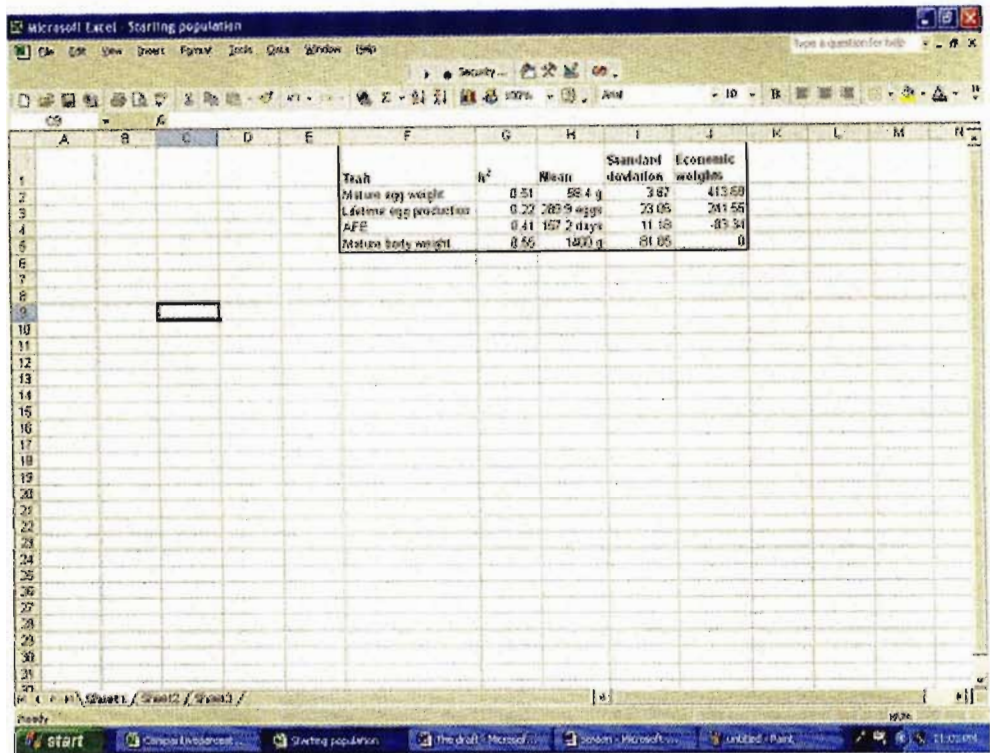
Figure 2.1   The range F1 to J5 in "Sheet 1" of the Microsoft Excel file "Starting population".

On the same spreadsheet a correlation matrix was set up and is illustrated in figure 2.2.

- In cell F7 the label "Genetic (above) and phenotypic (below) correlations" was entered.
- In cells F8 to F11 the names of the four traits were entered. The trait names were also entered, in the same order into cells G7, H7, I7 and J7.
- The genetic correlations, which were taken from the literature (Dalton, 1981), between each pair of traits were entered into the appropriate cells above the diagonal and the phenotypic correlations, also taken from the literature, were entered into the appropriate cells below the diagonal to produce the following correlation matrix:
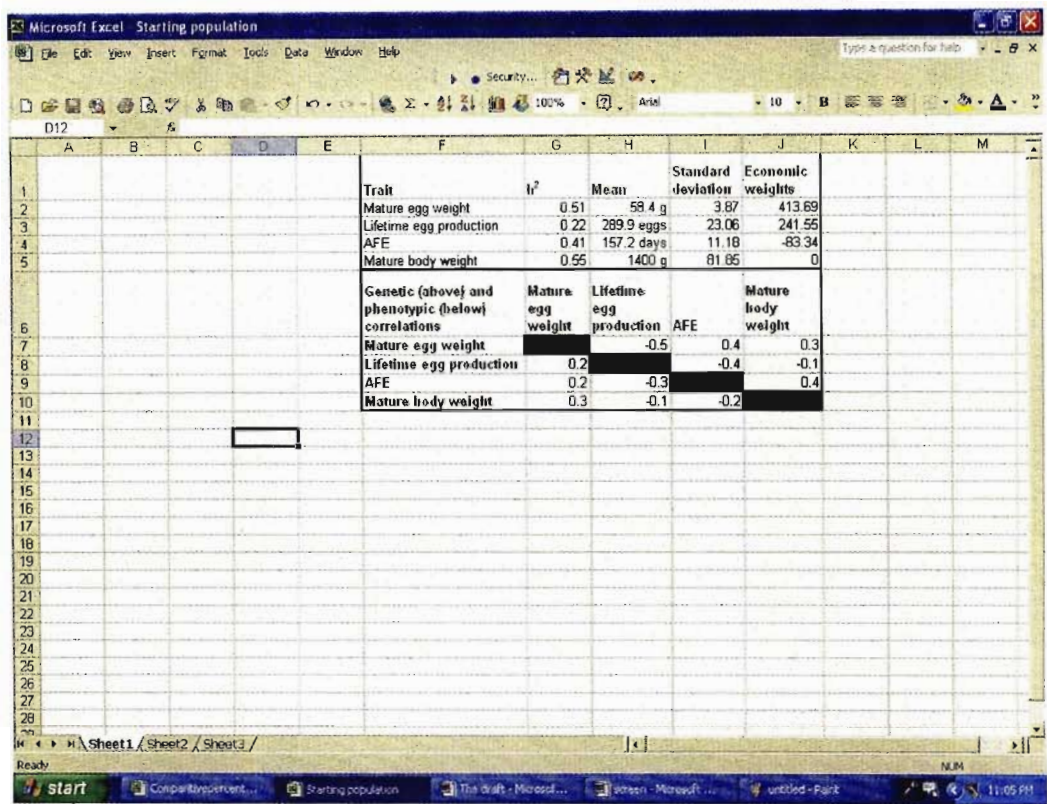
Figure 2.2   The range F6 to J11 in "Sheet 1" of the Microsoft excel file "Starting population".

On a separate spreadsheet ("Sheet 2") in the same file ("Starting population") four columns containing the values of the initial starting population were set up. The starting population consisted of 500 randomly generated individuals and for each individual the values of four traits were included. These four traits needed to be correlated with each other according to the correlation coefficients in figure 2.2. This was done as follows.

- In cell A1 a random number was entered using the following formula:

  "=SQRT(-2*LN(RAND()))*COS(2*3.141592653589*RAND()+RAND())"

- This formula was copied and pasted across to cell B1

- The formulae in cells A1 and B1 were each copied down for 500 cells so that there were two columns of 500 random numbers

- The first two traits to be correlated were egg weight and egg production, which have a correlation coefficient of r = -0.5.

- In cell D1 the following formula was entered.

=SQRT(1+(-0.5))/2*(A1+B1)+SQRT(1-(-0.5))/2*(A1-B1)

- In cell E1 the following formula was entered.

=SQRT(1+(-0.5))/2*(A1+B1)+SQRT(1-(-0.5))/2*(B1-A1)

- These formulae were each copied down for 500 cells so that there were two columns of random numbers that were correlated with each other (r = -0.5).

- The first column, representing egg weight, required a mean of approximately 58.4 and a standard deviation of approximately 3.87. The second column, representing egg production required a mean and standard deviation of approximately 289.9 and 23.06. Thus in cell G1 the following formulae was entered.

"=D1*3.87+58.4"

- And in cell H1 the following formula was entered.

"=F1*23.06+289.9"

- These formulae were each copied down for 500 cells.
- The values from columns A and B were copied and pasted as fixed values to columns J and K. The egg weight values in column G were copied and pasted as fixed values to column Q for later use.
- The formula that was entered into cell A1 was now entered into cell L1 and copied and pasted down for 500 cells so that there were two columns of fixed values and one column of random values in columns J, K and L.
- The next two traits which were to be correlated were AFE and egg production, with a correlation coefficient of r = -0.4.
- In cell N1 the following formula was entered.

=SQRT(1+(-0.4))/2*(K1+L1)+SQRT(1-(-0.4))/2*(K1-L1)

- In cell O1 the following formula was entered.

=SQRT(1+(-0.4))/2*(K1+L1)+SQRT(1-(-0.4))/2*(L1-K1)

- These formulae were each copied down for 500 cells so that there were two columns of random numbers that were correlated with each other with r = -0.4.
- The first column, representing egg production, required a mean of approximately 289.9 and a standard deviation of approximately 23.06. The second column, representing AFE,

required a mean and standard deviation of approximately 157.2 and 11.18 respectively. Thus, in cell R1 the following formula was entered.

```
=N1*23.06+289.9
```

- In cell S1 the following formula was entered.

```
=O1*11.18+157.2
```

- These two formulae were each copied down for 500 cells.
- Columns Q, R and S now contained values for egg weight (fixed values), egg production (random numbers) and AFE (random numbers) respectively.
- In cells S501, S502 and S503 the correlation coefficients were computed for egg weight and egg production, egg weight and AFE and egg production and AFE respectively using the following formulae:

"=CORREL(Q1:Q500,R1:R500)" " =CORREL(Q1:Q500,S1:S500)"
"=CORREL(R1:R500,R1:R500)"

- The F9 button was now pushed (this button changes each random number) until the best combination of correlation coefficients appeared (in other words until the three correlation coefficients best matched those in figure 2.2).
- Once the best correlations were determined, the values in columns J, K and L which produced the correlations, were copied and pasted as fixed values to the columns U, V

and W respectively. Columns R and S (egg production and AFE) were copied and pasted as fixed values to columns AD and AE respectively for later use.

- The formula that was entered into cell A1 was now entered into cell X1 and copied down for 500 cells so that there were three columns of fixed values and one column of random values in columns U, V, W and X.

- The final two traits to be correlated were egg weight and body weight, with a correlation coefficient of r = 0.3.

- The following formula was entered into cell Z1.

=SQRT(1+(0.3))/2*(U1+X1)+SQRT(1-(0.3))/2*(U1-X1)

- The following formula was entered into cell AA1.

=SQRT(1+(0.3))/2*(U1+X1)+SQRT(1-(0.3))/2*(X1-U1)

- These formulae were each copied down for 500 cells so that there were two columns of random numbers that were correlated with each other with r = 0.3.

- The first column, representing egg weight, required a mean of approximately 58.4 and a standard deviation of approximately 3.87. The second column, representing body weight, required a mean and standard deviation of approximately 1400 and 81.85 respectively. Thus, in cell AC1 the following formula was entered.

```
=Z1*3.87+58.4
```

- In cell AF1 the following formula was entered.

```
=AA1*81.85+1400
```

- Columns AC, AD, AE and AF contained the values for egg weight and body weight (both random numbers) and egg production, AFE (both fixed).

- The six different correlation coefficients between the four traits were computed in cells AF501 to AF506, in the manner described previously.

- The F9 button was pushed until the best correlation coefficients were determined, i.e., until the six correlations best matched the correlations in figure 2.2.

- Subsequently, the values in columns AC, AD, AE and AF which produced these correlations were then all copied and pasted as fixed values into the range A2 to D501 on "Sheet 1".

- The mean and standard deviation of egg weight was entered into cells A501 and A502 respectively, by entering the following formulae:

```
"=AVERAGE(A2:A501)"    "=STDEV(A2:A501)"
```

- Similarly the means and the standard deviations for the other three traits were determined and entered into cells B501, B502, C501, C502, D501 and D502.

- Appropriate headings were assigned to the four traits to produce the spreadsheet illustrated in figure 2.3.
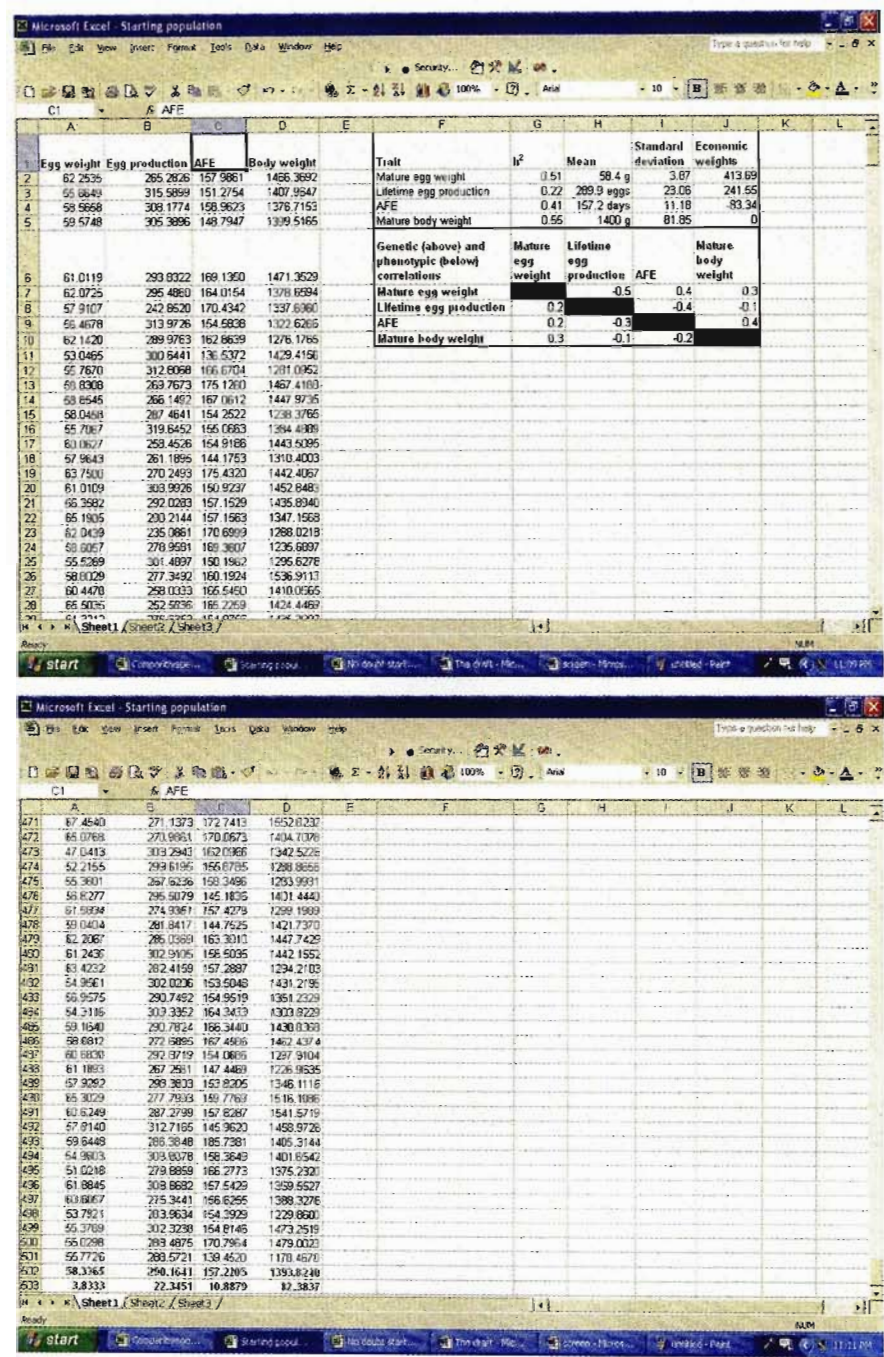
Figure 2.3 The range A1 to D503 in "Sheet 1" of the Microsoft excel file "Starting population".

2.4 INDIVIDUAL SELECTION

- A Microsoft excel file was opened and named "Model, Individual selection".
- The name of the first spreadsheet was changed from "sheet 1" to "Working".
- Cell A1 on this sheet was labelled "h^2", cell A2 was labelled "Proportion" and cell A3 was labelled "Intensity".
- The first trait that was used was egg weight. The heritability of egg weight (0.51) was entered into cell B1, the desired proportion of individuals selected (0.22) was entered into cell B2 and the selection intensity, which was determined using a selection intensity table and finding what value corresponded with 0.22 (the proportion selected), was entered into cell B3. The resultant spreadsheet is illustrated in figure 2.4.
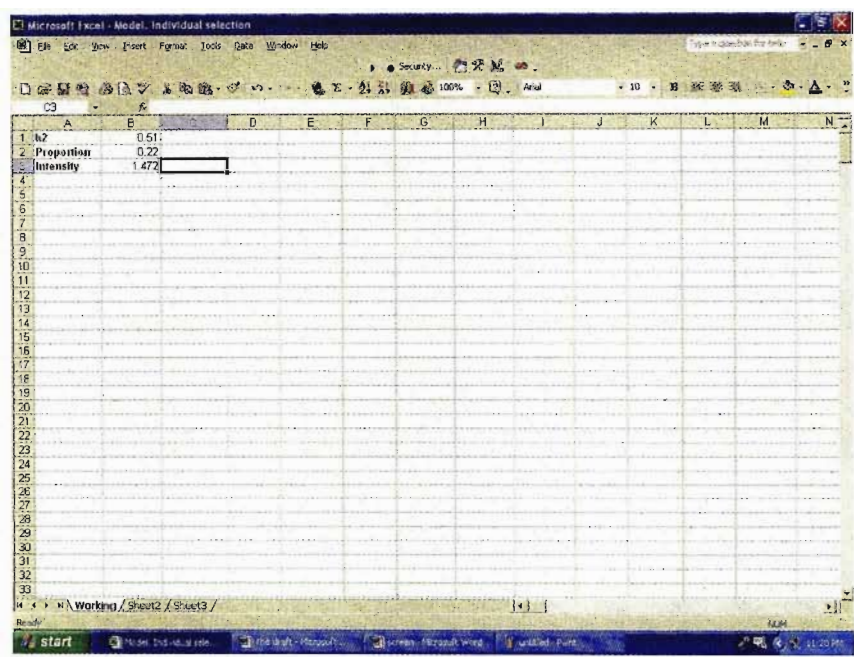
Figure 2.4   The range A1 to B3 in the "Working" spreadsheet of the Microsoft excel file "Model, Individual selection".

- Cell A5 was labelled "1", as it was the heading for the first generation.

- The values of the average egg weights of the 500 individuals in the first generation were represented in cells A6 to A505, with cells A506 and A507 representing the mean and the standard deviation respectively. Cells A6 to A507 were copied and pasted from the file "Starting population" (cells A2 to A503).

- In cell B6 the following formula was entered.

> "=PERCENTILE(A6:A505,1-$B2)"

- This formula took the values in cells A6 to A505 and computed a '1-B2' percentile value. The desired proportion selected was equal to the proportion of values in the range A6 to A505 that were greater than this percentile value.

- Cell B5 was labelled "Percentile". The spreadsheet at this point is illustrated in figure 2.5.
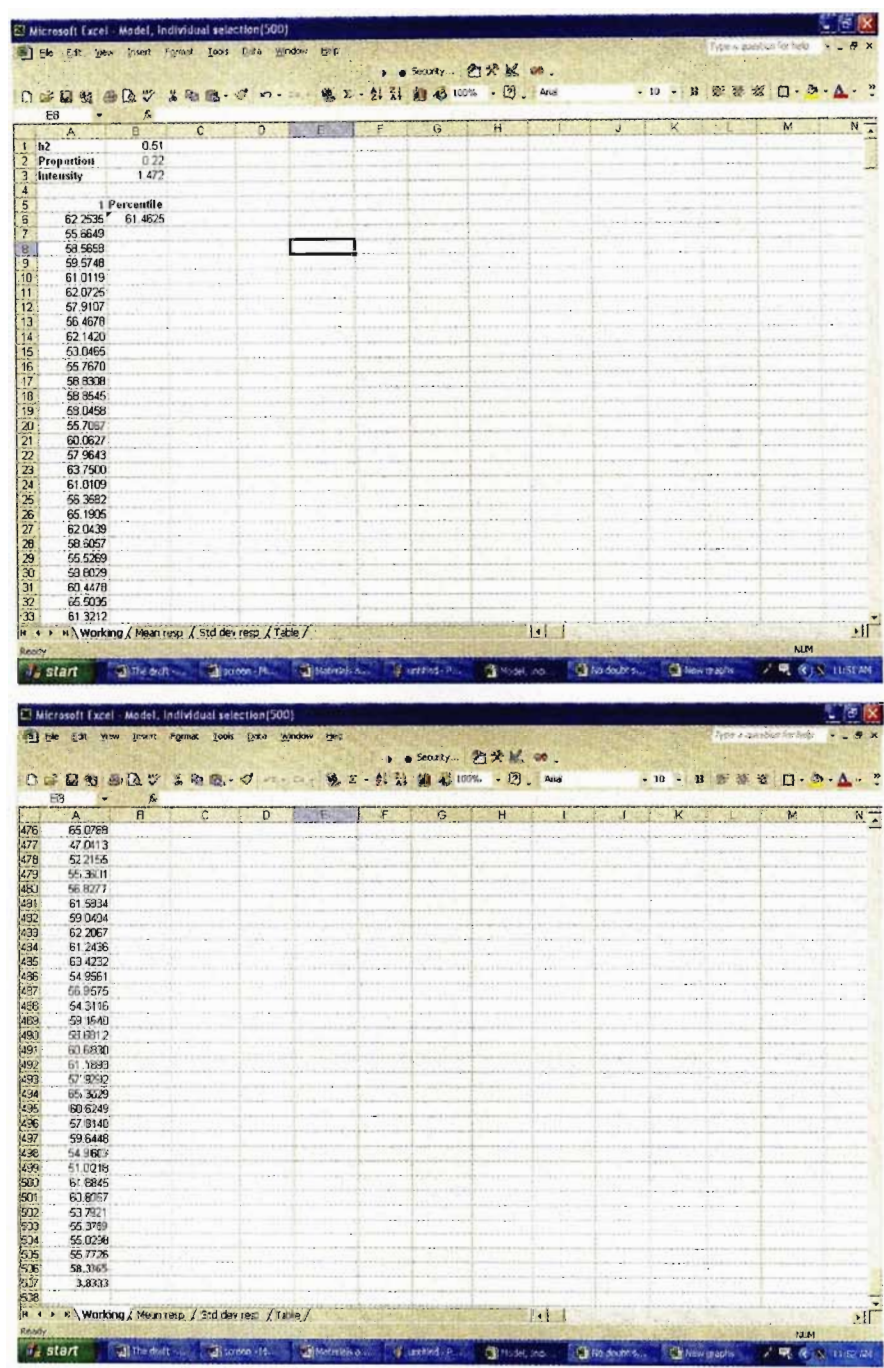
Figure 2.5   The range A1 to B507 in the "Working" spreadsheet of the Microsoft excel file "Model, Individual selection".

- In cell C6 the following formula was entered.

```
"=IF(A6>B$6,A6,0)"
```

- If the first individuals value for average egg weight (cell A6) was higher than the computed percentile (cell B6) then that individuals average egg weight value (cell A6) was displayed in cell C6, if it was lower than the percentile value then a '0' was displayed in cell C6.

- This formula was copied down for 500 cells, keeping the percentile value (cell B6) constant with the use of a dollar sign. The result being that the egg weight values of each of the 500 individuals was compared to the percentile value. This produced a column of numbers containing egg weight values for those individuals greater than the percentile and zeros for those individuals less than the percentile. The proportion of egg weight values in column C out of the 500 individuals was equal to the proportion specified in cell B2. Those cells containing values were the individuals that were to be used as parents for the next generation (the 22 percent of the population that had the highest egg weights).

- The label "Parents" was therefore entered at the top of this column (cell C5).

- Cell D5 was also labelled "Parents" and in cell D6 ">0" was entered.

- The mean of the parents (values in cells C6 to C505 that were not zeros) was computed in cell C506. This was done using the database average function and the equation that was entered into cell C506 was:

```
"=DAVERAGE(A5:C505,C5,D5:D6)"
```

- This formula took the average of all the values in column C5 that met the criteria specified in cell D6, which was ">0", and therefore computed the mean of all the egg weight values and ignored the zeros.

- In a similar way the standard deviation of the parents was computed in cell C507, the formula entered in this case was:

"=DSTDEV(A7:C507,C7,D7:D8)"

- In cell D506 the formula "=(C507+A507)/2" was entered, this formula computed a standard deviation that was half way between the standard deviation of the entire population (cell A507) and the standard deviation of the parents (cell C507). This was an assumption that had to be made in order to determine a realistic estimate of the standard deviation of the next generation. Figure 2.6 illustrates how the spreadsheet appeared at this point.
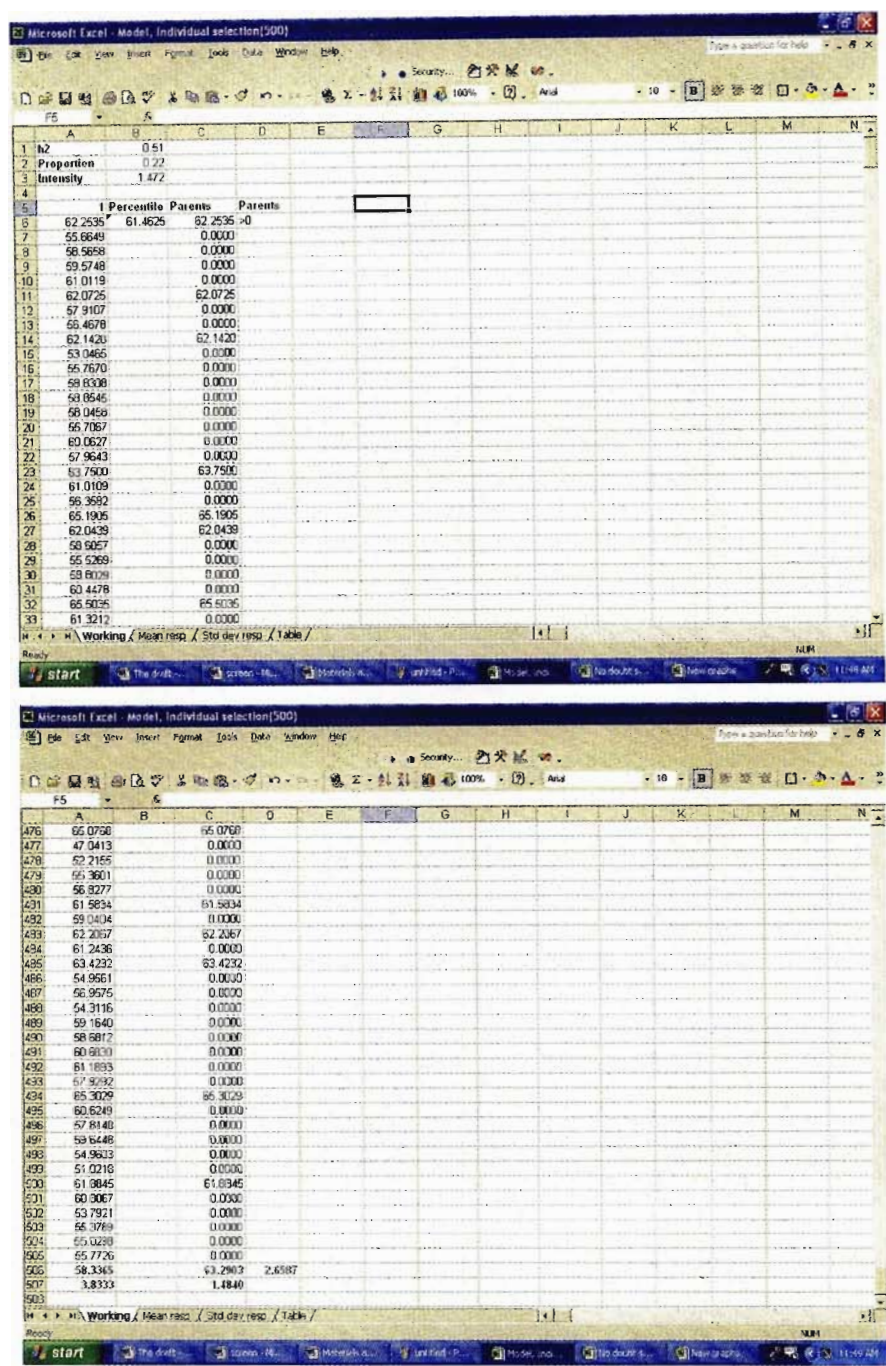
Figure 2.6 The range A1 to D507 in the "Working" spreadsheet of the Microsoft excel file "Model, Individual selection".

- Cell E5 was labelled "Ave P(Off)".

- The mean egg weight of the offspring of the following generation was calculated in cell E6. This was calculated by adding the response to selection for generation one to the mean value of generation one before selection using the following formula:

"=$B1*$B3*A507+A506".

Which represents the response formula $R = i.h^2.\sigma_p$ (Falconer and Mackay, 1996), added onto the mean of the previous generation.

Figure 2.7 illustrates the spreadsheet at this point.
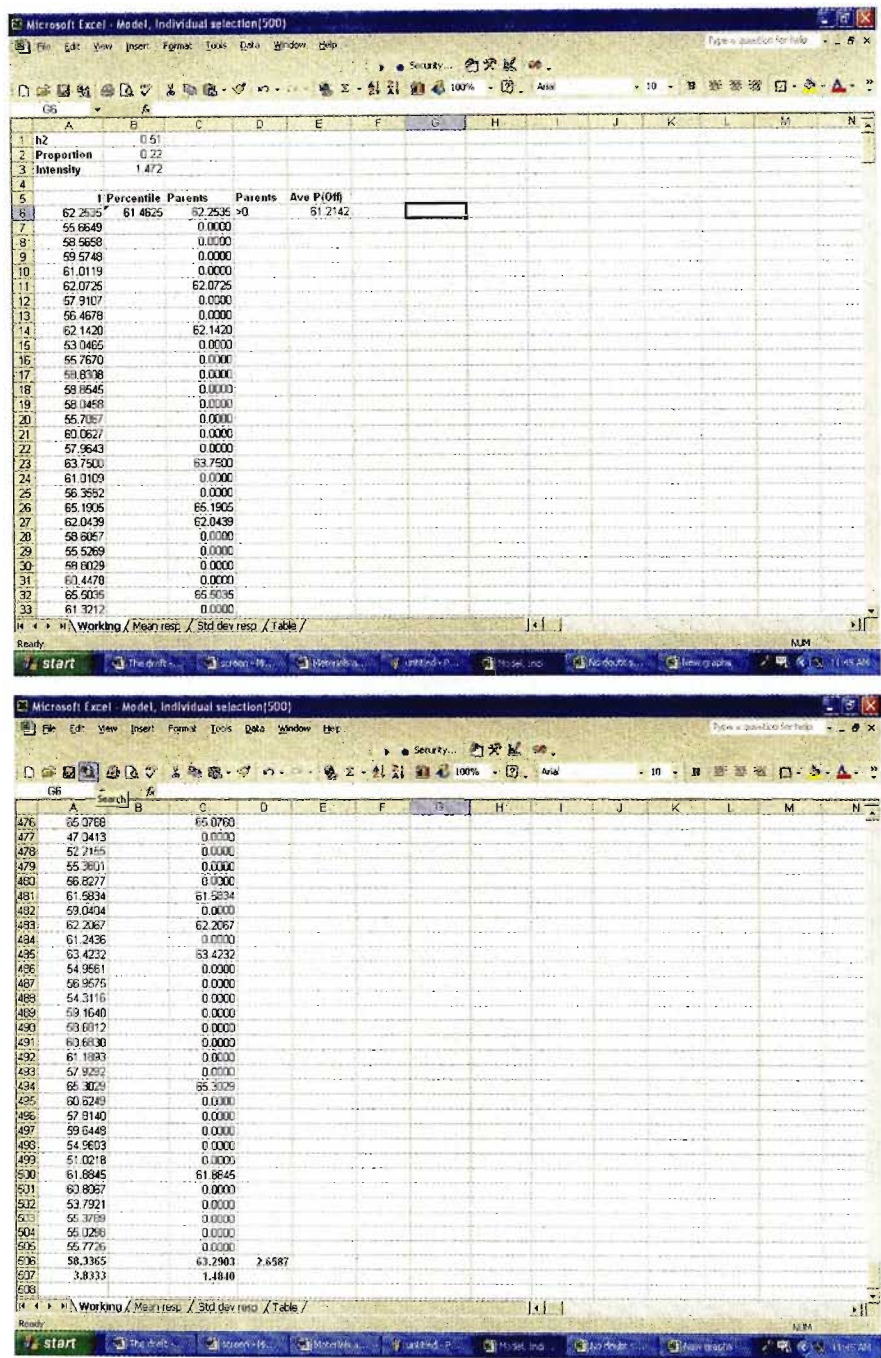
Figure 2.7 The range A1 to E507 in the "Working" spreadsheet of the Microsoft excel file "Model, Individual selection".

- In cell G5 the formula "=A5+1" was entered and the value computed by Microsoft excel was "2". This was the heading for generation two.

- The mean value of the offspring (cell E6) and the standard deviation (cell D506) was then used to randomly generate the next generation and the formula entered into cell G6 was:

"=(SQRT(-2*LN(RAND()))*COS(2*3.141592653589*RAND()+RAND()))*D$506+E$6".

- This formula was copied down for 500 cells to produce the second generation of 500 individuals. These values were random numbers, unlike the first generation, which was fixed.
- The mean and standard deviation of generation 2 was computed in cells G506 and G507 respectively using the following respective formulae:

"= AVERAGE(G6:G505)" "=STDEV(G6:G505)"

- The range B5 to E507 was then copied and pasted, as formulae, to the range H5 to K507, which is illustrated in figure 2.8.
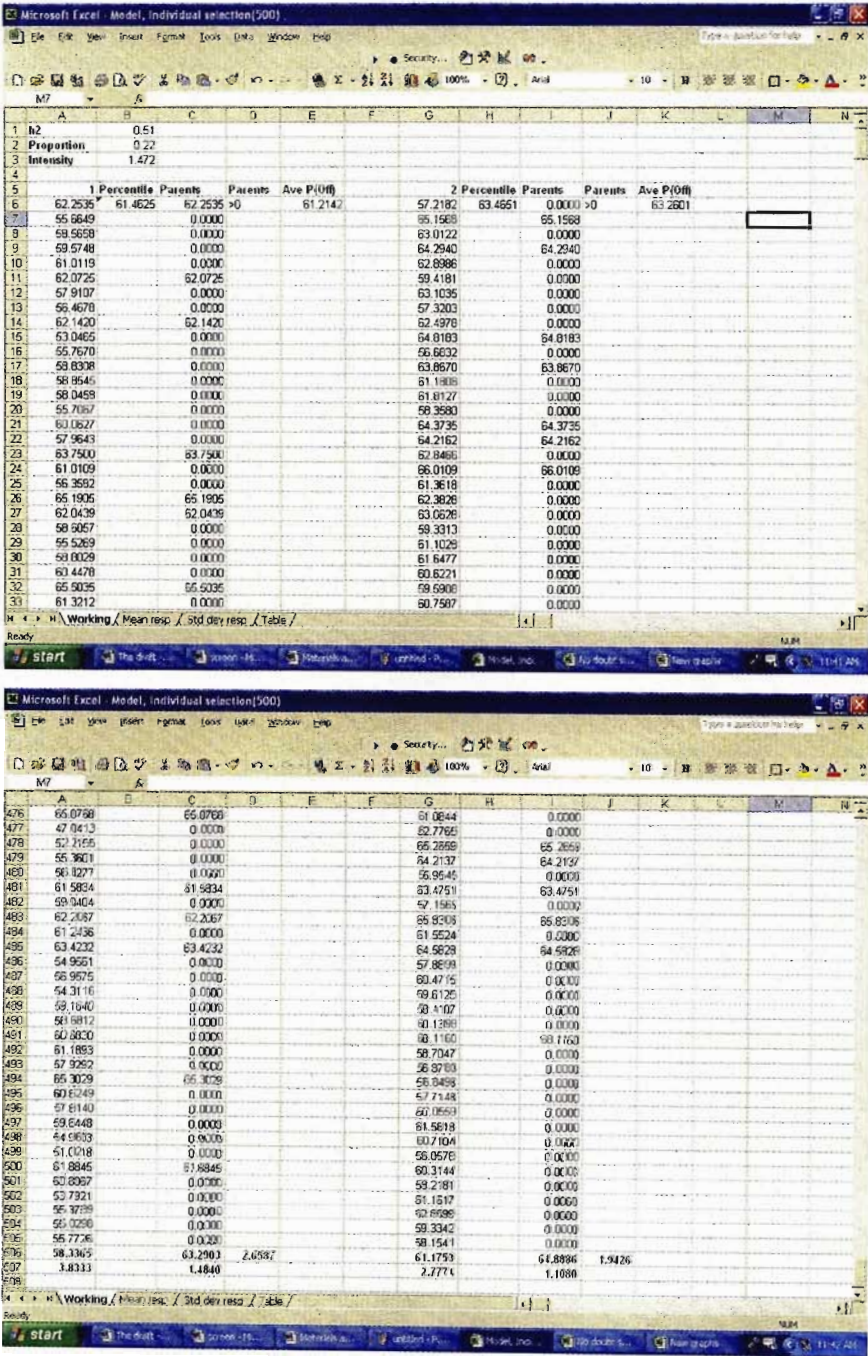
Figure 2.8   The range G5 to K507 in the "Working" spreadsheet of the Microsoft excel file "Model, Individual selection".

- The range G5 to K507 was then copied and pasted as formulae to the range M5 to Q507 and this range was then copied and pasted as formulae across to the next set of cells.

- This process was continued for 25 generations, as this provided sufficient time to study the selection response.

- The name of the next spreadsheet ("Sheet 2") was changed to "Table".
- On this spreadsheet cell A1 was labelled "Generation", cell B1 was labelled "Mean" and cell C1 was labelled "StDev".
- In cell A2 the number "1" was entered.
- In cell A3 the formula "=A1+1" was entered. This formula was then copied down until cell A26 so that the numbers 1 to 25 were entered in this column (these represented generation 1 to 25).
- In cell B2 the formula "=Working!A506" was entered. This formula meant that cell B2 (in the spreadsheet "Table") was equal to cell A506 in the "Working" spreadsheet, which was the mean of the first generation.
- The mean of the second generation was entered into cell B3 in a similar way ("=Working!G506") and the mean of the other 23 generations were entered into cells B4 to B26 similarly.
- In cell C2 the standard deviation of the first generation was entered using the formula ("=Working!A507").
- In cells C3 to C26 the standard deviations of generations 2 to 25 were entered in a similar way, and the resultant table is illustrated in figure 2.9.
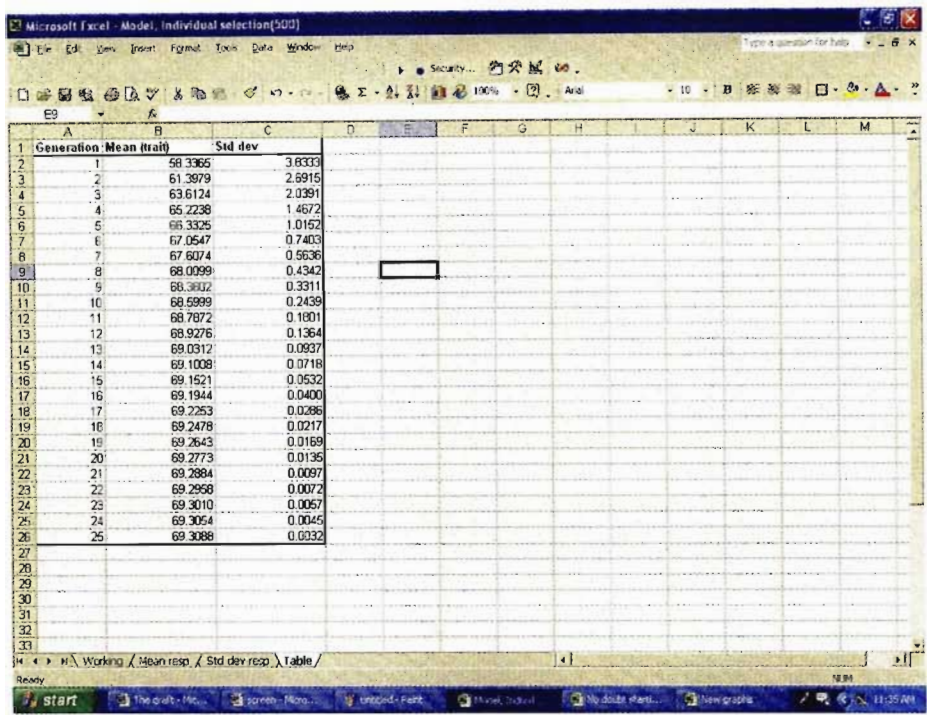
Figure 2.9 The range A1 to C26 in the "Table" spreadsheet of the Microsoft excel file "Model, Individual selection".

A graph showing the response in mean egg weight to individual selection was then set up in the following way.

- The active spreadsheet was still "Table".
- The "Chart wizard" option on the standard toolbar was selected, and a XY scatter plot was selected.
- The "series" tab was then selected.
- The values entered into the "X values" box were "=Table!$A2$:$A$26" and the values entered into the "Y values" box were "=Table!$B2$:$B$26".
- The "Next" button was then selected.
- Another dialog box appeared and the "Finish" button was selected.

The resulting graph plotted generation 1 to 25 on the X-axis against mean egg weight in each generation on the Y-axis.

- Under the "Chart" menu the "Chart location" option was selected.
- The "As new sheet" option was selected and the chart was named "Mean resp".

- Under the "Chart" menu the "Format plot area" option was selected and for "Border" the option "None" was selected, while for area a white colour was selected.
- Again the "Chart" menu" was selected, this time the "Chart options" option was selected.
- Under the "Titles" tab in the resulting dialog box appropriate titles were assigned.
- Under "Chart title" the title "Response in mean egg weight following individual selection" was entered, this was the title of the graph.
- Under "Value (X) axis" the title "Generation" was entered (the name of the X-axis) and under "Value (Y) axis" the title "Egg weight in grams" was entered (the name of the Y-axis).
- The "Gridlines" tab was then selected and all gridlines were removed.
- The "Legend" tab was then selected and the legend was also removed.
- The number of decimal places on the Y-axis was changed to two by right clicking on the Y-axis and selecting "Format axis", the "Numbers" tab in the resulting dialog box was selected and under "Category" the option "Number" was selected and in the "Decimal places" box "2" was entered.
- The data series, or curve was edited by right clicking on the curve and selecting "Format data series". In the resulting dialog box the "Patterns" tab was selected. In the "Style" box a circle was selected and in the "Size" box "3" was entered.

A graph showing the response in standard deviation was then set up. The procedure used was identical to the procedure used to set up the "Mean resp" graph, with the exception of the following:

- For this graph the values entered into the "Y-values" box were "=Table!$C2$:$C$26", which were the values of the standard deviations for each generation.
- Under "Chart location" this chart was placed as a new sheet and named "Std dev resp".
- The title of this chart was "Egg weight: Changes in standard deviation following individual selection" and the name given to the Y-axis this time was "Standard deviation".

Graphs of the mean response in egg weight to individual selection and the response in standard deviation were printed. A table of responses in mean egg weight and standard deviations of egg

weight was also printed. Because the whole model was based on random numbers each graph and each table would change every time F9 was pushed. For this reason 30 different copies of each table (and the graphs produced from those tables) were printed and using the mean egg weight value of generation 2 and generation 5 (cells B3 and B6 in the table respectively) average values for the mean egg weights at generation 2 and generation 5 were calculated for the 30 tables. The table that contained mean values at generation 2 and generation 5 closest to the average values that were calculated was then selected and the graphs produced from this table were also selected.

The file "Model, Individual selection" was saved. This model could now be used to produce results for the other three traits. The only changes that were made to the model, when using another trait were the following:

- The heritability (cell B1 in the "Working" spreadsheet) was changed according to the trait that was being used.

- The range A6 to A507 in the "Working" spreadsheet (which was the first generation and was a fixed set of values) was changed according to the trait's mean and standard deviation. The appropriate set of cells (depending on what trait was being used) from the file "Starting population" needed to be copied and pasted across into this range.

- The chart titles and the titles of the axes were also changed depending on what trait was used.

- In the case of the trait AFE the formula in cell B6 was changed to "=PERCENTILE(A6:A505,B2)" and the formula in cell C6 was changed to "=IF(A6>B$6,A6,0)". The formula in cell E6 was changed to "=A506-$B1*$B3*A507". This is because for age at first egg the aim was to lower the number of days to reach sexual maturity.

This model was then run for all four traits.

2.5   BETWEEN FAMILY SELECTION

- A new file was opened and saved as "Model, Between family selection". The method used to produce this model was similar to the method used to produce "Model, Individual selection".

- In this model, however, two new parameters were introduced into the "Working" spreadsheet, the degree of relatedness between sibs (r) and the family size (n). These values were entered into cells E1 and E2 respectively. In E1 "0.25" was entered because an assumption was made that half sibs were to be used and in cell E2 "5" was entered as this was the assumed family size.

- Cells D1 and D2 were labelled "r" and "n" respectively.

- Cells A5 to A507 were set up in the same way that they were set up in the case of individual selection, but in cell A508 the variance of cells A6 to A505 was calculated by entering the formula "=VAR(A6:A505)" into cell A508.

- This time a column was included to represent the family means. An assumption was made that the first five cells of the range A6 to A505 would represent the first family and the next five cells would represent the second family and the next five the third, this would continue so that there would be 100 families, each consisting of five consecutive individuals.

- Cell B5 was labelled "Family".

- In cell B6 the formula "=AVERAGE(A6:A10)" was entered.

- In cell B7 the formula "=B6" was entered this formula was copied down to the next three cells so that the five cells (B6 to B10) all had the same value, which was the average or the 'family mean' of cells A6 to A10, which were the individuals in the first family.

- The range B6 to B10 was then selected and copied. It was pasted onto the range B11 to B505. The range B6 to B505 represented the means of 100 families (each mean was repeated five times). Each individual in cells A6 to A505 had its family mean represented alongside it in cells B6 to B505.

- The variance of the family means (between family variance) was then calculated in cell B506 using the formula "=VAR(B6:B505)".

- In this case the percentile formula entered into cell C6 was:

```
"=PERCENTILE(B6:B505,1-$B2)"
```

- This formula took the values in cells B6 to B505 and computed a '1-B2' percentile value. The percentile value produced was therefore based on the family means and not the individual values.

- The following formula was entered into cell D6.

```
"=IF(B6>C$6,A6,0)"
```

- This formula functions so that if the family mean (cell B6) of individual one was greater than the percentile (cell C6) then the egg weight value (cell A6) of individual one was entered into cell D6, if not then a zero was entered into cell D6.

- This formula was copied down for 500 cells. The result was that the 22 percent of individuals with the highest family means were selected.

- The mean and standard deviation of this column were determined in the same way as they were in individual selection.

- In cell B509 the correlation of phenotypic values of members of a family (t) was computed using the equation "=B506/A508" (the between family variance divided by the total population variance) (Falconer and Mackay, 1996).

- Cell A509 was labelled "t".

- Cell A510 was labelled "h^2_b" (between family heritability).

- In cell B510 the following formula was entered to calculate the between family heritability.

"=$B1*((1+($E2-1)*$E1)/SQRT($E2*(1+($E2-1)*B511)))"

This formula represented the following formula taken from Falconer (1996):

$$h^2_f = h^2 \ x \sqrt{\frac{1+(n-1)r}{n\ [1+(n-1)t]}}$$

- The formula used to calculate the mean egg weight of the next generation was entered into cell F6. The formula was:

"=B510*$B3*A509+A508"

Which represents the response formula $R = i.h^2.\sigma_p$ (Falconer and Mackay, 1996) added onto the mean of the previous generation.

The resulting spreadsheet is illustrated in figure 2.10.
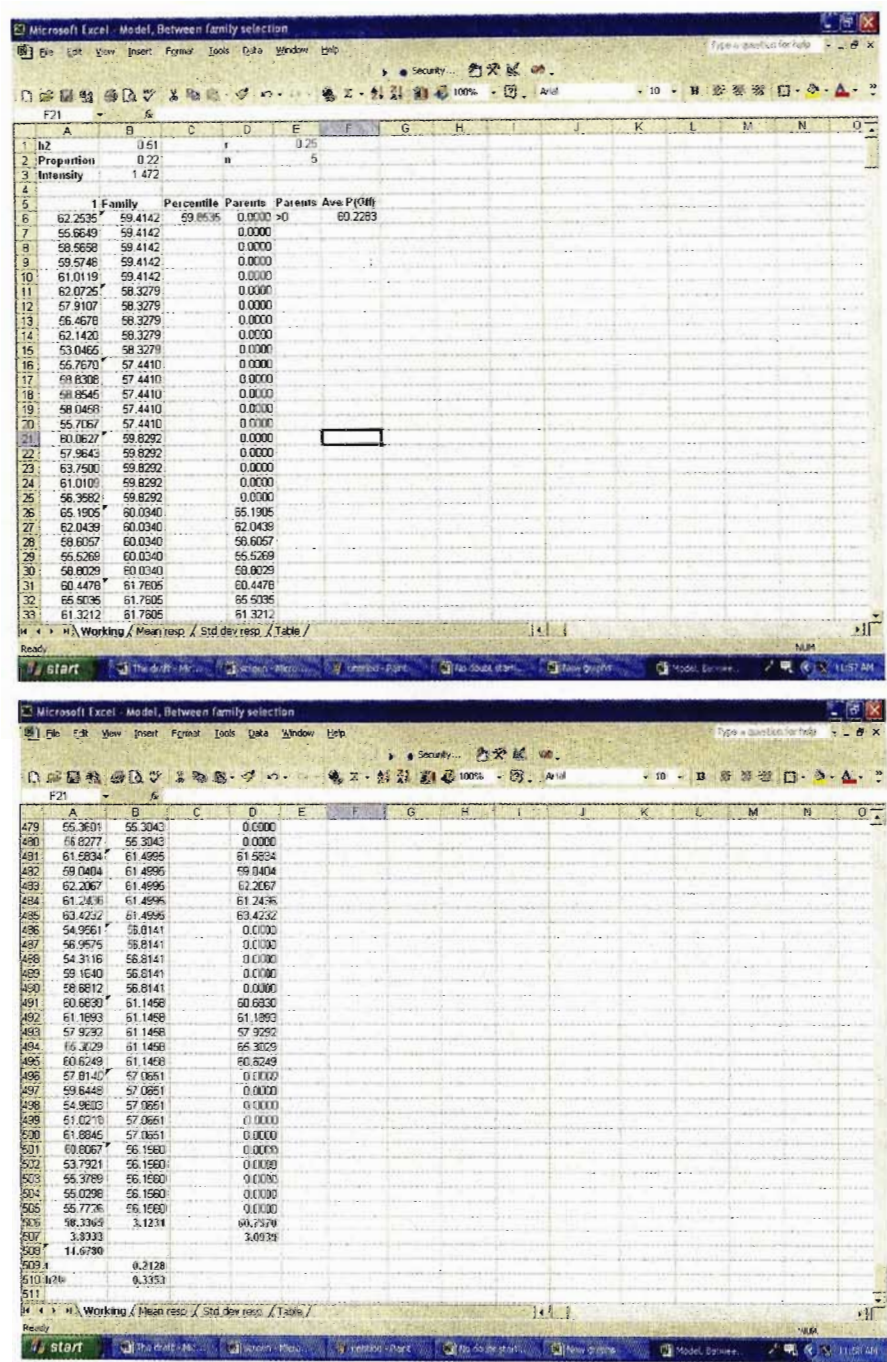
Figure 2.10 The range A1 to F510 in the "Working" spreadsheet of the Microsoft excel file "Model, Between family selection".

- In cell H5 the formula "=A5+1" was entered.
- The mean value of the offspring (cell F6) and the standard deviation (cell D507) was then used to generate the next generation and the formula entered into cell H6 was:

"=(SQRT(-2*LN(RAND()))*COS(2*3.141592653589*RAND()+RAND()))*D$507+F$6".

- This formula was copied down for 500 cells to produce the second generation of 500 individuals.
- The mean, standard deviation and variance of generation 2 was computed in cells H506, H507 and H508 respectively using the following respective formulae:

"=AVERAGE(H6:H505)" "=STDEV(H6:H505)" "=VAR(H6:H505)"

- The range B5 to F510 was then copied and pasted, as formulae, to the range I5 to M510.
- The 25 generations were then produced in the same way as they were in "Model, Individual selection".
- The table and graphs were set up and printed in the same way as was explained in "Model, Individual selection".
- Appropriate changes to chart titles and axis names were made. This model was then run for the other three traits, making the necessary changes that were explained previously.

2.6   WITHIN FAMILY SELECTION

- A new file was opened and saved as "Model, Within family selection".
- The range A1 to E3 and the range A5 to B509 (of the "Working" spreadsheet) were set up in the same way as they were in "Model, Between family selection".
- In cell C5 the heading "Difference" was entered.

- In cell C6 the formula "=A6-B6" was entered. The value computed in cell C6 as a result of this formula was individual one's phenotypic value (A6) subtract individual one's family mean value (B6).

- This formula was copied down for 500 cells so that the within family deviation was calculated for each of the 500 individuals.

- In this case the following percentile formula was entered into cell D6:

"=PERCENTILE(C6:C505,1-$B2)"

- This formula took the values in cells C6 to C505 and computed a '1-B2' percentile value. The percentile value produced was therefore based on the within family deviations.

- The following formula was entered into cell E6.

"=IF(C6>D$6,A6,0)"

- This formula functions so that if the within family deviation (cell C6) of individual one was greater than the percentile (cell D6) then the egg weight value (cell A6) of individual one was entered into cell D6, if not then a zero was entered into cell D6.

- This formula was copied down for 500 cells. The result was that the 22 percent of individuals with the highest within family deviations were selected.

- The mean and standard deviation of this column was calculated in the same way as they were in individual selection.

- In cell A510 the heading "h^2_w" was entered.

- In cell B510 the formula entered to calculate the within family heritability was:

"=$B1*(1-$E1)*SQRT(($E2-1)/($E2*(1-B511)))"

This formula represented the following formula taken from Falconer (1996):

$$h^2_w = h^2 \times (1-r) \times \sqrt{\frac{(n-1)}{[n(1-t)]}}$$

- In cell F506 the formula "=(E507+A507)/2" was entered. This formula calculated a standard deviation that was halfway between the standard deviation of the entire population (cell A507) and the standard deviation of the selected parents (cell E507).
- The formula used to calculate the mean egg weight of the next generation was entered into cell G6. The formula was:

"=B510*$B3*A509+A508"

Which represents the response formula $R = i.h^2.\sigma_p$ (Falconer and Mackay, 1996), added onto the mean of the previous generation.

Figure 2.11 illustrates how the spreadsheet appeared.

Figure 2.11   The range A1 to G510 in the "Working" spreadsheet of the Microsoft excel file "Model, Within family selection".

- In cell I5 the formula "=A5+1" was entered.
- The mean value of the offspring (cell G6) and the standard deviation (cell F506) was then used to generate the next generation and the formula entered into cell G6 was:

"=(SQRT(-2*LN(RAND()))*COS(2*3.141592653589*RAND()+RAND()))*F$506+G$6".

- This formula was copied down for 500 cells to produce the second generation of 500 individuals.
- The mean, standard deviation and variance of generation two was computed in cells I506, I507 and I508 respectively using the following respective formulae:

"=AVERAGE(I6:I505)" "=STDEV(I6:I505)" "=VAR(I6:I505)"

- The range B5 to G510 was then copied and pasted, as formulae, to the range J5 to O510.
- The 25 generations were then produced in the same way as they were in "Model, Individual selection".
- The table and graphs were set up and printed in the same way as was explained in "Model, Individual selection".
- Appropriate changes to chart titles and axis names were made.
- This model was then run for the other three traits, making the necessary changes that were explained previously.

2.7 FAMILY-INDEX SELECTION

- A new Microsoft excel file was opened and saved as "Model, Family-index selection".
- The ranges A1 to E3 and A5 to B509 (of the "Working" spreadsheet) were set up in the same way as they were in "Model, Between family selection".
- In cell C5 the heading "Pf" was entered.

- In cell C6 the formula "=B6-A$506" was entered. This formula computed the difference between the family mean of individual one (cell B6) and the population mean (cell A506).
- This formula was copied down for 500 cells and in each of these cells the population mean was kept constant due to the dollar sign.
- In cell D5 the heading "Index value" was entered.
- In cell D6 the following formula to calculate the family-index value of individual A6 was entered:

"=A6+(((E$1-B$509)/(1-E$1))*(E$2/(1+(E$2-1)*B$509)))*C6"

This formula represented the following formula taken from Falconer (1996):

$$I = P + \left\{ \frac{r - t}{1 - r} \times \frac{n}{1 + (n-1)t} \right\} \times P_f$$

- This formula was copied down for 500 cells so that an index value was calculated for each of the 500 individuals.
- The following percentile formula was entered into cell E6:

"=PERCENTILE(D6:D505,1-$B2)"

- This formula therefore produced a percentile value that was based on the index values in column D.
- The following formula was entered into cell F6:

```
"=IF(D6>E$6,A6,0)"
```

- If the index value of individual one (cell D6) was greater than the percentile (cell E6) then the egg weight value (cell A6) of individual one was entered into cell F6, if not then a zero was entered into cell F6.

- This formula was copied down for 500 cells. The result was that the 22 percent of individuals with the highest index values were selected.

- The mean and standard deviation of this column were calculated in the same way as they were in individual selection.

- In cell A510 the heading "h^2_{FI}" was entered.

- In cell B510 the following formula to calculate the family-index heritability was entered:

"=$B1*(SQRT(1+((($F1-B509)*($F1-B509))/(1-B509))*(($F2-1)/(1+($F2-1)*B509))))".

This formula represented the following formula taken from Falconer and Mackay, 1996:

$$h^2_c = h^2 \times \sqrt{1 + \frac{(r-t)^2}{(1-t)} \times \frac{(n-1)}{1+(n-1)t}}$$

- In cell G506 the formula "=(E507+A507)/2" was entered. This formula calculated a standard deviation that was halfway between the standard deviation of the entire population (cell A507) and the standard deviation of the selected parents (cell E507).

- The formula used to calculate the mean egg weight of the next generation was entered into cell H6 as:

"$B3*A507*B510+A506"

This formula represented the formula, $R = i.h^2.\sigma_p$, taken from Falconer (1996), added to the mean of the previous generation.

The spreadsheet is illustrated in figure 2.12.
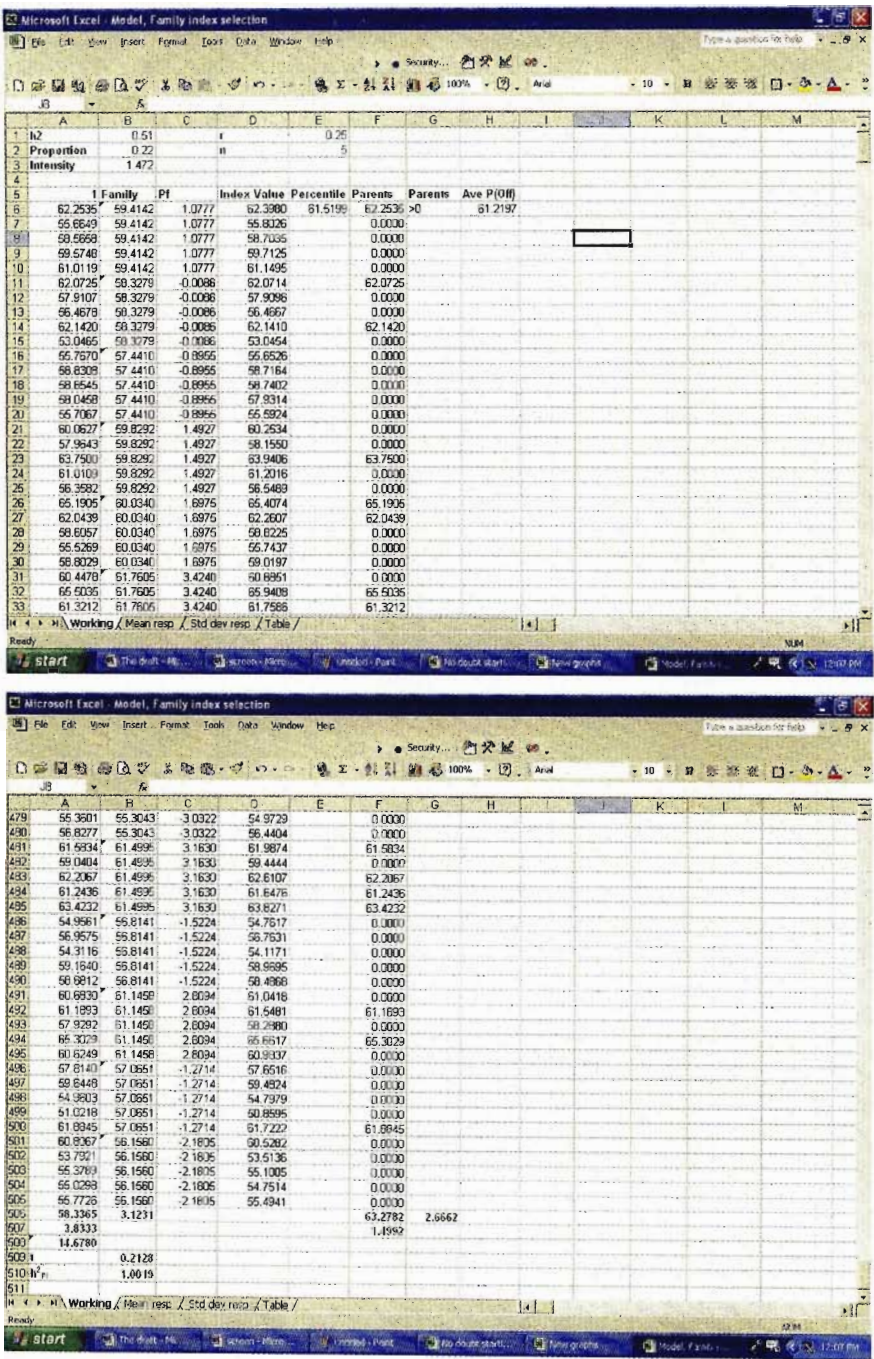
Figure 2.12 The range A1 to H507 in the "Working" spreadsheet of the Microsoft excel file "Model, Family-index selection".

- In cell J5 the formula "=A5+1" was entered.
- The mean value of the offspring (cell H6) and the standard deviation (cell G506) was then used to generate the next generation and the formula entered into cell J6 was:

> "=(SQRT(-2*LN(RAND()))*COS(2*3.141592653589*RAND()+RAND()))*G$506+H$6".

- This formula was copied down for 500 cells to produce the second generation of 500 individuals.
- The mean, standard deviation and variance of generation two was computed in cells J506, J507 and J508 respectively using the following respective formulae:

> "=AVERAGE(J6:J505)" "=STDEV(J6:J505)" "=VAR(J6:J505)"

- The range B5 to G510 was then copied and pasted, as formulae, to the range J5 to O510.
- The 25 generations were then produced in the same way as they were in "Model, Individual selection".
- The table and graphs were set up and printed in the same way as was explained in "Model, Individual selection".
- Appropriate changes to chart titles and axis names were made.
- This model was then run for the other three traits, making the necessary changes that were explained previously.

2.8 INDEX SELECTION

- A new Microsoft excel file was opened and saved as "Model, Index selection".
- This method will be explained using the traits egg weight and egg production.
- The name of the first spreadsheet was changed from "Sheet 1" to "b-values". The purpose of this spreadsheet was to calculate the b-values that were to be used in the index.

- In cell A7 of the spreadsheet "b-values" the heading "P" was entered, this heading represented the phenotypic matrix. Cells A8, B8, A9 and B9 were the cells into which the values of the phenotypic matrix were going to be entered.

- In cell D7 the heading "G" was entered, this represented the genotypic matrix. Cells D8, D9, E8 and E9 were the cells into which the values of the genotypic matrix were going to be entered.

- In cell G7 the heading "a" was entered. This heading represented the economic weights matrix. Cells G8 and G9 were the cells into which the economic weights of each trait were going to be entered.

- In cell I7 the heading "b" was entered and cells I8 and I9 were the cells in which the b-values would be displayed.

- Cells C8 and C9 were then merged, by highlighting the two cells, and then selecting the "Format" menu.

- The "Cells" option was then selected.

- In the dialog box that appears the "Alignment" tab was selected and the "Merge cells" option was selected.

- An "x" was then entered into the merged cell.

- The "x" was centred using the "Centre" button on the standard toolbar and the font size was changed to 20. The "x" represented a multiplication sign.

- In cells F8 and F9 the same procedure was followed.

- In cells I8 and I9 the same procedure was followed except that "=" was typed in instead of "x". Figure 2.13 illustrates how the spreadsheet appeared.
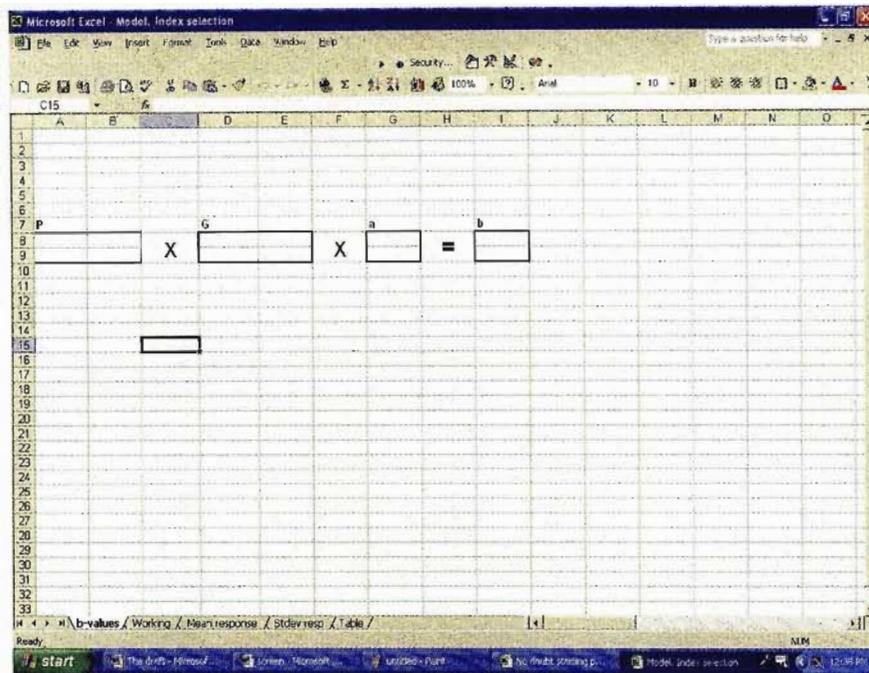
Figure 2.13 The range A7 to I9 in the "b-values" spreadsheet of the Microsoft excel file "Model, Index selection".

- In cell A8 the phenotypic variance of egg weight was entered. This value was obtained by taking the standard deviation of egg weight (cell I2 from the file "Fixed starting population") and squaring it.

- In cell B9 the phenotypic variance of egg production was entered similarly (cell I3 from the file "Fixed starting population").

- In cells A9 and B8 the phenotypic covariance between the two traits was entered. The phenotypic covariance was equal to the phenotypic correlation between the two traits (cell G9 in the "Fixed starting population" file) multiplied by the standard deviation of each trait. These values made up the P-matrix.

- The genetic variances of egg weight and egg production were entered into cells D8 and E9 respectively. The genetic variance of egg weight was calculated by multiplying the heritability of egg weight (cell G2 in the "Fixed starting population" file) by the phenotypic variance of egg weight (cell A8). The genetic variance of egg production was calculated by multiplying the heritability of egg production (cell G3 in the "Fixed starting population" file) by the phenotypic variance of egg production (cell B9).

- The genetic covariance between the two traits was entered into cells D9 and E8. The genetic covariance was calculated by multiplying the genetic correlation between the two traits (cell H8 of the "Fixed starting population" file) by the genetic standard deviation of each trait. The genetic standard deviation of egg weight was the square root of the genetic variance of egg weight (cell D8). The genetic standard deviation of egg production was the square root of the genetic variance of egg production (cell E9). These values made up the G-matrix.

- In cell G8 the economic weight of egg weight (cell J2 in the "Fixed starting population" file) was entered.

- In cell G9 the economic weight of egg production (cell J3 in the "Fixed starting population" file) was entered. These values made up the a-matrix.

- Once all these values had been entered the "Tools" menu was selected and the "Macro" option was selected.

- The "Record macro" option was then selected and the name "b-values" was entered into the "Macro name" box (the matrix algebra that had to be done to get the b-values was going to be recorded by the "b-value" macro).

- The "OK" button was then pushed. Every keystroke that was made from that point was then recorded by the macro until the "stop" button, which appeared in a separate dialog box, was pushed.

While the macro was recording the P-matrix (cells A8, A9, B8 and B9) was inverted.
- This was done by entering the formulae "=A8", "=B8", "=A9" and "=B9" into the cells W2, X2, W3 and X3 respectively.
- In cells Y2 and Z3 a "1" was entered.
- In cells Z2 and Y3 a "0" was entered.
- In cells W5 and W6 the formulae "=W2/$W2" and "=W3" were entered.
- Cell W5 was then copied and pasted across for three cells to the right so that cells W2, X2, Y2 and Z2 were all divided by W2.
- The cell W6 was also copied and pasted across for three cells.
- In cells W8 and W9 the formulae "=W5" and "=W6-($W6*W5)" were entered.
- These two cells were then copied and pasted across to the right for three cells.

- In cells W11 and 12 the formulae "=W8" and "=W9/$X9" were entered.
- These two cells were then copied and pasted across for three cells to the right.
- In cells W14 and W15 the formulae "=W11-($X11*W12)" and "=W12" were entered.
- These two cells were then copied and pasted across for three cells to the right.
- The values in cells Y14, Y15, Z14 and Z15 were the values of the inverted P-matrix.

The inverted P-matrix was then multiplied by the G-matrix (cells D8, D9, E8 and E9) as follows:

- In cell Y17 the formula "=Y14*D8+D9*Z14" was entered.
- In cell Y18 the formula "=Y15*D8+D9*Z15" was entered.
- In cell Z17 the formula "=Y14*E8+E9*Z14" was entered.
- In cell Z18 the formula "=Y15*E8+E9*Z15" was entered.
- The values in cells Y17, Y18, Z17 and Z18 were the values of the P^{-1} x G matrix.

The P x G matrix was then multiplied by the a-matrix (cells G8 and G9).

- In cell I8 the formula "=G8*Y17+Z17*G9" was entered.
- In cell I9 the formula "=G8*Y18+Z18*G9" was entered.
- The "Stop" button was then pushed and the "b-values" macro stopped recording. The output value in cell I8 was the b-value for trait 1 (egg weight in this case) and the output value in cell I9 was the b-value for trait 2 (egg production in this case).

A macro button was then inserted as follows:

- The mouse pointer was placed on the toolbar at the top of the screen and the right mouse button was clicked, a list appeared.
- The "Forms" option on the list was chosen and the "Button" option on the resulting dialog box was then selected.
- The mouse cursor was then placed on the top left hand corner of cell B2 and dragged four cells down and two cells across to produce a button that covered eight cells.
- The macro "b-values" was then assigned to that button.
- The button text was then edited to say "Calculate economic weighting factors (b1 and b2)". Figure 2.14 illustrates how the resulting spreadsheet appeared.
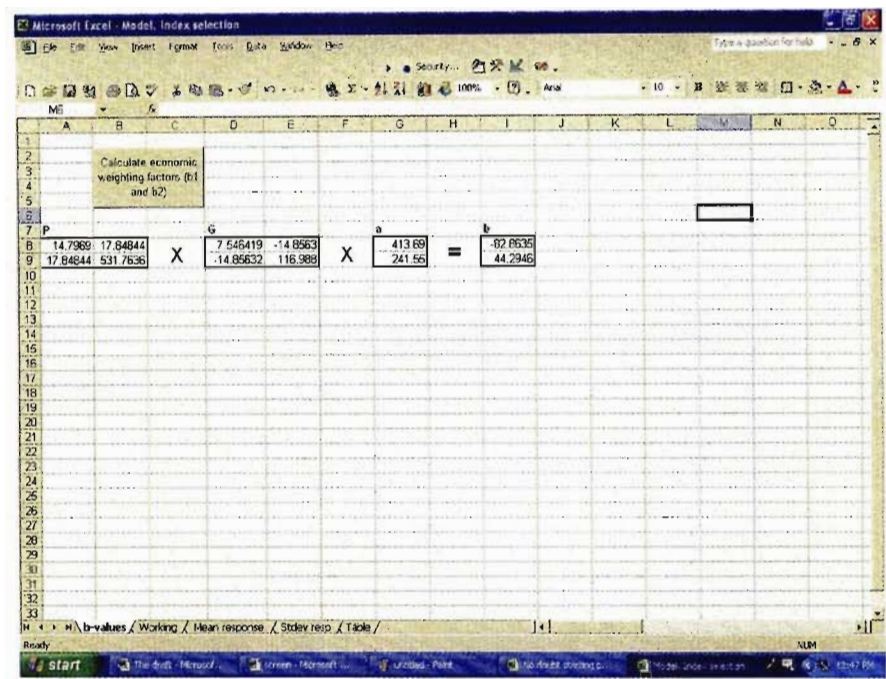
Figure 2.14 The range A1 to I9 in the "b-values" spreadsheet of the Microsoft excel file "Model, Index selection".

The b-values of any two traits could now be calculated with the following minor changes:

- Phenotypic variances and co-variances of the desired traits needed to be entered into the P-matrix.

- Genetic variances and co-variances of the desired traits needed to be entered into the G-matrix.

- Weighting values of the desired two traits needed to be entered into the a-matrix.

- The "Calculate economic weighting factors (b1 and b2)" button could then be pushed and the new b-values would then be displayed in cells I8 and I9.

- In the same file ("Model, Index selection") the name of the next spreadsheet was changed from "Sheet 2" to "Working".

- In cells A1 and A2 of this spreadsheet the headings "Ppn" and "i" were entered.

- The desired proportion selected and intensity of selection were entered into cells B1 and B2 respectively.

- In cells D1 and D2 the headings "b1" and "b2" were entered.

- In cells E1 and E2 the formulae "='b-values'!I8" and "='b-values'!J3" were entered. These were the b-values calculated in the "b-values" spreadsheet.
- In cells G1 and G2 the headings "h^2_1" and h^2_2" were entered.
- In cells H1 and H2 the heritabilities of trait one and trait two were entered respectively.
- In cell A4 the heading "1" was entered to represent the first generation.
- In cells A5 and B5 the headings "1" and "2" were entered.
- The initial values of trait one (egg weight in this case) were copied from the file "Fixed starting population", cells A2 to A503 and pasted into cells A6 to A507.
- The initial values for trait two (egg production in this case) were copied from the file "Fixed starting population", cells B2 to B503 and pasted into cells B6 to B507.
- In cell C5 the heading "Index" was entered.
- In cell C6 the following formula to calculate the index value of individual one was entered.

"=A6*$E$1+B6*$E$2"

This formula represented the formula: $I = b_1 P_1 + b_2 P_2$ (Falconer and Mackay, 1996).

- The formula was copied down for 500 cells so that each of the 500 individuals had an index value.
- The following percentile formula was entered into cell D6

"=PERCENTILE(C6:C505,1-$B1)"

- This formula took the values in cells C6 to C505 and computed a '1-B2' percentile value. The percentile value produced was therefore based on the index values.

- In cells E5 and F5 the headings "Parents(1)"and "Parents(2)" were entered respectively.
- In cells E6 and F6 the following formulae were entered respectively:

"=IF(C6>D$6,A6,0)" and "=IF(C6>D$6,B6,0)"

- If the index value of individual one (cell C6) was greater than the calculated percentile value (cell D6) then individual one's phenotypic value for trait one (cell A6) was displayed in cell E6 and individual one's phenotypic value for trait two (cell B6) was displayed in cell F6. If the phenotypic value of individual one was less than the percentile value then zeros were displayed in cells E6 and F6.
- These two formulae were copied down for 500 cells. The result was that the 22 percent of individuals with the highest index values were selected.
- The mean and standard deviation of these columns were calculated in the same way as they were in individual selection.
- In cells E508 and F508 the formulae "=(E507+A507)/2" and "=(F507+A507)/2"were entered. These formulae calculated the standard deviations that were halfway between the standard deviation of the entire population and the standard deviation of the selected parents.
- The headings "Ave 1" and "Ave 2" were entered into cells H5 and I5 respectively.
- In cells H6 and I6 the following respective formulae used to calculate the mean egg weight and the mean egg production of the next generation were entered.

"$H1*(E506-A506)+A506" and "$H2*(F506-B506)+B506".

The formulae both represent the formula: $R = i.h^2.\sigma_p$, taken from Falconer (1996), added onto the mean of the previous generation.

Figure 2.15 illustrates the resulting spreadsheet.
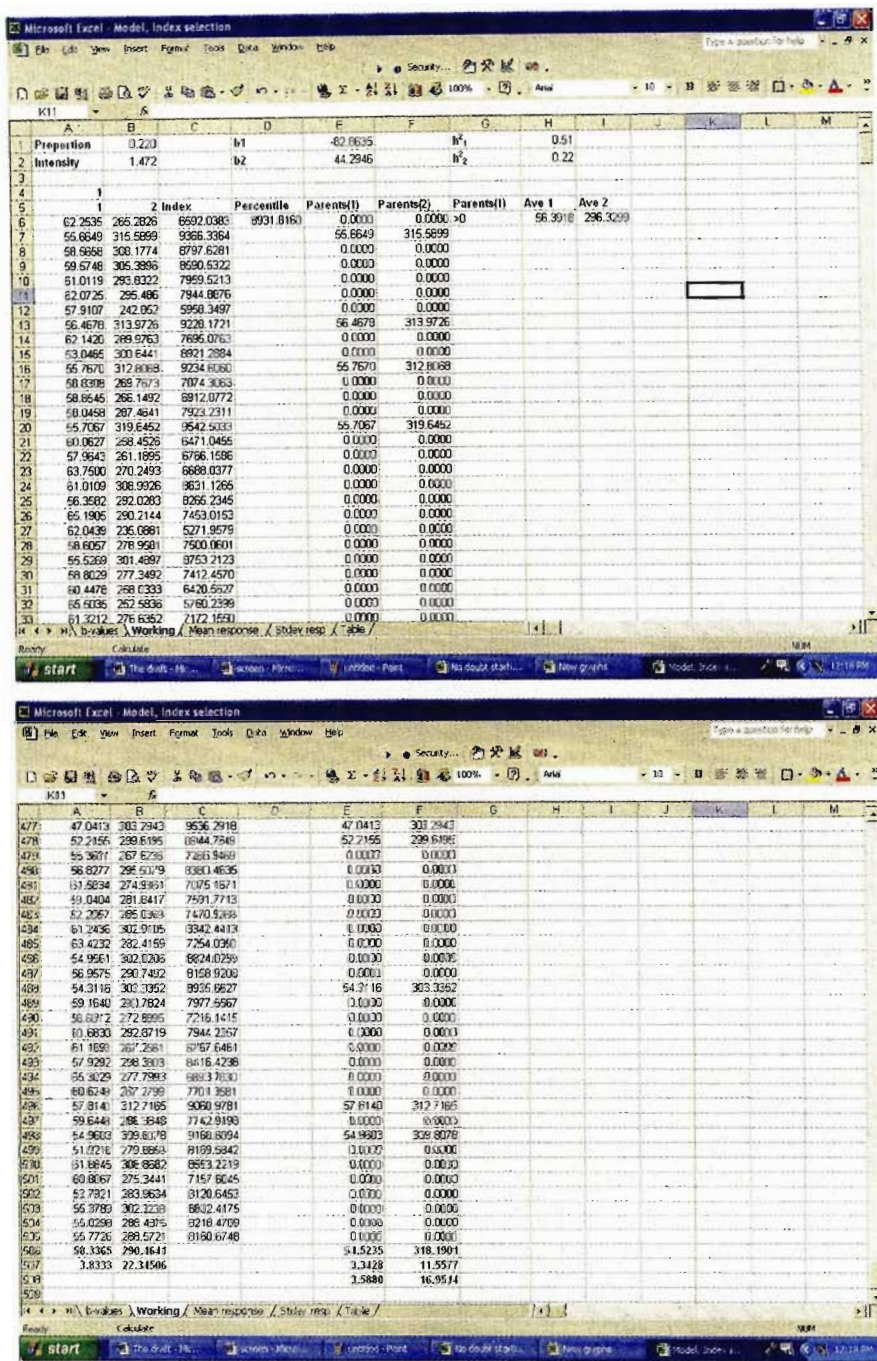
Figure 2.15 The range A1 to I508 in the "Working" spreadsheet of the Microsoft excel file "Model, Index selection".

- The table was set up in a similar way to the method explained in "Model, Individual selection".

- In this case, however, two extra columns were included in the table, one for the mean of the additional trait and one for the standard deviation of the second trait. The resultant table therefore had five columns and is illustrated in figure 2.16.
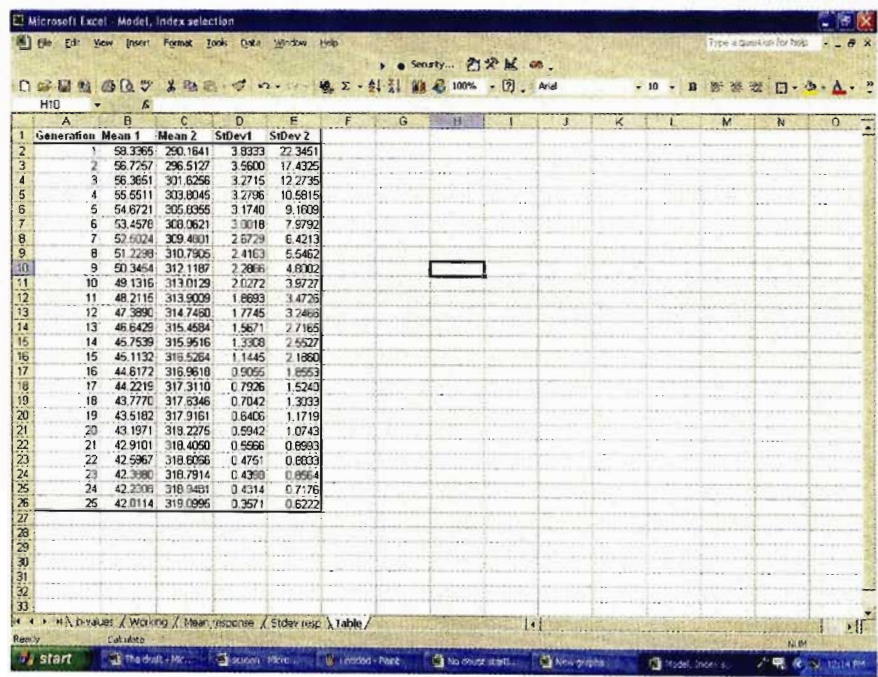
Figure 2.16   The range A1 to E26 in the "Table" spreadsheet of the Microsoft excel file "Model, Index selection".

A graph showing the response in the mean values of the two traits to individual selection was then set up in the following way.

- The active spreadsheet was "Table".

- The "Chart wizard" option on the standard toolbar was selected, and a XY scatter plot was selected.

- The "series" tab was then selected.

- The values entered into the "X values" box were "=Table!$A2$:$A$26" and the values entered into the "Y values" box were "=Table!$B2$:$B$26".

- A second series was then added. For this series the same values were added into the "X values" box and the values entered into the "Y values" box were "=Table!$C2$:$C$26".

The resulting graph plotted generation 1 to 25 on the X-axis against mean values of trait one and two on the Y-axis. The graph was edited and formatted in a similar way as explained in "Model' Individual selection".

- In this case the axis of the second data series (or the curve of trait two) was changed by right clicking on the curve and selecting "Format data series".
- In the resulting dialog box the "Axis" tab was selected and "Secondary axis" was selected. Appropriate changes were then made to the title and axis names.

A graph showing the response in the standard deviations of the two traits to individual selection was then set up in the following way.

- The active spreadsheet was "Table".
- The "Chart wizard" option on the standard toolbar was selected, and a XY scatter plot was selected.
- The "series" tab was then selected. The values entered into the "X values" box were "=Table!$A2$:$A$26" and the values entered into the "Y values" box were "=Table!$D2$:$D$26".
- A second series was then added. For this series the same values were added into the "X values" box and the values entered into the "Y values" box were "=Table!$E2$:$E$26".

The resulting graph plotted generation 1 to 25 on the X-axis against standard deviations of trait one and two on the Y-axis. The graph was formatted and edited in the same way as was the "Mean resp" graph explained previously.

The file "Model, Index selection" was saved and could then be used to determine the simultaneous responses to index selection of any of the two traits.

CHAPTER 3
RESULTS

3.1 INTRODUCTION

Firstly the efficiency of the first four selection techniques, namely individual selection, between family selection, within family selection and family-index selection will be compared. A graph and a table of the response to each of these techniques are presented for each trait. An idea of the efficiency of the four techniques at different heritabilities and different variances can therefore be established.

Secondly the results of multiple trait selection or index selection will be presented. Graphs and tables will be presented showing how two traits respond simultaneously to index selection.

3.2 EGG WEIGHT

Figure 3.1 illustrates that the responses to individual selection and family-index selection are superior to those of within family selection and between family selection in the early generations (generations one to twelve). At approximately generation ten the responses to individual selection and family-index selection begin to level off. The responses to within family selection and between family selection are slower at first but the two methods do not level off as fast and in the later generations the response to between family selection is superior to the response to the other three methods.
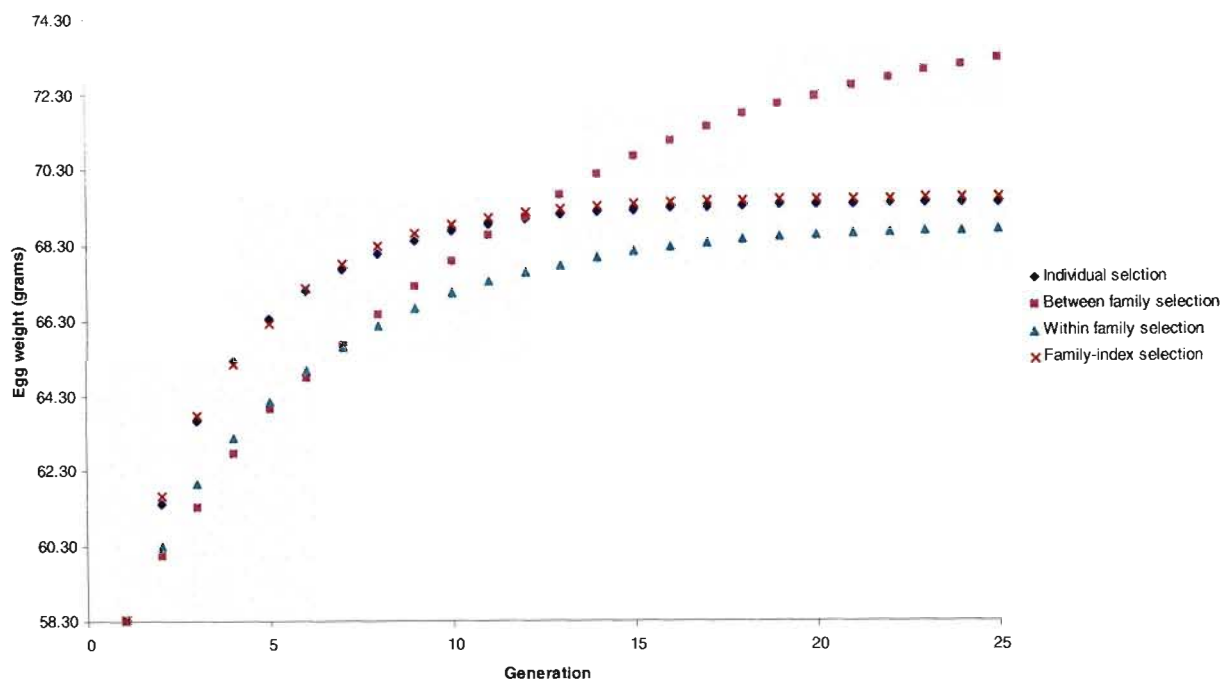
Figure 3.1 Response in egg weight ($h^2 = 0.51$) to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

The decline in the standard deviation of egg weight following individual selection, between family selection, within family selection and family-index selection is illustrated in figure 3.2. Individual selection and family-index selection produce the quickest drop in the standard deviation. The drop in the standard deviation following within family selection is slightly slower. The drop in the standard deviation as a result of between family selection is a lot slower than the other three selection methods and by generation 25 the standard deviation has not yet reached zero.
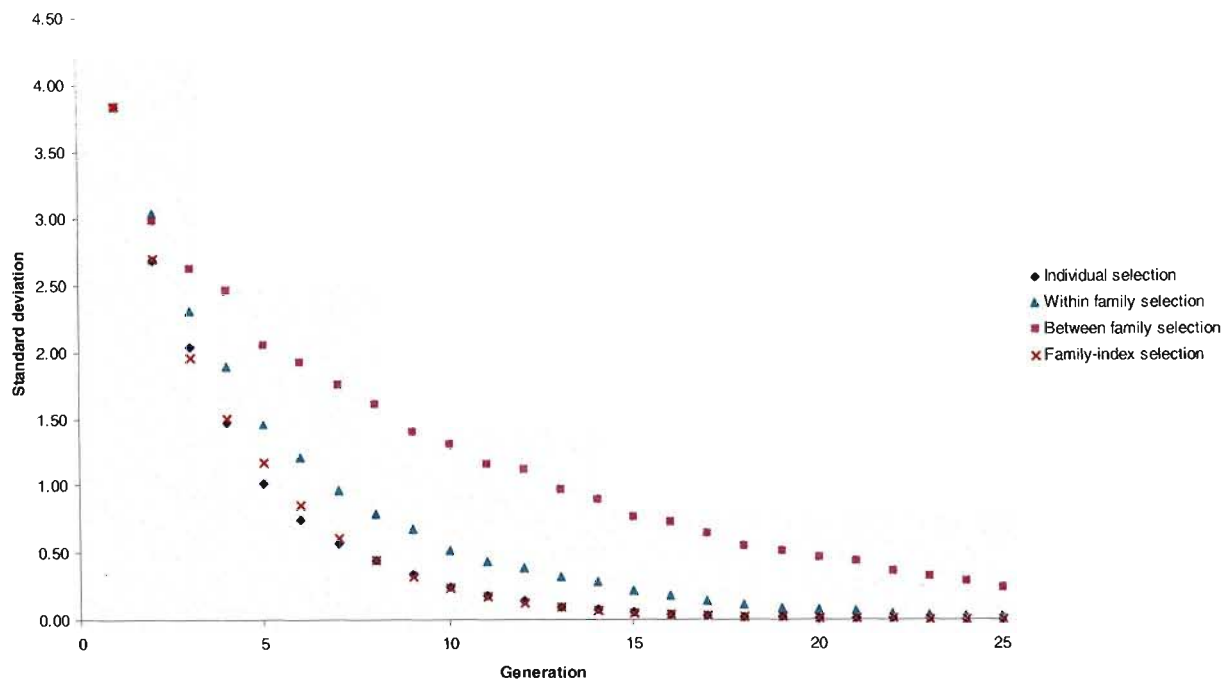
Figure 3.2   Change in the standard deviation of egg weight $(h^2 = 0.51)$ due to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Table 3.1 illustrates that from generations two to eleven individual selection and family-index selection produce the heaviest eggs. Between family selection initially results in the lightest eggs, however, from generation twelve onwards between family selection produces the heaviest eggs.

Table 3.1 Egg weight in grams at each generation as a result of the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	58.3365	58.3365	58.3365	58.3365
2	61.3979	60.0258	60.2741	61.5929
3	63.6124	61.3107	61.9210	63.7485
4	65.2238	62.7344	63.1646	65.1218
5	66.3325	63.9307	64.1221	66.2158
6	67.0547	64.7553	64.9381	67.1299
7	67.6074	65.6037	65.5856	67.7584
8	68.0099	66.4361	66.1263	68.2297
9	68.3602	67.1526	66.5924	68.5432
10	68.5999	67.8238	67.0008	68.7845
11	68.7872	68.4674	67.2777	68.9569
12	68.9276	68.9418	67.5295	69.0824
13	69.0312	69.5307	67.7289	69.1777
14	69.1008	70.1142	67.9133	69.2440
15	69.1521	70.5674	68.0790	69.2967
16	69.1944	70.9516	68.1989	69.3354
17	69.2253	71.3381	68.2943	69.3612
18	69.2478	71.6657	68.3720	69.3818
19	69.2643	71.9450	68.4324	69.3976
20	69.2773	72.1607	68.4803	69.4081
21	69.2884	72.4156	68.5163	69.4153
22	69.2958	72.6117	68.5538	69.4209
23	69.3010	72.8107	68.5756	69.4248
24	69.3054	72.9394	68.5935	69.4275
25	69.3088	73.0950	68.6092	69.4295

Table 3.2 illustrates that after each generation of selection the standard deviation is highest following between family selection. Within family selection produces the second highest standard deviation at each generation. The standard deviations resulting from individual selection and family-index selection are comparatively low.

Table 3.2 The standard deviation of egg weight at each generation as a result of the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	3.8333	3.8333	3.8333	3.8333
2	2.6915	2.9872	3.0420	2.6934
3	2.0391	2.6217	2.3036	1.9541
4	1.4672	2.4541	1.8843	1.4929
5	1.0152	2.0413	1.4548	1.1603
6	0.7403	1.9190	1.1957	0.8459
7	0.5636	1.7506	0.9554	0.6068
8	0.4342	1.6036	0.7799	0.4411
9	0.3311	1.3898	0.6661	0.3126
10	0.2439	1.2892	0.5125	0.2328
11	0.1801	1.1419	0.4319	0.1708
12	0.1364	1.1062	0.3834	0.1236
13	0.0937	0.9541	0.3180	0.0898
14	0.0718	0.8837	0.2749	0.0659
15	0.0532	0.7545	0.2142	0.0491
16	0.0400	0.7158	0.1722	0.0352
17	0.0286	0.6332	0.1388	0.0262
18	0.0217	0.5352	0.1073	0.0199
19	0.0169	0.4981	0.0880	0.0146
20	0.0135	0.4523	0.0747	0.0101
21	0.0097	0.4321	0.0604	0.0073
22	0.0072	0.3540	0.0472	0.0054
23	0.0057	0.3146	0.0350	0.0035
24	0.0045	0.2822	0.0296	0.0025
25	0.0032	0.2303	0.0249	0.0018

3.3 EGG PRODUCTION

Figure 3.3 illustrates that in the early generations (generations 2 to 6) the response of egg production was very similar in all four selection methods, with family index selection producing the best response to selection. From generation eight onwards between family selection produces the best responses. The responses to between family selection and within family selection continue to rise in the later generations (between family more so than within family). The responses to individual selection and family-index selection level off at approximately generation ten and from generation ten onwards individual selection produces the worst response to selection.
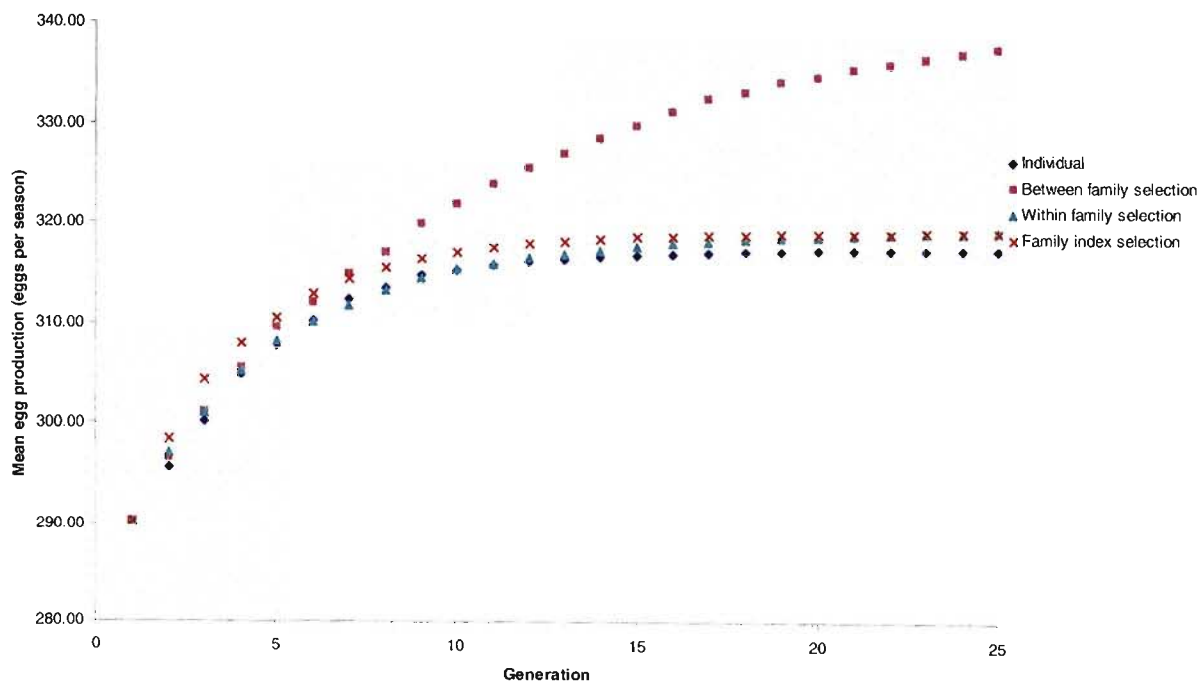
Figure 3.3 Response in egg production ($h^2 = 0.22$) to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

The decline in the standard deviation of egg production following individual selection, between family selection, within family selection and family-index selection is illustrated in figure 3.4. Individual selection and family-index selection produce the quickest drop in the standard deviation. The drop in the standard deviation following within family selection is slightly slower. The drop in the standard deviation as a result of between family selection is a lot slower than the other three selection methods and by generation 25 the standard deviation has not yet reached zero.
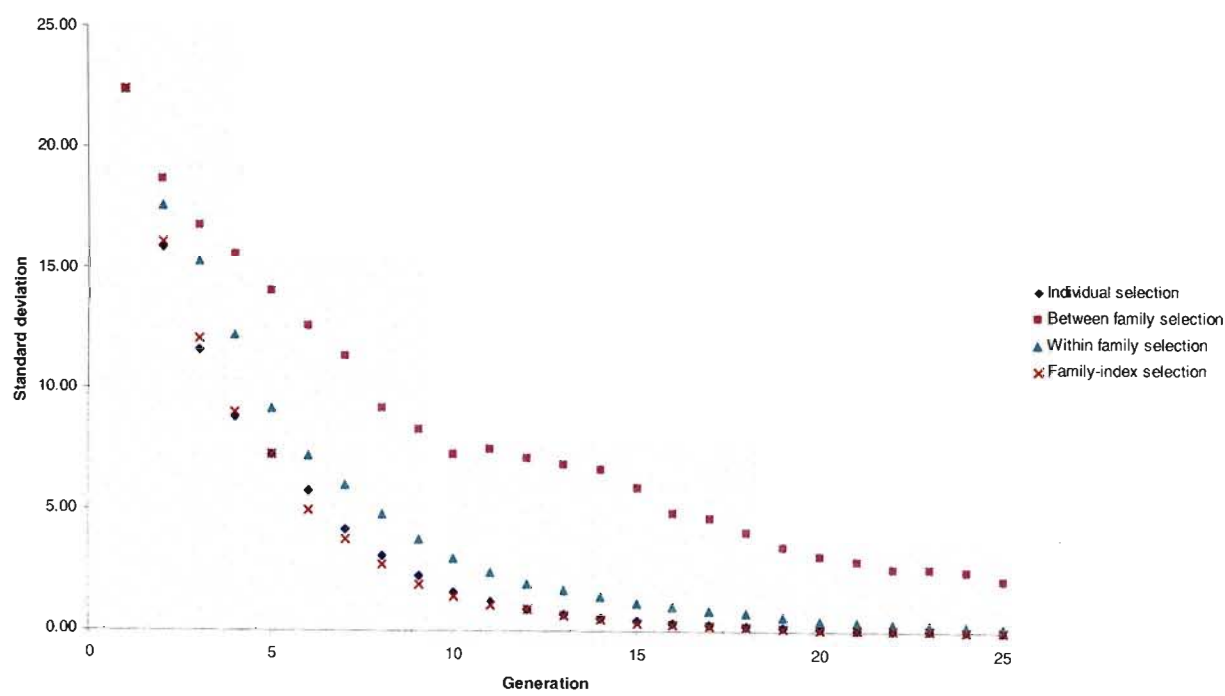
Figure 3.4   Change in the standard deviation of egg production ($h^2 = 0.22$) due to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Table 3.3 illustrates that initially (generation one to six) family-index selection produced the best response and individual selection produced the worst response to selection. Between family selection, from generation seven onwards produces the best responses. In most generations the family-based methods of selection all produced better responses than individual selection.

Table 3.3   Egg production (measured as number of eggs produced per season) at each generation following individual selection, between family selection, within family selection and family-index selection.

Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	290.1641	290.1641	290.1641	290.1641
2	295.6119	296.5364	297.0372	298.4372
3	300.1600	301.0147	300.9635	304.2510
4	304.6657	305.3309	305.0637	307.8048
5	307.6704	309.4200	308.1213	310.4721
6	310.2383	311.9862	310.0605	312.7885
7	312.2478	314.8335	311.6308	314.3280
8	313.4454	316.8727	313.2066	315.4024
9	314.6382	319.7629	314.4144	316.3128
10	315.2131	321.7189	315.2317	316.9341
11	315.6734	323.6915	315.8233	317.4012
12	316.0321	325.2999	316.4124	317.7236
13	316.2769	326.8293	316.7571	318.0404
14	316.4811	328.2841	317.1294	318.2809
15	316.6642	329.5158	317.4548	318.4536
16	316.8075	330.9462	317.8336	318.5428
17	316.9227	332.1277	318.0605	318.6089
18	316.9862	332.8437	318.2362	318.6838
19	317.0555	333.7656	318.4149	318.7344
20	317.0953	334.2840	318.5502	318.7679
21	317.1305	334.9698	318.6668	318.7926
22	317.1551	335.5443	318.7677	318.8119
23	317.1747	336.0343	318.8339	318.8275
24	317.1858	336.5147	318.8965	318.8378
25	317.1977	337.0541	318.9456	318.8466

Table 3.4 illustrates that after each generation of selection the standard deviation is highest following between family selection, and after 25 generations of between family selection the standard deviation is 2.05. Within family selection produces the second highest standard

deviation in every other generation. The standard deviations resulting from individual selection and family-index selection are comparatively low and by generation 20 they are nearing zero.

Table 3.4 The standard deviation of egg production at each generation as a result of the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	22.3451	22.3451	22.3451	22.3451
2	15.8458	18.6324	17.5755	16.0411
3	11.5959	16.7480	15.2451	12.0391
4	8.7937	15.5688	12.1943	9.0066
5	7.2446	13.9852	9.1194	7.2349
6	5.7471	12.5711	7.1939	4.9756
7	4.1900	11.3082	5.9993	3.7886
8	3.1114	9.1683	4.7925	2.7162
9	2.2732	8.2575	3.7657	1.9195
10	1.5382	7.2199	2.9624	1.4197
11	1.2053	7.4285	2.3904	1.0460
12	0.8600	7.0545	1.9196	0.8560
13	0.6858	6.8106	1.6508	0.6254
14	0.5372	6.6087	1.4091	0.4673
15	0.4165	5.8899	1.1443	0.3256
16	0.3102	4.8366	0.9803	0.2383
17	0.2522	4.6422	0.8384	0.1887
18	0.1811	4.0857	0.7164	0.1438
19	0.1462	3.3990	0.5529	0.1070
20	0.1068	3.0540	0.4261	0.0772
21	0.0768	2.8647	0.3471	0.0581
22	0.0559	2.5309	0.2927	0.0450
23	0.0419	2.5155	0.2346	0.0344
24	0.0305	2.4396	0.1929	0.0250
25	0.0237	2.0510	0.1579	0.0182

3.4 AGE AT FIRST EGG

Figure 3.5 illustrates that the response to individual selection and family-index selection increase at a greater rate than within family selection and between family selection in the early generations (generations one to eleven). From generation ten onwards the response to individual selection and family-index selection levels off. The response to within family selection slowly nears the response to individual selection and family-index selection but is never quite as efficient. Between family selection is slow at first but does not level off as fast and, in the later generations it is the method producing the best responses.

Figure 3.5   Response in age at first egg (h^2 = 0.41) to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

The decline in the standard deviation of AFE following individual selection, between family selection, within family selection and family-index selection is shown in figure 3.6. Individual

selection and family-index selection produce the quickest drop in standard deviation. The drop in the standard deviation following within family selection is slightly slower and nears zero at approximately generation 23. The drop in the standard deviation as a result of between family selection is a lot slower than the other three selection methods and by generation 25 the standard deviation has not yet reached zero.
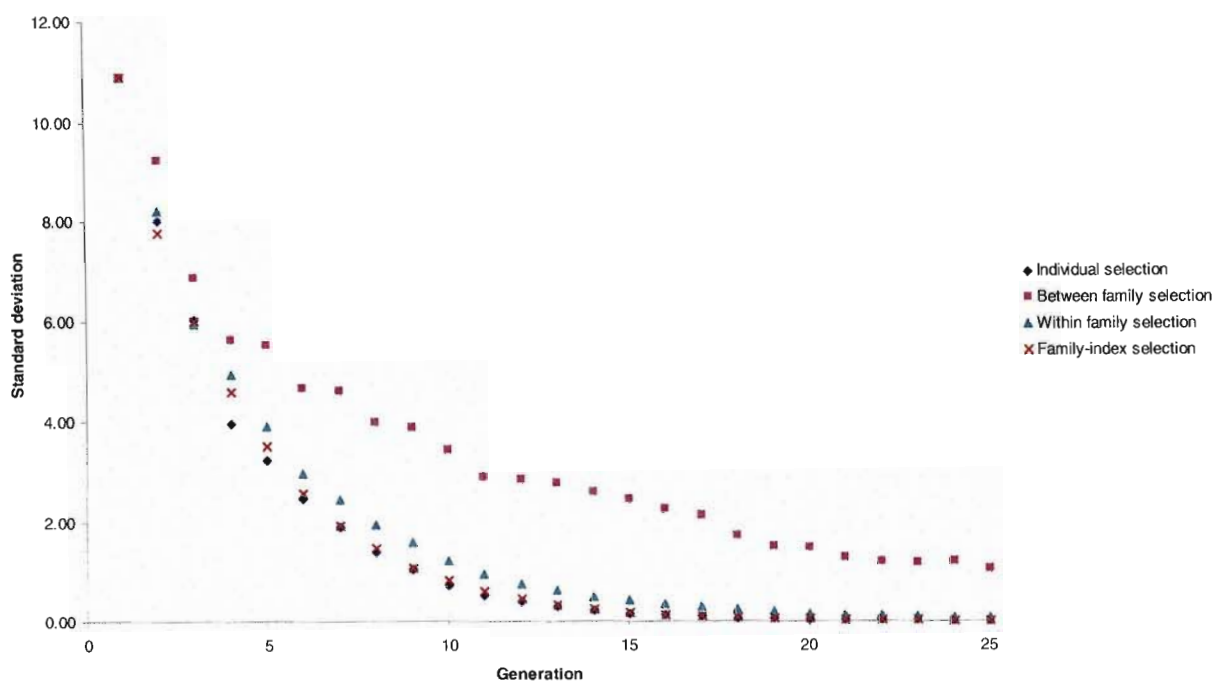
Figure 3.6   Change in the standard deviation of age at first egg ($h^2 = 0.41$) due to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Table 3.5 illustrates the response (a decline in days taken to reach sexual maturity) of AFE to the four selection methods in each generation. From generations two to eleven individual selection and family-index selection produce the best responses. From generation twelve onwards between family selection results in the best responses.

Table 3.5   Age at first egg (measured in days) at each generation following individual selection, between family selection, within family selection and family-index selection.

Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	157.2205	157.2205	157.2205	157.2205
2	150.4209	152.9070	152.4289	150.2687
3	145.8348	149.0230	149.0285	145.4446
4	142.1127	146.8645	145.8058	141.5723
5	139.5465	144.1775	143.5481	138.5623
6	137.4130	141.8481	141.9098	136.4202
7	135.9928	139.6624	140.5851	134.9677
8	134.7668	137.7426	139.4224	133.7702
9	133.8805	136.2399	138.5216	132.9303
10	133.2398	134.6498	137.7810	132.2436
11	132.8224	133.3425	137.2502	131.7697
12	132.5151	131.9622	136.8501	131.3690
13	132.2556	130.7154	136.4837	131.1113
14	132.0831	129.7913	136.1911	130.9368
15	131.9414	128.8153	135.9550	130.7713
16	131.8440	127.7707	135.7300	130.6580
17	131.7696	127.0617	135.5645	130.5700
18	131.7179	126.2458	135.4302	130.5080
19	131.6836	125.6191	135.3022	130.4593
20	131.6560	125.0224	135.2056	130.4272
21	131.6350	124.3554	135.1321	130.4006
22	131.6197	123.8489	135.0650	130.3845
23	131.6087	123.4287	135.0142	130.3708
24	131.6007	123.0196	134.9715	130.3609
25	131.5940	122.4738	134.9315	130.3539

Table 3.6 illustrates that after each generation of selection the standard deviation is highest following between family 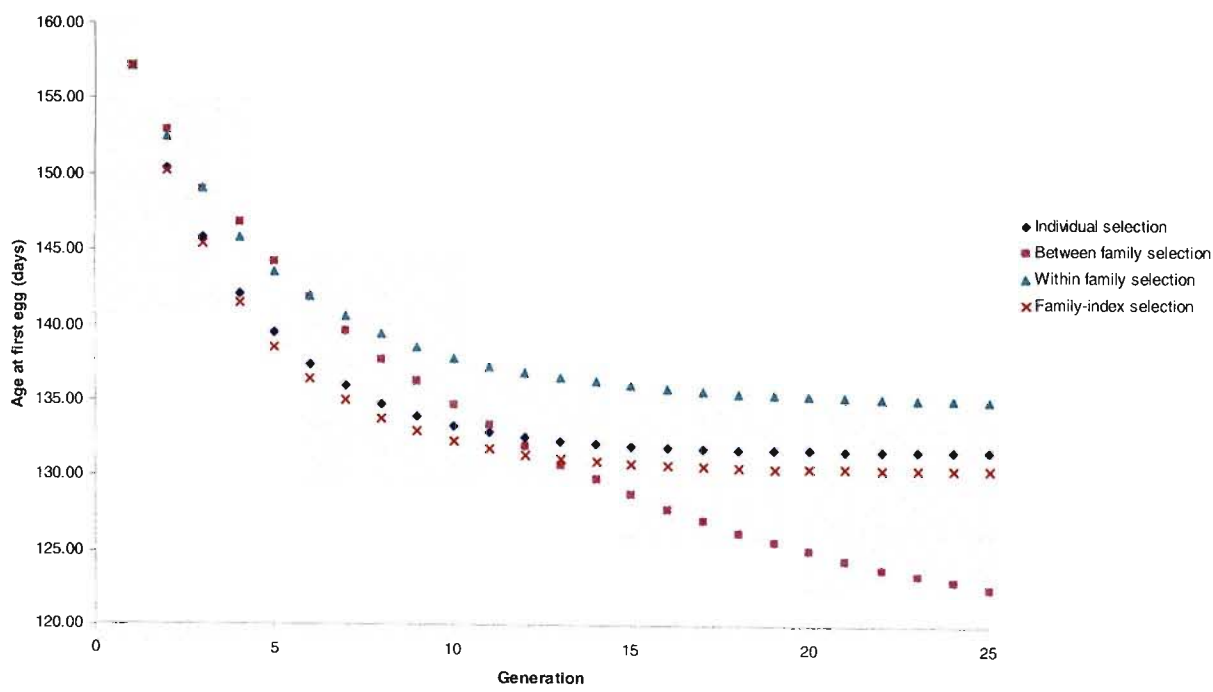selection. Within family selection produces the second highest standard deviation at each generation. The standard deviations resulting from individual selection and family-index selection are comparatively low.

Table 3.6 The standard deviation of age at first egg at each generation following the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	10.8879	10.8879	10.8879	10.8879
2	7.9972	9.2165	8.1948	7.7606
3	6.0216	6.8449	5.9463	5.9950
4	3.9546	5.6210	4.9161	4.5710
5	3.2346	5.5079	3.9000	3.4962
6	2.4710	4.6342	2.9606	2.5576
7	1.8897	4.5846	2.4468	1.9080
8	1.4030	3.9826	1.9436	1.4735
9	1.0324	3.8688	1.5819	1.0765
10	0.7282	3.4204	1.2236	0.8078
11	0.5335	2.8761	0.9489	0.5902
12	0.4030	2.8271	0.7339	0.4442
13	0.2868	2.7515	0.6124	0.3219
14	0.2188	2.5830	0.5033	0.2524
15	0.1601	2.4380	0.4134	0.1793
16	0.1188	2.2257	0.3503	0.1355
17	0.0881	2.1093	0.3060	0.1033
18	0.0606	1.7166	0.2519	0.0779
19	0.0455	1.5002	0.2098	0.0560
20	0.0338	1.4615	0.1604	0.0394
21	0.0256	1.2726	0.1348	0.0283
22	0.0188	1.1815	0.1174	0.0215
23	0.0148	1.1636	0.0985	0.0153
24	0.0113	1.1824	0.0830	0.0110
25	0.0088	1.0393	0.0656	0.0075

3.5 BODY WEIGHT

Figure 3.7 illustrates that the response to individual selection and family-index selection is superior to the response to between family selection and within family selection in the early generations (generations one to eight). At approximately generation ten the response to individual selection and family-index selection levels off. The response to within family selection and between family selection is slower at first but the two methods do not level off as fast. The response to within family selection only begins to level off at approximately generation fifteen. The response to between family selection levels off very slowly.

Figure 3.7   Response in body weight (h^2 = 0.55) to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

The decline in the standard deviation of body weight following individual selection, between family selection, within family selection and family-index selection is illustrated in figure 3.8.

Individual selection and family-index selection produce the quickest drop in the standard deviation. The standard deviation nears zero after approximately 18 generations of selection when using these two methods. The drop in the standard deviation following within family selection is slightly slower and nears zero at approximately generation 25. The drop in the standard deviation as a result of between family selection is a lot slower than the other three selection methods and by generation 25 the standard deviation has not yet reached zero.
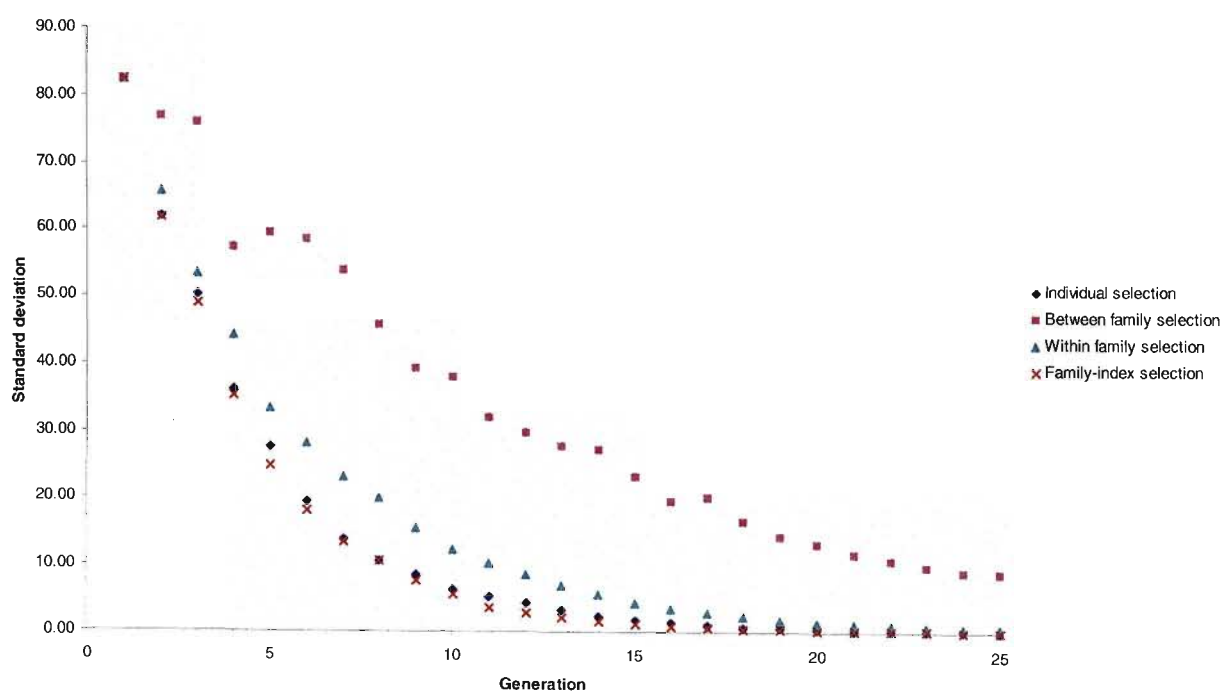
Figure 3.8   Change in the standard deviation of body weight ($h^2 = 0.55$) due to the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Table 3.7 illustrates that from generations two to seven individual selection and family-index selection produce the best responses. Between family selection initially (generations one to five) results in poor responses, from generation eight onwards, however, between family selection results in the best responses.

Table 3.7 Body weight in grams at each generation following the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

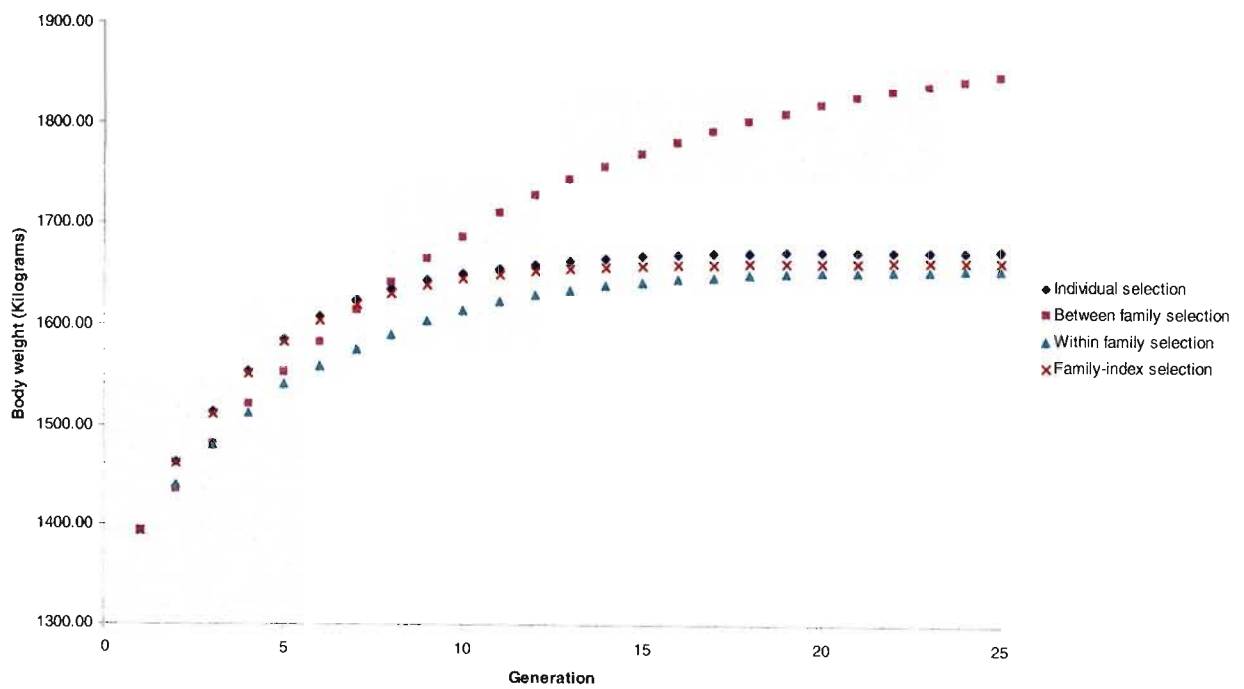| Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	1393.8240	1393.8240	1393.8240	1393.8240
2	1462.6183	1435.6867	1440.5438	1460.7696
3	1512.8278	1480.8528	1480.2418	1511.1543
4	1553.6650	1521.1572	1511.8872	1552.2639
5	1584.7836	1552.7133	1540.0579	1582.4088
6	1607.0495	1582.6632	1559.4170	1603.7453
7	1623.4327	1613.5878	1575.7159	1619.0971
8	1634.5146	1640.7541	1590.3690	1630.0312
9	1643.0337	1664.0559	1603.4471	1638.7728
10	1649.4412	1685.4544	1613.9496	1644.4579
11	1654.6132	1709.1344	1621.7405	1648.8357
12	1658.7182	1726.1966	1628.2138	1651.8735
13	1661.9945	1742.3395	1633.5135	1654.1270
14	1664.5533	1755.5123	1637.9961	1655.7599
15	1666.4574	1767.8161	1641.3143	1657.0494
16	1667.8380	1778.8918	1644.0822	1657.9307
17	1668.8360	1790.1306	1646.4751	1658.6052
18	1669.5475	1799.5387	1648.1946	1659.1415
19	1670.0526	1807.2220	1649.4308	1659.5187
20	1670.4569	1815.8353	1650.4827	1659.7913
21	1670.7483	1822.6162	1651.2852	1660.0084
22	1670.9573	1829.1240	1652.0370	1660.1593
23	1671.1206	1834.5952	1652.5986	1660.2722
24	1671.2345	1839.4511	1653.1155	1660.3636
25	1671.3266	1844.3342	1653.5118	1660.4265

Table 3.8 illustrates that after each generation of selection the standard deviation is highest following between family selection. Within family selection has produces the second highest standard deviation at each generation. The standard deviations resulting from individual selection and family-index selection are comparatively low.

Table 3.8 The standard deviation of body weight at each generation following the four different selection methods, individual selection, between family selection, within family selection and family-index selection.

Generation	Individual selection	Between family selection	Within family selection	Family-index selection
1	82.3837	82.3837	82.3837	82.3837
2	61.9625	76.7298	65.6718	61.7588
3	50.2713	75.8446	53.3046	48.9865
4	36.0671	57.1300	44.1589	35.0561
5	27.4649	59.1504	33.3625	24.7439
6	19.2513	58.1968	28.0265	18.0935
7	13.7981	53.7843	23.1020	13.4222
8	10.5762	45.6440	19.8935	10.6711
9	8.5029	39.1298	15.3797	7.6527
10	6.2528	37.8041	12.2664	5.5686
11	5.1374	31.7722	10.2939	3.6121
12	4.2473	29.6129	8.5775	2.8666
13	3.0978	27.4611	6.8984	2.0274
14	2.2909	26.9492	5.5960	1.5154
15	1.7158	23.0087	4.3620	1.1079
16	1.2373	19.2847	3.3549	0.8189
17	0.8731	19.8625	2.7953	0.5996
18	0.6236	16.3051	2.2699	0.4562
19	0.4992	14.1343	1.7658	0.3282
20	0.3581	12.9685	1.3667	0.2561
21	0.2595	11.5787	1.1444	0.1958
22	0.1974	10.5200	0.9172	0.1394
23	0.1493	9.6292	0.7870	0.1035
24	0.1153	8.9146	0.6438	0.0782
25	0.0856	8.6809	0.5083	0.0549

3.6 INDEX SELECTION

Figure 3.9 illustrates the response to multiple trait selection when egg production and egg weight were included in the index. While egg production increased dramatically as a result of multiple trait selection, egg weight dropped as a result of this selection method.
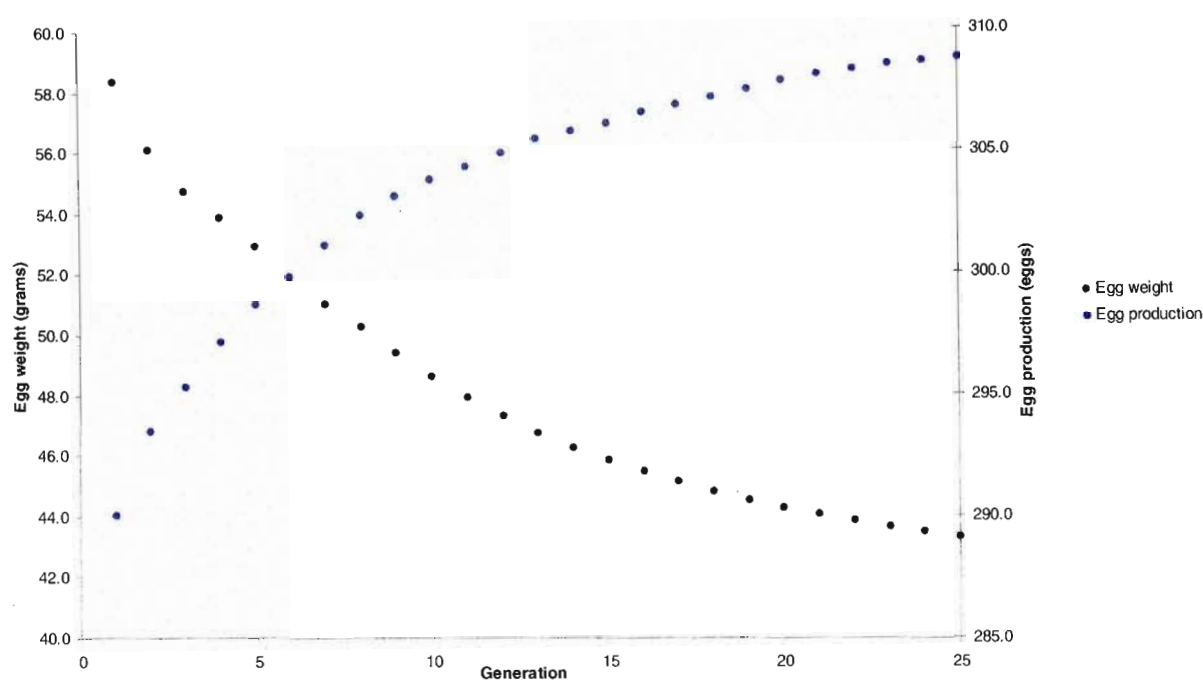
Figure 3.9 Combined response of egg weight and egg production to multiple trait selection.

Table 3.9 illustrates the response to multiple trait selection when egg production and egg weight were included in the index. It also illustrates the change in the standard deviations of these traits as a result of multiple trait selection. While egg production increased dramatically as a result of multiple trait selection, egg weight dropped as a result of this selection method. The figures in table 3.9 also illustrate that the standard deviation of both traits decline but not at a very rapid rate and after 25 generations of index selection the standard deviation of both traits has not yet reached zero.

Table 3.9 Values of egg weight and egg production and the standard deviations of these traits after each generation of multiple trait selection.

Generation	Mean egg weight (grams)	Egg production (eggs)	Egg weight standard deviation	Egg production standard deviation
1	58.3365	290.0321	3.8333	11.1725
2	56.0838	293.4960	3.4787	9.0970
3	54.7289	295.3312	2.8953	7.4344
4	53.8512	297.1706	2.6374	6.5680
5	52.9082	298.7597	2.2251	5.7081
6	51.8738	299.8501	2.1262	4.8024
7	50.9935	301.1728	1.9048	4.3414
8	50.2553	302.3677	1.7590	3.8008
9	49.3774	303.1431	1.6428	3.2464
10	48.5889	303.8350	1.3351	2.6344
11	47.9218	304.3655	1.2621	2.3503
12	47.2693	304.8889	1.1467	2.2509
13	46.7080	305.4825	1.0010	2.0424
14	46.2178	305.7640	0.8656	1.8938
15	45.8196	306.0786	0.8313	1.7121
16	45.4426	306.5714	0.7414	1.4858
17	45.0988	306.8462	0.6568	1.3684
18	44.7805	307.1862	0.6088	1.2811
19	44.5050	307.4950	0.5648	1.1191
20	44.2311	307.8255	0.5056	1.0102
21	44.0214	308.1013	0.4631	0.9103
22	43.8233	308.2960	0.3893	0.8194
23	43.6307	308.5036	0.3441	0.6615
24	43.4451	308.6276	0.2948	0.5683
25	43.3058	308.7408	0.2401	0.5104

Figure 3.10 illustrates the response to multiple trait selection when body weight and egg weight were included in the index. Initially egg weight increased dramatically as a result of multiple trait selection, however the response of egg weight levelled off at about generation ten. Body

weight increased slowly in the initial generations but then responded well in the later generations.

Figure 3.10   Combined response of egg weight and body weight to multiple trait selection.

Table 3.10 illustrates the response to multiple trait selection when body weight and egg weight were included in the index. It also illustrates the response in the standard deviations of these traits as a result of multiple trait selection. The figures in table 3.10 indicate an initial increase in the response of egg weight followed by a plateau and a slow initial increase in the response of body weight followed by a rapid increase in the later generations. The figures in table 3.10 also illustrate that the standard deviation of egg weight declines rapidly after each generation of selection and the standard deviation of body weight increases at first and then declines slowly after each generation of selection.

Table 3.10   Values of egg weight and body weight and the standard deviations of these traits after each generation of multiple trait selection.

Generation	Mean egg weight (grams)	Body weight (grams)	Egg weight standard deviation	Body weight standard deviation
1	58.3365	1393.8240	3.8333	82.3837
2	60.6852	1409.2085	2.5851	84.3336
3	62.4513	1409.3545	1.9516	83.7510
4	63.8173	1418.8719	1.4036	86.2873
5	64.7846	1427.9248	1.0525	79.7393
6	65.4681	1428.6421	0.7927	79.0232
7	66.0419	1427.7604	0.5677	80.5029
8	66.4055	1437.8389	0.4334	79.7965
9	66.7139	1443.3228	0.3217	82.2756
10	66.9232	1450.1931	0.2248	84.6091
11	67.0620	1463.1419	0.1809	83.7530
12	67.1739	1474.8777	0.1368	82.3944
13	67.2673	1504.2670	0.1057	79.9745
14	67.3180	1536.9798	0.0854	75.6526
15	67.3706	1563.5135	0.0703	75.2978
16	67.4127	1589.0107	0.0594	68.1361
17	67.4503	1617.5242	0.0477	68.4163
18	67.4779	1646.5253	0.0413	60.6030
19	67.4979	1675.1195	0.0373	57.1169
20	67.5160	1704.8409	0.0280	51.3097
21	67.5283	1733.1606	0.0246	42.1427
22	67.5420	1754.3360	0.0220	38.2443
23	67.5514	1773.6504	0.0197	32.5732
24	67.5609	1789.1434	0.0181	29.6857
25	67.5689	1803.6924	0.0166	26.8303

Figure 3.11 illustrates the response to multiple trait selection when egg weight and AFE were included in the index. Multiple trait selection for these two traits resulted in a significant improvement in egg weight over the 25 generations and a significant rise in the number of days taken to reach sexual maturity.

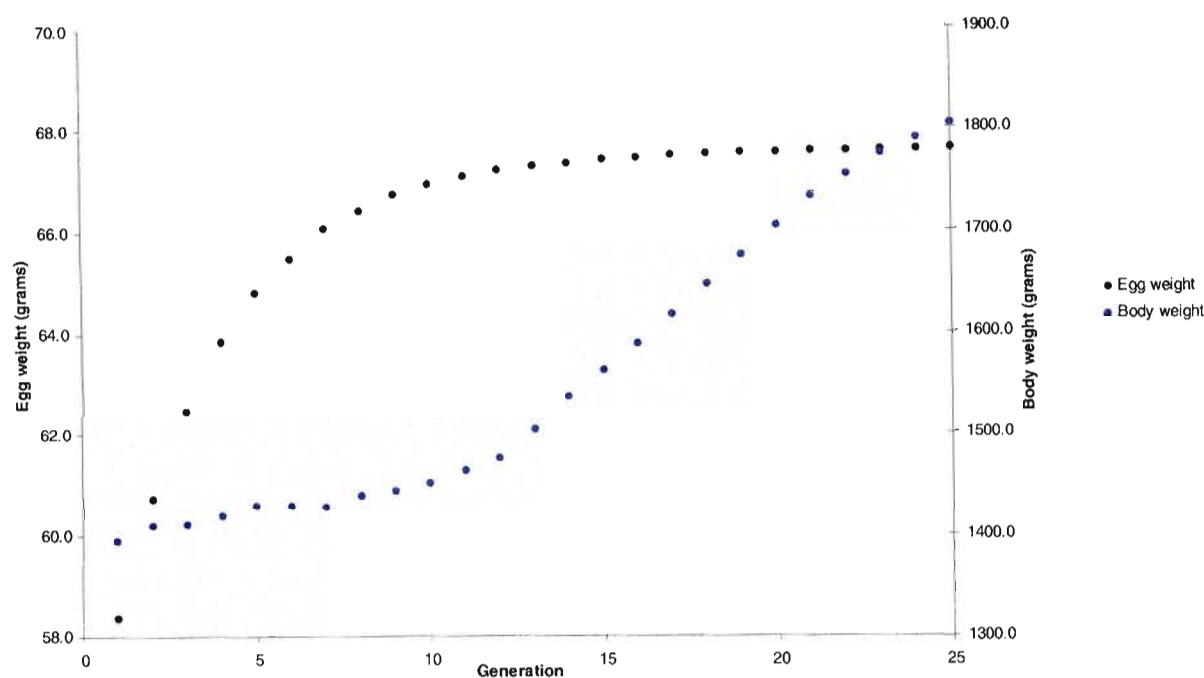**Figure 3.11** Combined response of egg weight and AFE to multiple trait selection.

Table 3.11 illustrates the response to multiple trait selection when egg weight and AFE were included in the index. It also illustrates the response in the standard deviations of these traits as a result of multiple trait selection. The average egg weight increased in each generation from 58.3365 in generation one to 70.8798 in generation 25. While the days taken to reach sexual maturity increased from 157.2205 in generation one to 200.1782 in generation 25. The standard deviation of both traits declined steadily and by generation 25 the standard deviation of both traits was very near to zero.

Table 3.11   Values of egg weight and AFE and the standard deviations of these traits after each generation of multiple trait selection.

Generation	Mean egg weight (grams)	AFE (days)	Egg weight standard deviation	AFE standard deviation
1	58.3365	157.2205	3.8333	10.8879
2	60.5218	160.8241	3.0253	10.3950
3	62.0486	163.6872	2.4734	9.2242
4	63.3152	167.2548	2.1179	9.0060
5	64.3927	170.7462	1.8037	8.5267
6	65.1065	174.0056	1.6163	7.0379
7	65.8482	176.8079	1.3397	6.8122
8	66.4665	180.0055	1.1235	5.9246
9	66.9838	182.5899	0.9983	5.4210
10	67.4411	184.9253	0.9435	4.6763
11	67.8197	186.5640	0.8459	4.3766
12	68.2588	188.2425	0.7323	4.3253
13	68.5806	190.1306	0.6407	3.7691
14	68.8937	191.3881	0.5854	3.1961
15	69.1585	192.8164	0.5475	2.7997
16	69.4032	193.7600	0.4925	2.5502
17	69.6312	194.7576	0.4142	2.2675
18	69.8597	195.8221	0.4008	2.1067
19	70.0430	196.7142	0.3550	1.9076
20	70.2207	197.4551	0.3143	1.6034
21	70.3882	198.1259	0.2837	1.4736
22	70.5339	198.6931	0.2473	1.2952
23	70.6639	199.2439	0.2233	1.1571
24	70.7919	199.6813	0.1912	1.1492
25	70.8798	200.1782	0.1826	0.9770

Figure 3.12 illustrates the response to multiple trait selection when body weight and egg production were included in the index. The figure indicates that there was an initial rise in egg production and then a slow levelling off at about generation 15. There was a slow decline in the response of body weight.
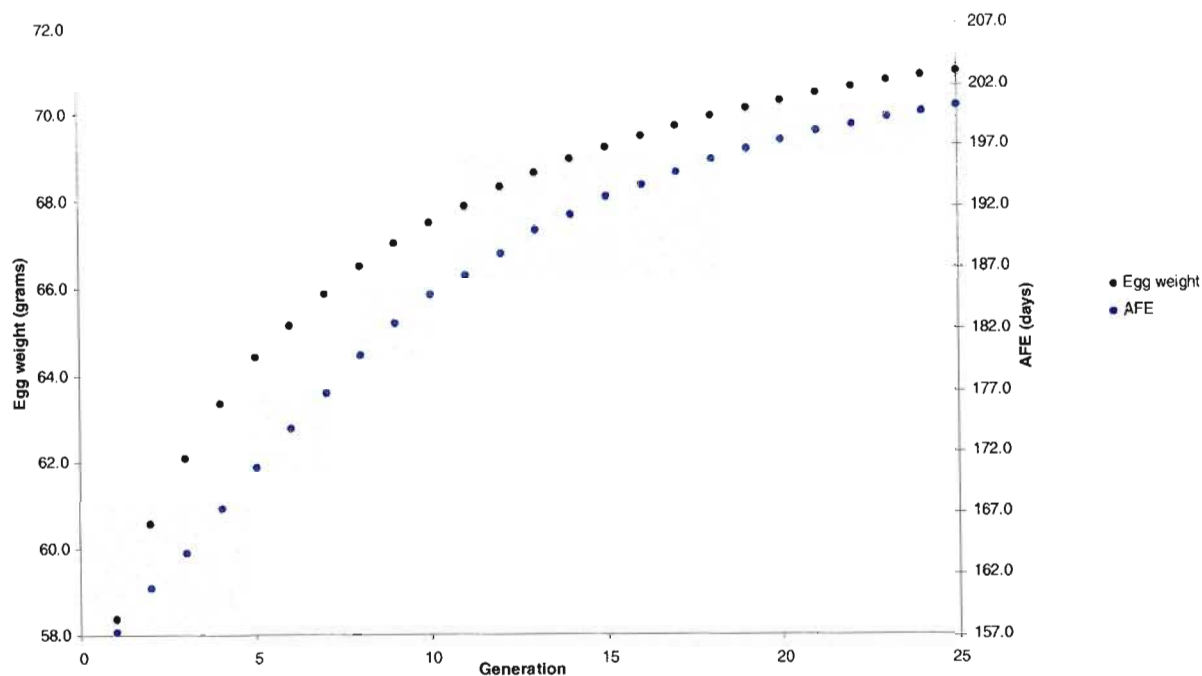
Figure 3.12   Combined response of body weight and egg production to multiple trait selection.

Table 3.12 illustrates the response to multiple trait selection when body weight and egg production were included in the index. It also illustrates the response in the standard deviations of these traits as a result of multiple trait selection. The figure illustrate that egg production rises rapidly in the initial generations (generations two to seven). This rapid response slows and levels off in the later generations. The figures illustrate that the body weight of the birds dropped slowly but steadily after each generation of multiple trait selection. The standard deviations of these two traits decreased steadily after each generation of multiple trait selection but did not reach zero after the 25 generations of selection.

Table 3.12   Values of body weight and egg production and the standard deviations of these traits after each generation of multiple trait selection.

Generation	Egg production (eggs)	Body weight (grams)	Standard Deviation of egg production	Standard deviation of body weight
1	290.1641	1393.8240	22.3451	82.3837
2	297.0778	1384.3584	16.4626	81.7020
3	301.5634	1392.6580	13.2158	79.8311
4	305.2724	1389.8342	9.0731	81.8544
5	307.6639	1390.5614	7.0888	80.2400
6	309.5360	1386.5838	5.0962	79.1458
7	310.9145	1372.1020	3.9188	76.4599
8	311.8353	1360.6287	3.0281	71.5672
9	312.6444	1342.7056	2.4563	70.2078
10	313.3169	1317.2340	1.9850	65.2000
11	313.7518	1288.2534	1.5900	64.0492
12	314.1972	1268.3963	1.3665	58.2206
13	314.5591	1241.8062	1.2805	56.4008
14	314.8986	1214.3798	1.0827	49.2399
15	315.1636	1193.6256	0.9802	46.1680
16	315.4340	1172.9059	0.8572	44.4395
17	315.5971	1150.1092	0.7258	37.2889
18	315.7391	1132.5112	0.6336	34.7572
19	315.8738	1117.2995	0.5638	30.1735
20	315.9987	1102.4215	0.4927	28.1190
21	316.0969	1089.0419	0.4513	26.6173
22	316.2087	1076.6183	0.4191	23.0838
23	316.2890	1065.4486	0.3488	21.0731
24	316.3501	1055.5014	0.3261	18.6200
25	316.3898	1045.7761	0.3044	16.6667

Figure 3.13 illustrates the response to multiple trait selection when body weight and AFE were included in the index. Multiple trait selection for these two traits resulted in a steady decline in both traits with AFE dropping at a faster rate than body weight.

Figure 3.13 Combined response of body weight and AFE to multiple trait selection.
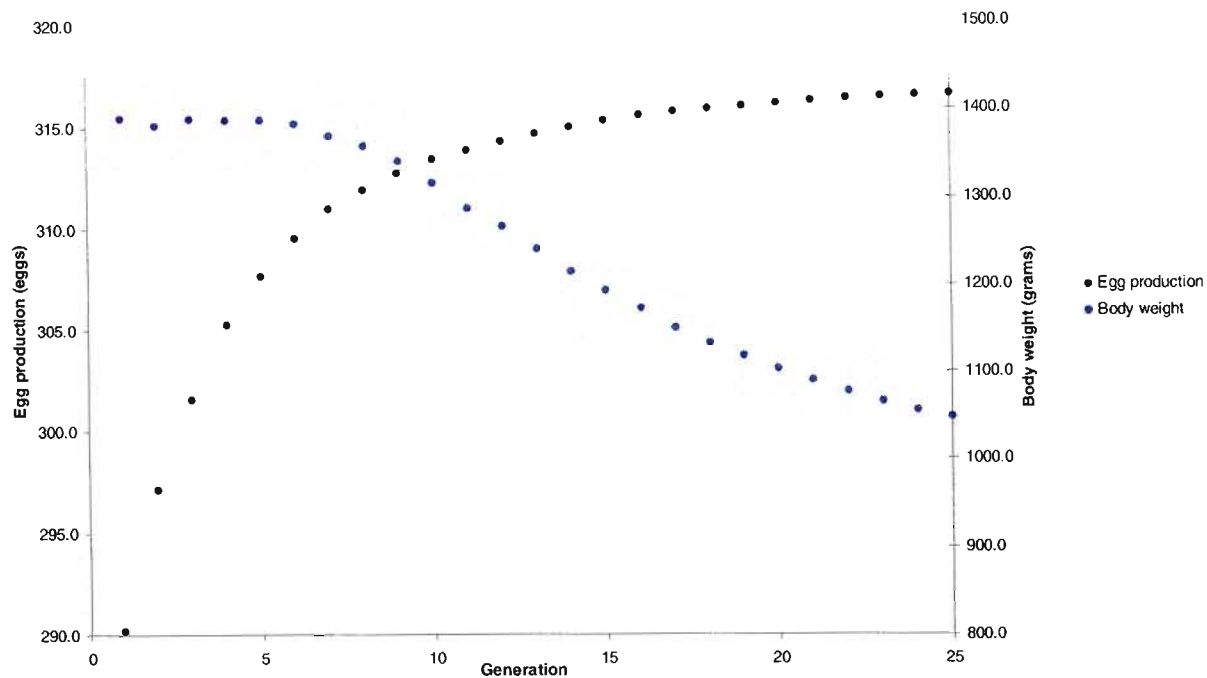
Table 3.13 illustrates the response to multiple trait selection when body weight and AFE were included in the index. It also illustrates the response in the standard deviations of these traits as a result of multiple trait selection. Both traits declined as a result of multiple trait selection. The standard deviation of both traits declined steadily and by generation 25 the standard deviation of AFE was very near zero.

Table 3.13   Values of body weight and AFE and the standard deviations of these traits after each generation of multiple trait selection.

Generation	Body weight (grams)	AFE (days)	Standard Deviation of body weight	Standard deviation of AFE
1	1393.8240	157.2205	82.3837	10.8879
2	1368.2063	151.5925	75.6414	9.3095
3	1331.7658	147.6650	72.2912	7.6391
4	1294.6211	144.5043	63.8290	6.7822
5	1268.7481	141.6071	63.6440	5.5864
6	1235.3693	139.1921	60.3649	4.9007
7	1200.8305	137.3918	52.4805	4.7910
8	1180.5481	135.3882	47.9396	4.5158
9	1153.1499	133.2280	42.8027	3.8995
10	1133.5728	131.6796	40.5085	3.5946
11	1115.5988	130.1873	34.3175	3.1676
12	1097.6349	128.6571	29.6442	2.7527
13	1082.7647	127.4834	26.7989	2.4541
14	1069.9460	126.3163	25.5510	2.0935
15	1057.2168	125.5182	22.8325	1.7981
16	1045.1797	124.9548	19.8130	1.5816
17	1034.9166	124.2731	17.1275	1.3975
18	1026.5458	123.8199	15.0294	1.2983
19	1018.0608	123.2987	13.1154	1.1620
20	1011.7175	122.8664	12.1436	1.0913
21	1006.5458	122.4232	11.1673	0.9827
22	1000.4395	122.0737	10.3810	0.8347
23	994.8593	121.7793	9.1460	0.7330
24	989.6220	121.4959	8.6113	0.6586
25	985.3925	121.2396	7.9128	0.5901

Figure 3.14 illustrates the response to multiple trait selection when egg production and AFE were included in the index. Multiple trait selection for these two traits resulted in a significant improvement in egg production and a steady decline in AFE.
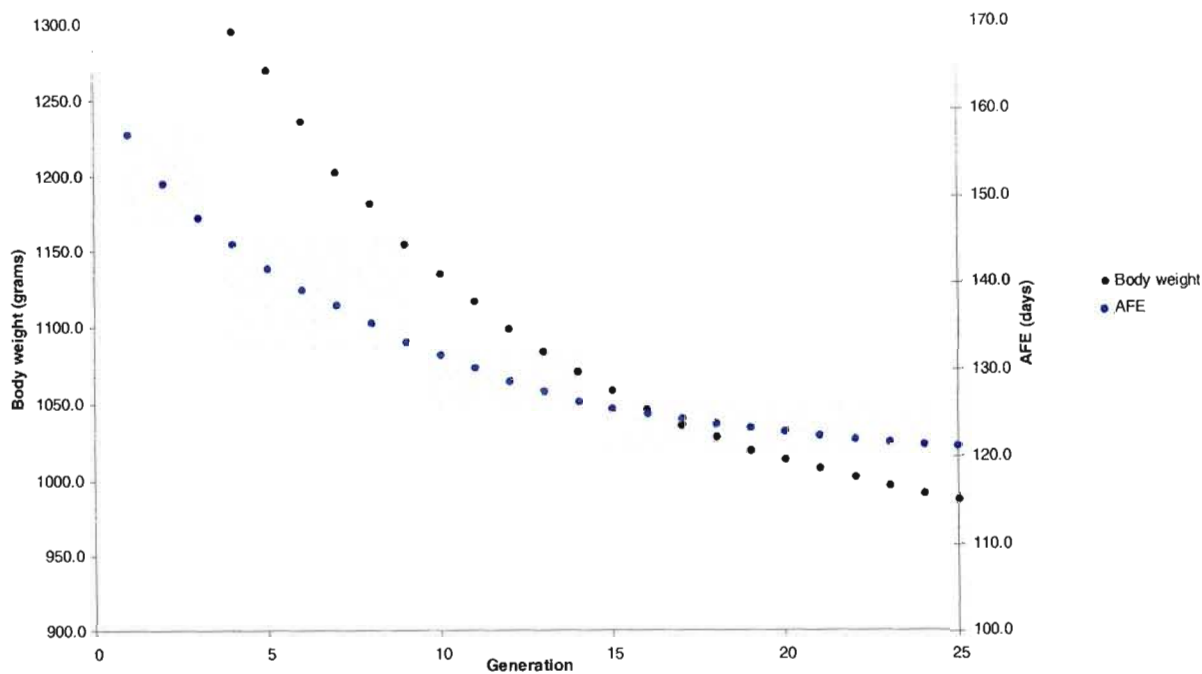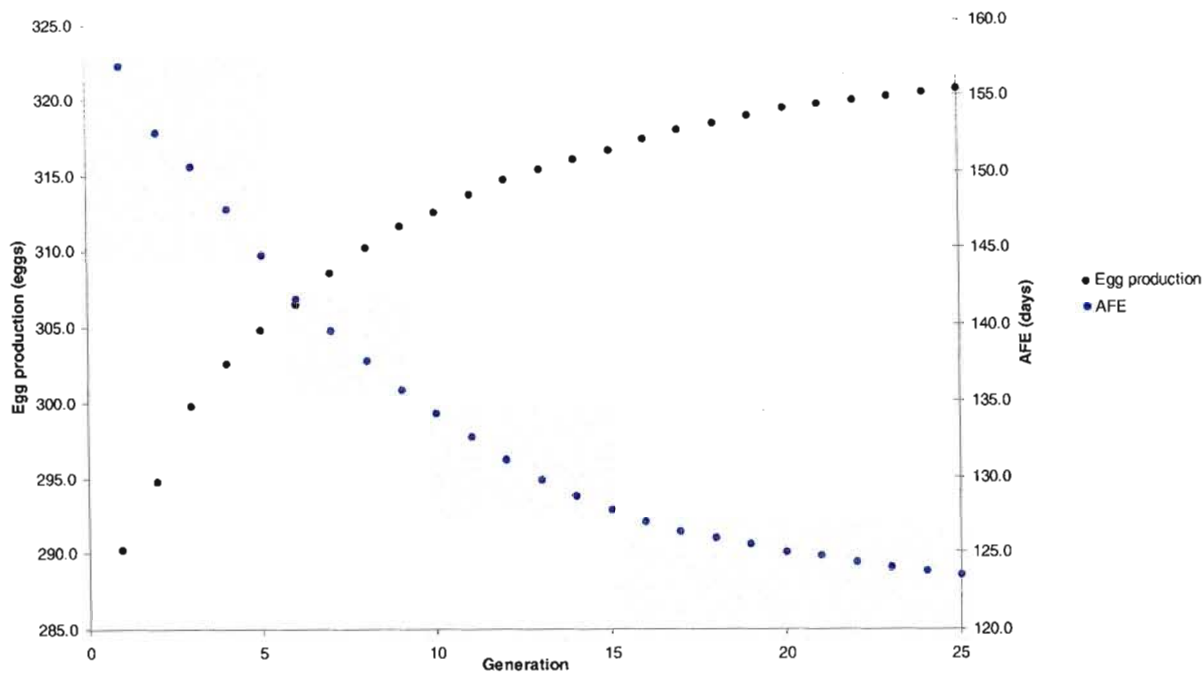
Figure 3.14 Combined response of egg production and AFE to multiple trait selection.

Table 3.14 illustrates the response to multiple trait selection when egg production and AFE were included in the index. It also illustrates the response in the standard deviations of these traits as a result of multiple trait selection. Egg production increased in each generation from 290.1641 eggs in generation one to 320.3645 eggs in generation 25. While the days taken to reach sexual maturity decreased from 157.2205 in generation one to 123.4811 in generation 25. The standard deviation of both traits declined steadily.

Table 3.14   Values of egg production and AFE and the standard deviations of these traits after each generation of multiple trait selection.

Generation	Egg production (eggs)	AFE (days)	Standard Deviation of egg production	Standard deviation of AFE
1	290.1641	157.2205	22.3451	10.8879
2	294.7135	152.7204	16.7271	8.6755
3	299.7621	150.5303	13.1764	8.3824
4	302.5400	147.7555	11.1182	7.4188
5	304.7143	144.7126	9.5858	6.8018
6	306.3916	141.7671	8.5292	5.8524
7	308.4945	139.6477	7.3683	4.9789
8	310.1430	137.6798	6.4024	4.3865
9	311.4626	135.8321	5.6395	4.1885
10	312.4073	134.1944	5.2651	3.9007
11	313.5915	132.5736	4.5393	3.4836
12	314.5361	131.0815	3.9234	2.9709
13	315.1741	129.7998	3.5946	2.5614
14	315.9045	128.7634	3.1268	2.3539
15	316.4790	127.8032	2.6908	1.9879
16	317.2024	126.9277	2.4365	1.6639
17	317.7799	126.2599	2.1310	1.4151
18	318.2051	125.8043	1.8859	1.3249
19	318.7030	125.4063	1.6102	1.1484
20	319.1157	124.9683	1.4405	1.0219
21	319.4252	124.6863	1.2079	0.8876
22	319.6535	124.3163	1.1069	0.8292
23	319.9219	123.9584	1.0451	0.7221
24	320.1209	123.6809	0.8747	0.5986
25	320.3645	123.4811	0.7862	0.5216

CHAPTER 4

DISCUSSION

4.1 USE OF COMPUTER MODELS

Computer models have previously been used to simulate selection strategies. For example, Muir (1997) used computer simulations to model the relationship between selection accuracy and response to selection as well as the relationship between selection intensity and effective population size. In this study, five computer models were developed to simulate the five selection techniques under comparison. The development of the models was a trial and error process. Each model was created and tested, only to discover that there was an error of some sort or that there was room for improvement. Each model would then be recreated and retested. This reiterative process of developing models and testing them continued until the best possible models were created.

An advantage of the models is that they could be created in a relatively short space of time and at a minimal cost. Once the best models had been created, all four traits could be run through one model in less than five minutes. Small changes needed to be made whenever a new trait was run through the model, such as changing the heritability and changing the starting population. The results were obtained without the costs of measuring characters, implementing breeding systems, feeding programs and housing chicken populations. However, the accuracy of the results of these models cannot be as accurate as if all these real life procedures had been implemented. Thus, the models and the results obtained from them can only be used as guidelines by breeders who must be made aware of the underlying assumptions of the models.

The models may also be useful from an educational perspective. The five models could be used to teach students the affects that different parameters (heritability, selection intensity and

standard deviation) have on the response to selection. The responses to different selection techniques as well as the changes in standard deviation following selection are displayed graphically and in table form providing students with a clear and visual summary of the effects of altering population parameters.

There are, however, a number of disadvantages to the models. A model will never exactly mimic a real life system or process as a number of assumptions need to be made before constructing a model, to take the place of the processes that the model cannot incorporate. Assumptions tend to decrease the accuracy of a model. There were a number of assumptions made when developing the models used in this investigation which have been listed in the materials and methods chapter (pages 31 and 32).

4.2 RESPONSE TO SELECTION MEASURED AS THE PERCENTAGE INCREASE AT EACH GENERATION

Each trait is measured in different units, it is thus difficult to compare the response to selection for the four traits. For example it is difficult to compare the response of egg production with the response of egg weight because egg numbers are being compared to grams. Table 4.1 therefore illustrates the percentage increases in each trait at selected generations for each selection method. Table 4.1 allows comparisons to be made because it standardizes the response in each generation for each trait into a percentage and these percentages are then comparable.

The last column in Table 4.1 labelled "$h^2 = 0.09$" was generated by running egg weight through the models, but instead of using the actual heritability of egg weight (0.51) a very low heritability was used (0.09). The reason for this is that it allows the effect of heritability to be tested without it being confounded with the effect of any other factors such as the variance. Comparisons can be made between the column "egg weight" and the column "$h^2 = 0.09$" to test the effect of heritability alone as all other factors are kept constant.

Table 4.1   Percentage increases in each trait at generation two and generation five for individual selection, between family selection, within family selection and family-index selection.

Selection method	Generation	Egg weight	Egg production	AFE	Body weight	$H^2 = 0.09$
Individual	2	5.2478	1.8775	4.3249	4.9357	1.0542
	5	13.7067	6.0332	11.2415	13.7004	2.6131
Between family	2	2.8958	2.1961	2.7436	3.0034	0.8023
	5	9.5896	5.2270	8.2960	11.3995	2.2903
Within family	2	3.3214	2.3687	3.0477	3.3519	0.9029
	5	9.9177	6.1886	8.6963	10.4916	2.2281
Family-index	2	5.5822	2.8512	4.4217	4.8030	1.2701
	5	11.6313	6.9988	11.8676	13.5300	2.6990

The next four sections will provide a brief comparison of the efficiencies of the four selection techniques.

4.3   INDIVIDUAL SELECTION

Individual selection is a technique where only the best few individuals are selected for breeding. Notwithstanding that this is useful in that the individuals with the best breeding values are selected (provided the trait has a reasonably high heritability), it does result in very similar individuals being selected in each generation (provided the selection intensity is sufficiently high), meaning that the variation will drop very rapidly in each generation until there is little to no variation left in the population to gain any significant response. The most striking result obtained from the model for individual selection was indeed the rapid drop in the standard deviation of all the traits (figures 3.2, 3.4, 3.6 and 3.8).

The implication of this rapid decrease in the standard deviation (σ_p) is that the response to individual selection (R) is going to slow down each generation and level off rapidly. The formula $R = i.h^2.\sigma_p$, which represents the selection response (Falconer and Mackay, 1996), highlights that as the standard deviation tends towards zero, so does the selection response. The response to individual selection for all traits showed favourable increases over approximately the first ten generations. This is because there is still sufficient variation in the population to gain a significant response to selection. Figures 3.1, 3.3, 3.5 and 3.7 illustrate how the selection response levels off after approximately ten generations. Due to the rapid loss of variation due to individual selection, this technique should not be applied to these traits for many more than fifteen generations. This was the result that was expected and correlated well with experimental results. Liu *et al.* (1994) reported a similar response to individual selection to the results obtained in this study when individual selection was applied to body weight at eight weeks of age. The response obtained by Liu *et al.* (1994) was about five times greater in the first half of the selection period than in the second, highlighting the effect of individual selection on the variation in a population.

The efficiency of individual selection for different traits can be compared using the values in table 4.1. Traits with high heritabilities, such as body weight (0.55) and egg weight (0.51), are expected to respond better to individual selection than traits with low heritabilities. After one cycle of individual selection (generation two) body weight had increased by 4.9357 percent and egg weight had increased by 5.2478 percent. By generation five body weight had increased by 13.7004 percent and egg weight had increased 13.7076 percent. These were the highest increases implying that these two traits responded best to individual selection.

AFE and egg production are traits with moderate to low heritabilities (0.41 and 0.22 respectively) and are not expected to respond as well to individual selection. This was shown to be the case as after one cycle of selection AFE had increased by 4.3249 percent and egg production had increased by 1.8775 percent. After five generations of selection AFE had increased by 11.2415 percent and egg production had increased by 6.0332 percent.

By comparing egg weight (h^2 = 0.51) with egg weight (h^2 = 0.09) it is clear that traits with high heritabilities respond a lot better to individual selection than traits with low heritabilities. The responses after one cycle of selection were 5.2478 and 1.0542 percent respectively. This very large difference in response is due only to the large difference in the heritabilities used, as all other factors were kept constant. When using this method of selection individuals are selected on the basis of there own phenotypic values and for traits with a high heritability the phenotype is a reliable indicator of the genotypic value. For this reason traits with a high heritability respond better to individual selection than traits with a low heritability (Lynch and Walsh, 2000).

4.4   BETWEEN FAMILY SELECTION

Between family selection involves selecting entire families with the best phenotypic family means (Lynch and Walsh, 2000). The most important implication of this is that by selecting entire families some individuals with poor phenotypic values will be selected for breeding based on the fact that their family means are high. Although this seems to be a disadvantage because individuals with lower breeding values are being used for mating, it is however very useful in maintaining the variation in the population. By selecting entire families some poor individuals, some moderate individuals as well as the better individuals will be selected. The variation amongst the individuals selected as parents will therefore be very high in comparison to the other selection methods. Figures 3.2, 3.4, 3.6 and 3.8 illustrate that after 25 generations of between family selection the standard deviation of the four traits has not yet reached zero.

Another reason as to why the standard deviation dropped so slowly when this method was implemented is that the assumption was made that there was no inbreeding. Under normal circumstances between family selection is expected to have the highest level of inbreeding out of all the selection techniques (Falconer and Mackay, 1996). Between family selection will result in fewer families being represented among the parents unless a large proportion of families are selected, which is undesirable as this would reduce the intensity of selection. Thus, with fewer families mating at random the chances of inbreeding are greater (Falconer and Mackay, 1996; Muir, 1997). This high occurrence of inbreeding would, in practice, result in a loss in variation

in the population especially over many generations of selection, as well as a reduction in the response to selection because inbreeding, in conjunction with selection, results in the loss of favourable alleles (Falconer and Mackay, 1996; Muir, 1997). The models constructed were, however, unable to incorporate inbreeding and because of this a lot of the variation that would have been lost due to inbreeding was kept in the population and therefore the response to selection was inflated.

The implication of the assumption of no inbreeding is that the response to between family selection will take a lot longer to level off than the response to any of the other selection methods and that this method will be more effective in the later generations. This is illustrated in figures 3.1, 3.3, 3.5 and 3.7. These figures illustrate that at generation 25 the curves for response to between family selection are yet to level off. In addition, because some poorer individuals, with lower breeding values, are being selected the response to between family selection rises slightly slower than the response to the other selection methods in the initial generations (tables 3.1, 3.3, 3.5 and 3.7).

Traits with high heritabilities are expected to respond worse to between family selection than they do to individual selection (Fairfull and Gowe, 1990). Egg weight increased by 5.2478 percent after one cycle of individual selection and by 13.7067 percent after five generations of individual selection (table 4.1). Egg weight only increased by 2.8958 percent after one cycle of between family selection and by 9.5896 percent after five generations of between family selection (table 4.1). This is evidence that a trait with a high heritability will not respond as well to between family selection as it will to individual selection.

Traits with low heritabilities (such as egg production) are expected to respond better to between family selection than they do to individual selection because the phenotypes of individuals for traits with a low heritability are poor indicators of the genotypic values (Falconer and Mackay, 1996). Information from a large number of the individual's relatives would therefore be a more accurate indicator of that individual's genotypic value than his single phenotypic value (Lynch and Walsh, 2000). Egg production increased by 1.8775 percent after one cycle of individual selection and by 6.0332 percent after five generations of individual selection. The same trait

increased by 2.1961 percent after one cycle of between family selection and by 5.2270 percent after five generations of between family selection (table 4.1). These results illustrate a very similar percentage response between the two methods. Between family selection produced a slightly higher response after one cycle of selection, which was expected, but produced a slightly lower response after five generations, which was unexpected, as egg production was expected to respond better to between family selection in all generations due to its low heritability. The effectiveness (87 percent as effective) of between family selection compared to individual selection for egg production (a trait with a low heritability) at generation five was, however, higher than the effectiveness (70 percent as effective) of between family selection compared to individual selection for egg weight (a high heritability trait) at generation five. Therefore, although between family selection did not always produce better responses than individual selection for egg production it was always comparatively more effective than individual selection for egg weight.

An explanation as to why between family selection produced slightly lower responses, on occasions, than individual selection for the traits with a low heritability is that environmental effects were not taken into account by the models. Between family selection is most useful when a large amount of individual-specific environmental effects (environmental effects unique to each individual) contribute towards the phenotypic variation (Falconer and Mackay, 1996; Lynch and Walsh, 2000). The large individual specific environmental deviations tend to cancel each other out in the family mean making the selection of entire families advantageous (Lynch and Walsh, 2000). This highlights the fact that a model is never an exact replica of the real life process that it is attempting to mimic and that there are often factors that cannot be incorporated into the model. It is important that people using the models are made aware of their limitations.

In previous experimental studies Kinney *et al.* (1970) used full sib family selection and half sib family selection to gain a 3.8 percent response in egg production and Garwood and Lowe (1979) used half sib family selection to gain a 0.7 percent increase in egg production. The results of the model developed in this study show slightly better responses to Garwood and Lowe (1979) and Kinney *et al.* (1970) with a response of 5.2270 percent after five generations of half sib family selection.

4.5 WITHIN FAMILY SELECTION

Within family selection involves selecting the individuals with the greatest deviation from the mean of the family to which they belong (Lynch and Walsh, 2000). The variation amongst the individuals selected as parents will be low because the most desirable individuals, which will be selected, from the population will generally be similar. This is particularly true when the selection intensity is suitably high and that there is a large amount of variation common to family members (Lynch and Walsh, 2000). There will, however, be more variation maintained in subsequent generations compared to individual selection because of the additional variation due to differences between families. Figures 3.2, 3.4, 3.6 and 3.8 illustrate the decline in the standard deviation and show that although the standard deviation drops very rapidly when using within family selection, the decline is intermediate between that of between family selection and individual selection. The standard deviation reaches zero in approximately generation 23 when using within family selection compared to individual selection where the standard deviation reaches zero at approximately generation 17.

In general the response to within family selection, like the response to individual selection, will decrease in each generation and level off at a certain point due to the decreasing standard deviation. The response to within family selection will increase favourably for approximately 15 generations and level off once the standard deviation begins to approach zero (figures 3.1, 3.3, 3.5 and 3.7).

Traits with high heritabilities are not expected to respond as well to within family selection as they do to individual selection (Falconer and Mackay, 1996). This is illustrated by the results of these two models where egg weight increased by 5.2478 percent after one cycle of individual selection and by 13.7067 percent after five generations of individual selection. The same trait only increased by 3.3214 percent after one cycle of within family selection and by 9.9177 percent after five generations of within family selection (table 4.1).

Traits with low heritabilities (such as egg production) are expected to respond better to within family selection than they do to individual selection, because the phenotypic values of traits with a low heritability are poor indicators of the genotypic values. Thus information from many relatives usually proves to be a more accurate indicator of an individuals breeding value (Lynch and Walsh, 2000). In this study, egg production increased by 1.8775 percent after one cycle of individual selection and by 6.0332 percent after five generations of individual selection. The same trait increased by 2.3687 percent after one cycle of within family selection and by 6.1886 percent after five generations of within family selection (table 4.1). At generation two and five the response to within family selection was only slightly higher than the response to individual selection.

One possible explanation as to why within family selection was only slightly more effective than individual selection for the traits with a low heritability is that environmental effects were not taken into account by the models. Within family selection is most useful when there is a large amount of environmental variation common to members of a family, and selecting within families helps to eliminate this large non-genetic variation and make selection more effective (Lynch and Walsh, 2000). This is an advantage that within family selection has over individual selection that could not be taken into account by the models.

4.6 FAMILY-INDEX SELECTION

Family-index selection involves calculating a weighted index of the between family and the within family components for each individual. Individuals with the highest index values are then selected as parents (Falconer and Mackay, 1996). The most desirable individuals will therefore be selected using all sources of information about the individual, implying that the standard deviation will again drop very rapidly because there will be very little genetic variation amongst the parents selected in each generation. Figures 3.2, 3.4, 3.6 and 3.8 illustrate this drop in standard deviation. The drop in standard deviation of the four traits as a result of family-index selection is very similar to the drop in standard deviation as a result of individual selection and reaches zero at about generation 17.

In the initial generations the response to family-index was generally higher than the responses to any of the other selection methods for all traits at any heritability value (tables 3.1, 3.3, 3.5 and 3.7). This result was expected as family-index selection takes all sources of information about an individual into account in the index value and thus the individuals with the best breeding values are selected under all circumstances. The reason this method is not widely used in breeding programs is that it is often economically and practically inefficient due to the costs of combining the selection methods, such as the necessity to obtain pedigrees (Falconer and Mackay, 1996; Lynch and Walsh, 2000).

For traits with high heritabilities (egg weight and body weight) the response was similar to the response to individual selection. This may be due to the fact that there is not a lot of environmental variance in highly heritable traits and that the little environmental variance that was present could not be accounted for in the model. The phenotypic value of an individual will, in such cases, be the best indicator of the genotypic value and thus individual selection will be almost as effective as family-index selection.

Sharma *et al.* (1998) used family-index selection to select for 40-week egg production and reported the following results. Over 16 generations of selection 80 percent of the total genetic gain was accounted for in the first eight generations after which the response slowed and levelled off. Poggenpoel *et al.* (1996) also reported positive progress over only the first ten generations of selection for egg production. The model for family-index selection produced results in line with these two studies. The model showed an initial rapid drop in the standard deviation and a good selection response, with a levelling off after approximately eight generations.

A selection method that retains the variation in the population for longer periods of time such as between family selection and within family selection, to a lesser degree, will produce better responses to selection in later generations. Figures 3.1, 3.3, 3.5 and 3.7 illustrate that the response to between family selection does indeed catch up to and exceed the response to family-index selection from approximately generation eight onwards. The response to within family selection nears the response to family-index selection in the later generations. This is also illustrated in tables 3.1, 3.3, 3.5 and 3.7.

4.7 SUMMARY OF SINGLE TRAIT SELECTION

The four selection techniques discussed all select for one trait at a time. The aims of the breeder will determine what trait is selected for. In chickens the majority of single trait selection experiments are applied to egg production and to a lesser degree, egg weight, as these are the most economically important traits in terms of total egg production. They are also the easiest to measure and most obvious traits to select for (Fairfull and Gowe, 1990). The genetic gain in all four traits in the first ten generations of selection will be compared in this section as after ten generations most of the responses tended to level off except that of between family selection.

Egg production is the most common trait used in selection programs and the majority of single trait selection experiments for this trait have shown positive genetic progress (Fairfull and Gowe, 1990). This trait has a relatively large amount of genetic variance for selection to act on and because it has a low heritability a family based method of selection is usually implemented. Results produced by the models show the sound reasoning for the use of family based methods. Individual selection for egg production resulted in a 25 egg increase after ten generations (a 2.5 percent increase per generation), family-index selection a 26.7 egg (2.7 percent) increase, within family selection a 25 egg (2.5 percent) increase and between family selection a 31.5 egg (3.2 percent) increase. These responses are in agreement with the results reported by Sharma *et al.* (1998) where egg production increased by 2.38 eggs per generation following family-index selection and Poggenpoel *et al.* (1996) where a response of 5.18 eggs per year was reported following ten generations of selection for part-record egg production.

Single trait selection for egg weight is common, due to its high heritability, but not as common as in egg production because there is a lot less variation in egg weight than there is in egg production (Sharma *et al.*, 1998). The average egg weight increased by 1.03 grams per generation in the first ten generations as a result of individual selection, 0.95 grams per generation as a result of between family selection, 0.87 grams per generation as a result of within family selection and 1.05 grams per generation as a result of family-index selection.

Age at sexual maturity may also be selected for. The models showed that individual selection resulted in birds taking on average 2.4 days fewer to reach sexual maturity per generation in the first ten generations, between family selection: 2.26 days fewer per generation, within family selection: 1.94 days fewer per generation and family-index selection: 2.5 days fewer per generation. AFE and egg production are negatively correlated and thus selection for increased egg production results in the desired decrease in the days taken to reach sexual maturity. Because of this correlation not a lot of emphasis is given to single trait selection for AFE but instead this trait is usually selected for in combination with egg production (Fairfull and Gowe, 1990; Poggenpoel *et al.*, 1996; Sharma *et al.*, 1998). In addition, the age at which hens begin to lay is physiologically limited. Birds need time to build up sufficient energy reserves before they begin laying, and hens that begin to lay too early will lay very light eggs (Gowe and Fairfull, 1995) and the implication of this is that too much selection pressure cannot be given to AFE. This physiological limit on AFE could not be taken into account by the models, which therefore may have produced birds that begin laying too early. In addition because birds that begin laying early will produce more eggs the models may have produced inflated egg production results.

The models highlighted that body weight showed a positive response to single trait selection, especially to individual selection and family-index selection, because of its high heritability. There is, however, very little benefit gained from attempting to increase body weight in egg laying birds due to the additional feeding costs for heavier birds that tend to cancel out the benefits gained. Very little attention is thus given to single trait selection for body weight when egg production is of primary interest (Appleby *et al.*, 1992). Body weight is, however, correlated to many of the important egg production traits and therefore cannot be totally ignored when dealing with egg laying birds. These correlations will be discussed in the following section.

4.8   INDEX SELECTION

The models for individual selection, between family selection, within family selection and family-index selection discussed previously have assumed that there are no correlations between traits. However, when selecting for a particular trait, there will often be correlated responses in other economically important traits.   These correlated responses may be favourable or unfavourable and must thus be taken into account. A model for index selection was developed in order to study the effect of selecting for two traits simultaneously in a chicken population. With the four traits being used in this study there were six possible combinations of traits that will be discussed in the following sections.

4.8.1   Egg weight and egg production

Egg weight and egg production are both traits with high economic weightings (413.69 and 241.55 respectively). It is therefore desirable to gain a response in both of these traits. Figure 3.9 illustrates that this did not happen when these two traits were included in an index together. Instead egg production responded well and egg weight did not respond well, with the average weight of eggs decreasing quite dramatically. The reason why this happened was that even though both traits had high economic weightings there was also a very high negative genetic correlation between the two traits ($r = -0.5$). It is therefore impossible to select for one of these traits and gain a positive correlated response in the other using index selection.

The possible reason as to why egg production increased in preference to egg weight was that even though egg weight had a higher economic weighting than egg production, it had a much lower standard deviation (3.87 as opposed to 23.06). The response to selection is directly proportional to the variance of a trait; it would thus be easier to gain an improvement in egg production because there is more variation present. Egg production therefore received a more favourable index weighting value (b-value).

Similar results have been found in breeding experiments when egg weight and egg production have been considered simultaneously. Sharma *et al.* (1998) reported a negatively correlated response between these two traits. An increase in egg number (4.46 to 4.72 eggs per generation in the first eight generations) was accompanied by a decrease in egg weight of between -1.67 and -0.79 grams per generation in the first eight generations. In addition, Poggenpoel *et al.* (1996) used an independent culling method to select for these two traits simultaneously. A hen's index for egg number as well as her egg weight was taken into account. Using this method they were able to gain an increase in egg weight; however, egg production declined slightly.

4.8.2   Egg weight and body weight

Multiple trait selection was applied to egg weight and body weight, using the model for index selection. These two traits have a genetic correlation of 0.3 and a phenotypic correlation of 0.3. The implication of this is that larger birds will produce larger eggs. Figure 3.10 illustrates the response of these two traits to multiple trait selection showing that both traits increase simultaneously. Egg weight increased rapidly at first and then levelled off due to a loss in the standard deviation (table 3.10). The opposite was true for body weight, where the response was slow at first but faster in the later generations. The results obtained by Sharma *et al.* (1996) were in accordance with these results, with egg weight showing a genetic gain of -0.51 grams per generation and body weight showing a genetic gain of –11.73 grams per generation, indicating that the two traits are positively correlated and do respond in the same direction.

The reason why the response to selection was greater for egg weight in the initial generations was that the economic weighting of body weight was zero, implying that there will be no economic gain as a result of improving this trait. In contrast, the economic weighting of egg weight was high (413.69). It is therefore expected that egg weight will initially respond well to multiple trait selection in this case and that the slow increase in body weight was due to its positive genetic correlation with the more economically favourable egg weight. The reason for the increased response to selection in body weight in the later generations was that the standard deviation of egg weight reached zero at about generation 17. There was therefore no variation in

egg weight left for selection to act upon. There was, however, a large amount of variation left in body weight leading to substantial increases in the later generations.

4.8.3 Egg weight and AFE

Egg weight and AFE are positively correlated both genetically (0.4) and phenotypically (0.2), implying that birds that take longer to reach sexual maturity will produce heavier eggs. Poggenpoel *et al.* (1996) reported that when egg weight increased so did AFE. However, when the weight of eggs decreased, the number of days taken to reach sexual maturity also dropped. Breeders therefore need to decide between hens that take fewer days to reach sexual maturity (and therefore lay more eggs) but produce lighter eggs on average and hens that take longer to reach sexual maturity but produce heavier eggs.

The results of the selection index used in this study indicated that hens that take longer to reach sexual maturity and produce heavier eggs will produce higher economic gains than hens that take fewer days to reach sexual maturity (figure 3.11). The model thus implies that this would be the better selection strategy.

4.8.4 Body weight and egg production

Body weight and egg production have a genetic correlation of -0.1 and a phenotypic correlation of -0.1. These correlations are quite low implying that there is only a slight negative relationship between these two traits. The response of these two traits to multiple trait selection is illustrated in figure 3.12, which indicates that egg production increases rapidly until it reaches a plateau at approximately generation 15 and body weight declines steadily. This result is to be expected due to the small negative correlation between the two traits and because egg production has higher economic weighting value (241.55 as opposed to 0). Similar results were reported by Poggenpoel *et al.* (1996) and Sharma *et al.* (1998) where an increase in egg production was accompanied by a decrease in body weight.

4.8.5 Body weight and AFE

The genetic correlation between body weight and AFE is 0.4, which is a high positive correlation. The two traits are therefore expected to respond to selection in the same manner, which was evident from the results reported by Sharma *et al.* (1996). An increase in body weight would thus result in an increase in the number of days taken to reach sexual maturity and vice versa.

Figure 3.13 illustrates that both traits decrease. This result is expected because, even though body weight has a high standard deviation (81.85) it has an economic weighting of zero implying that there will be no economic gain if this trait is increased. Selection therefore acts by decreasing the number of days taken to reach sexual maturity and, therefore, increasing the number of eggs produced by each bird.

4.8.6 Egg production and AFE

Egg production and AFE are highly negatively correlated. The genetic correlation between the two traits is -0.4 and the phenotypic correlation between the two traits is -0.3. Therefore hens that begin to lay eggs sooner (decreased AFE) will produce more eggs.

Figure 3.14 illustrates the response of these two traits to multiple trait selection. Because egg production has a higher economic weighting value and a higher standard deviation that AFE the selection index favoured this trait over AFE (higher b-values were given to egg production). The result of this would be an increase in egg production and because of the high negative correlation between egg production and AFE there would also be a decline in the number of days taken to reach sexual maturity.

Sharma *et al.* (1998) reported that in the first eight generations of selection egg production increased by 4.46 to 4.72 eggs per generation while AFE decreased by 4.63 to 6.39 days per

generation. Poggenpoel *et al.* (1996) found similar relationship between these traits supporting the results obtained from the model.

4.9   CONCLUSION

The majority of the results produced by the five models were expected and in accordance with results from previous studies. There were, however, a few unexpected results due to the assumptions that had to be made in constructing the models. The most significant assumption was that of no inbreeding which lead to the slow decline in the variation of the traits when between family selection was applied and as a result an inflated response to this method of selection. In addition, the inability to account for environmental effects lead to the results of the model for within family selection not being as effective as desired for traits which have a low heritability. The development of models that can relax some of these assumptions and therefore improve the accuracy of the results is an area that can be worked on in future studies of this nature.

Nevertheless, it can still be concluded from the results that at higher heritabilities individual selection is more effective than between and within family selection and at lower heritabilities some form of family based selection is more effective. It is, however, most beneficial to use family-index selection in most cases provided that the cost involved in implementing this method of selection is not too high.

The results obtained from the index selection model illustrate that correlations between traits must be considered in any breeding program. For example, when selecting for egg laying birds, egg production is usually selected for, but this trait is negatively correlated with the desirable trait of egg weight. In contrast, the age at first egg is negatively correlated with egg production which is desirable.

There are a number of different parameters that have to be considered by breeders when making selection decisions. Breeders need to formulate their breeding goals and determine the best

method of achieving them. One method of planning a breeding strategy may be the use of computer simulations.

REFERENCES

Appleby, M.C., B.O. Hughes and H.A. Elson. 1992. *Poultry production systems: Behaviour, management and welfare.* 1-8. C.A.B. International, Great Britain.

Burnside, E.B., G.B. Jansen, G. Civati and E. Dadati. 1992. Observed and theoretical trends in a large dairy population under intensive selection. *Journal of Dairy Science.* 76: 2242-2253.

Crawford, R.D. 1990. Origin and history of poultry species. In: *Poultry breeding and genetics.* (Ed. Crawford R.D). 705-760. Elsevier Science Publishers, Netherlands.

Crawford, R.D. 1995. Origin, history and distribution of commercial poultry. In: *World animal science: Poultry production, volume C9.* (Ed. Hunton P). 1-20. Elsevier Science Publishers, Netherlands.

Dalton, C. 1981. *An introduction to practical animal breeding.* Granada Publishing Limited, Great Britain.

Fairfull, R.W. and R.S. Gowe. 1990. Genetics of egg production in chickens. In: *Poultry breeding and genetics.* (Ed. Crawford R.D). 705-760. Elsevier Science Publishers, Netherlands.

Falconer, D.S. and T.F.C. Mackay. 1996. *Introduction to quantitative genetics, 4th ed.* Longman Group, New York.

Flock, D.K. and R. Preisinger. 2002. Breeding plans for poultry with emphasis on sustainability. *Proc.7thWCGALP.* 33: 273-280.

Francesch, A., J. Estany, L. Alfonso and M. Iglesias. 1997. Genetic parameters for egg number, egg weight and eggshell colour in three Catalan poultry breeds. *Poultry Science*. 76: 1627-1631.

Garwood, V.A. and P.C. Lowe. 1979. Comparison of individual, sire family and index selection for short term rate of egg production in chickens. *Poultry Science*. 58: 751-753.

Gowe, R.S. and R.W. Fairfull. 1995. Breeding and genetics of egg laying chickens. In: *World animal science: Poultry production, volume C9*. (Ed. Hunton P). 435-451. Elsevier Science Publishers, Netherlands.

Hartmann, C., K. Johansson, E. Strandberg and L. Rydhmer. 2003. Genetic correlations between the maternal genetic effect on chick weight and the direct genetic effects on egg composition traits in a white leghorn line. *Poultry Science*. 82: 1-8.

Hastings, A. 1997. *Population biology: concepts and models*. Springer, New York.

Hicks, C., W.M. Muir and D. A. Stick. 1998. Selection index updating for maximizing rate of annual genetic gain in laying hens. *Poultry Science*. 77: 1-7.

Jiang, X., A.F. Groen and E.W. Brascamp. 1998. Economic values in broiler breeding. *Poultry Science*. 77: 934-943.

Kennewell, S. E. 2000. The role of computer modelling in the teaching and learning of algebra to pupils aged 11-14. *Unpublished PhD Thesis*. University of Wales, Swansea.

Kinney, T.B., B.B. Bohren, J.V. Craig and P.C. Lowe. 1970. Responses to individual, family or index selection for short term rate of egg production in chickens. *Poultry Science*. 49: 1052-1064.

Ledur, M.C., R.W. Fairfull, I. McMillan and L. Asseltine. 2000. Genetic effects of aging on egg production traits in the first laying cycle of White Leghorn strains and strain crosses. *Poultry Science.* 79: 296-304.

Ledur, M.C., L.E. Liljedahl, I. McMillan, L. Asseltine and R.W. Fairfull. 2002. Genetic effects of aging on egg quality traits in the first laying cycle of White Leghorn stains and strain crosses. *Poultry Science.* 81: 1439-1447.

Lewis, P.D., T.R. Morris and G.C. Perry. 1999. Light intensity and age at first egg in pullets. *Poultry Science.* 78: 1227-1231.

Liu, G., E.A. Dunnington and P.B. Siegel. 1994. Responses to long-term divergent selection for eight-week body weight in chickens. *Poultry Science.* 73: 1642-1650.

Lynch, M. and B. Walsh. 1998. *Genetics and analysis of quantitative traits.* Sinauer Associates, Inc., Massachusetts, U.S.A.

Lynch, M. and B. Walsh. 2000. *Evolution and selection of quantitative traits.* 239-292.

Manson, J.M. 1972. Body weight, egg weight and egg production. In: *Egg formation and production.* (Eds. Freeman, B.M. and P.E. Lake). 115-138. British Poultry Science Ltd., Edinburgh.

Mills, J.D. 2002. Using computer simulation methods to teach statistics: A review of the literature. *Journal of statistics education.* [Online], 10(1). (www.amstat.org/publications/jse/v10v1/mills.html)

Muir, W.M. 1997. Genetic selection strategies: Computer modelling. *Poultry Science.* 76: 1066-1070.

Podlich, D.W. and M. Cooper. 1998. Qu-gene: A simulation platform for quantitative analysis of genetic models. *Bioinformatics*. 14: 632-653.

Poggenpoel, D.G., G.F. Ferreira, J.P. Hayes and J.J. Du Preez. 1996. Response to long term selection for egg production in laying hens. *British Poultry Science*. 37: 743-756.

Rishell, W.A. 1997. Symposium: Genetic selection-strategies for the future breeding and genetics-historical perspective. *Poultry Science*. 76: 1057-1061.

Robinson, S. 1994. *Successful simulation: A practical approach to simulation projects*. McGraw-Hill Book Company, England.

Sharma, D., D.C. Johari, M.C. Kataria, R.C. Hazary, D. Choudhari and S.C. Mohapatra. 1998. Factors affecting direct and correlated responses in a White Leghorn population under long term selection for egg number. *British Poultry Science*. 39: 31-38.

Siegel, P.B. and E.A. Dunnington. 1997. Genetic selection strategies-population genetics. *Poultry Science*. 76: 1062-1065.

Snustad, D.P. and M.J. Simmons. 2003. *Principles of genetics 3rd ed*. John Wiley & Sons, Inc., U.S.A.

Soderberg, P. 2003. An examination of problem-based teaching and learning in population genetics and evolution using EVOLVE, a computer simulation. *International Journal of Science Education*. 25, 1: 35-55.

Spies, A.A.B., F.E. Robinson, R.A. Renema, J.J.R. Feddes, M.J. Zuidhof and R.C. Fitzsimmons. 2000. The effects of body weight and long ahemeral days on early production parameters and morphological characteristics of broiler breeder hens. *Poultry Science*. 79: 1094-1100.

Starfield, A.M. and A.L. Bleloch. 1991. *Building models for conservation and wildlife management*. 1-15. Macmillan Publishing Company, England.

Starfield, A.M., K.A. Smith and A.L. Bleloch. 1990. *How to model it. Problem solving for the computer age*. 1-14. McGraw-Hill Publishing Company, England.

Szydlowski, M and T. Szwaczkowski. 2001. Bayesian segregation analysis of production traits in two strains of laying chickens. *Poultry Science*. 80: 125-131.

Tai, G.C.C., A. Murphy and H. De Jong. 1996. Comparison of efficiency of alternative selection strategies: An example of selection for resistance to common scab in potatoes. *Canadian Journal of Plant Science*. 76: 849-852.

Zhao, B., I.J. Mackay, P.D.S. Caligari and R. Mead. 1997. The efficiency of between and within full-sib family selection in a recurrent selection program in sugar beet. *Euphytica*. 95: 355-359.