STUDIES ON GENETIC DRIFT AND INBREEDING IN SMALL POPULATIONS UNDER ARTIFICIAL SELECTION

by

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ABSTRACT

The effects of population size, mating strategy, and selection on selection response, genetic drift, and variability of response were studied in small Japanese quail populations. The effects of population size on genetic gain, variability of response and inbreeding were examined for a 3 generation phenotypic selection experiment. Effective population sizes of 12 (Large) and 6 (Small) per replicate were evaluated at the same selection intensity. The selection criterion was Week 2 body weight in Japanese quail. Estimates of genetic gain at Generation 3 were 10.67 and 8.89 grams, respectively for the large and small populations.

A selection experiment involving 3 mating strategies was conducted in order to evaluate the efficiency of selection and effectiveness of reducing genetic drift and/or inbreeding in small populations. The mating strategies used were random (RM), minimum coancestry (MN), and maximum coancestry (MX) mating. Genetic gain at Generation 3 was 7.03, 7.36 and 6.62 grams and inbreeding levels were 6%, 4% and 12% in the RM, MN and MX lines, respectively. After 3 generations of selection, inbreeding effective population size had declined by 62% in the MX lines. In the MN lines, inbreeding effective population size increased by 16%.

The effects of inbreeding on reproductive performance were studied in the large and small populations (Experiment I) and the RM, MN and MX lines (Experiment II). Ten percent increase in the embryo's inbreeding caused about 10% reduction in fertility in both experiments. Ten percent increase in the embryo's inbreeding caused 10% reduction in hatchability in Experiment I and RM lines in Experiment II, and about 13% reduction in hatchability in MX lines.

The goal of short-term selection has been to maximize genetic gain. Results from the present study suggest that the goal of a breeding program for small populations should shift from
maximization of response to optimization of genetic gain and effective population size. Among the factors to be optimized are rate of selection, variability of response, inbreeding depression in the selection trait and fitness. Restriction of family size coupled with the use of either circular pair or maximum avoidance mating is preferred over within-family selection under random mating or mass selection with maximum avoidance in terms of reducing inbreeding in small populations undergoing artificial selection.
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DEDICATION

To my Mom and Dad

for the vision they gave me to pursue.

"I want to know the thoughts of God;
the rest are details". (Albert Einstein)
CHAPTER 1

1. GENERAL INTRODUCTION

1.1. POPULATION SIZE, RANDOM GENETIC DRIFT AND SELECTION

Wright (1922, 1939, 1978) has advocated the importance of sampling effects in small populations. Artificially selected populations of farm or laboratory animals usually have small effective population size \( (N_e) \) in the range of 10 to 100, rarely as large as 1000, with selection pressure on one or few traits is high (Hill and Keightley, 1988). The genes passed from one generation to the next are a sample of genes from the parent generation. Therefore, the gene frequencies are subject to sampling error between successive generations, and the smaller the number of parents, the greater the sampling variation (Wright, 1948; Falconer, 1989).

Wright (1922) was the first to discuss the effects of population structure on response to artificial selection. He proposed a structure of repeated cycles of subdividing a population and practising within and between-line selection and crossing to be more effective in bringing about genetic (gene frequency) changes than selecting within a single large population (Wright, 1939). The idea that population structure might be manipulated to alter gene frequency requires simultaneous consideration of all processes by which gene frequencies may change. Wright (1948, 1955) further characterized the mode of change of gene frequency according to the degree of determinacy. First, factors which tend to bring about directed changes according to some definite function of the gene frequencies. These are recurrent mutation, recurrent immigration and crossbreeding, and selection. Secondly, fluctuations that are indeterminate in direction but
determinate in variance. These include fluctuations about the mean values of the coefficients for the steady processes and fluctuations due to sampling in the parentage of each generation. The random fluctuations tend to cause random drift from an equilibrium point. Thirdly, changes in gene frequency that are best treated as indeterminate in both means and variance e.g. nonrecurrent mutations, unique hybridization, nonrecurrent selective events, unique extreme reduction in numbers.

There is an extensive theory in quantitative genetics for predicting the variance in mean performance between replicated small populations and the expected genetic variance within such populations (Crow and Kimura, 1970; Falconer, 1989). Results are obtained readily in the absence of selection (Hill, 1980). Gene frequency can change by chance due to mendelian sampling. The problem arises as to how important is the role played by random fluctuations. Kimura (1955a) and Dobshansky and Pavlovsky (1957) noted that the role played by chance during sampling depended on the prevailing population structure, especially its size. All variations in gene frequencies which are indeterminate in direction have been classified by Wright (1949a) as random genetic drift. The magnitude of these effects can be described by introducing the concept of idealized random breeding population (Crow, 1954) in which the offspring come from pairs of gametes drawn randomly from an infinite pool to which each parent has contributed equally. The number of progeny contributed by individual parents will have a binomial distribution. Small shifts in the gene ratios of all segregating factors do occur from generation to generation due to the errors in random sampling in the process by which the gametes available in any one generation are chosen to constitute the next. This may also cause an increase in the frequencies of homozygotes at the expense of heterozygotes. Such chance deviation will be
greater when the population size is small (Wright, 1931, 1932, 1938, 1948). Errors in sampling are negligible in large populations but are of great importance in small populations (Kimura, 1955b).

Artificial selection is considered by most geneticists as the main force for changing gene frequency. Selection changes gene frequencies and induces linkage disequilibrium between selected loci (Lush, 1945; Bulmer, 1971). In case of directional selection, the induced disequilibrium consists of a lack of extreme combinations, which leads to negative covariances between gene effects, and therefore, leads to a reduction in genetic variance in the selected parents. The linkage disequilibrium is only halved by recombination during meiosis (if there is no physical linkage between the loci). Therefore, even with no change in gene frequencies, the genetic variance in the offspring is lower than the initial generation. The relative magnitude of these two effects depends on the number of loci involved and the initial gene frequencies. When the number of loci is large, this change and its consequences can be neglected (Crow and Kimura, 1970).

Quantitative geneticists usually assume that a quantitative trait is determined by an infinite number of additive (nonepistatic) and unlinked loci. However, simulation studies by Mäki-Tanila and Kennedy (1988) suggest that animal models provide a good approximation of breeding values for traits controlled by a small number of loci (even if selection has occurred) if the genetic model is additive. Their results on response to three generations of selection were estimated with an animal model for a trait controlled by two loci with a heritability of .5. Three frequencies of the favourable alleles were considered (q = .1, .5 and .9). Selection response tended to be underestimated slightly if frequency of the favourable allele was low and
overestimated if frequency was high. For low frequency, the genetic model assumed tended to underestimate true genetic variance because the additive genetic variance would increase as q increased up to .5. For high frequency, true genetic variance was slightly underestimated as q approached fixation. A finite number of loci and recombination rates different from half introduce difficulties: (i) the linkage equilibrium induced by selection is not simply halved by recombination, (ii) the usual coefficient of inbreeding is lower than the probability of gene identity at selected loci (Robertson, 1977; Chevalet, 1988). The lower the number of loci and the higher their linkage, the faster is the decrease in genetic variance and the lower is the cumulated genetic gain expressed in initial genetic standard deviation units (Verrier et al., 1991).

Artificial selection theory has been concerned almost entirely with the prediction of the rate of response to various selection pressures. Selection may be expected to increase the frequency of favourable alleles until they reach fixation. However, in small populations there is a possibility that one allele may be fixed by chance even though there are more desirable ones in the population (Robertson, 1960). Thus, the cumulative effects of selection and genetic drift over generations may yield a mean response less than predicted from selection alone. The influence of drift on selection has been demonstrated for traits controlled by single genes (Kerr and Wright, 1954a, b) but has received little experimental consideration for quantitative traits.

In small populations, genetic drift causes variation among selection lines resulting in variation in mean response (Hill, 1971) as well as variation in within-line additive genetic variance (Bulmer, 1976; Avery and Hill, 1977). This increased variance means that drift leads to a dispersion of gene frequencies between replicates, up to the doubling of the initial variance and at fixation there is no variability within lines. In small populations, the additive genetic
variance within lines and consequently the response to selection are reduced by random genetic
drift (Madalena and Hill, 1972). A small effective size will give rise to a higher chance of drift
and will also limit the long-term response in both the utilization of desirable genes and failure
to capture valuable mutants (Hill, 1985; 1986). Since genetic drift is related to effective
population size, it should be possible to determine an effective population size required in a
selection program to minimize the effects of genetic drift.

1.2. INBREEDING

Inbreeding is the mating of related individuals and the degree of relationship between
individuals depends on the population size (Wright, 1931). Inbreeding causes random changes
in gene frequency and increases the proportion of less favourable recessive alleles made
homozygous (Robertson, 1960; Hill and Robertson, 1966; Dickerson, 1972). In small
populations, inbreeding may lead to an initial increase in the within-line genetic variance for traits
controlled by recessive genes (Robertson, 1952). The increase in the within-line variance occurs
only for rare recessive genes which are almost hidden in outbred populations but may appear at
a greatly increased frequency within inbred lines. Within-line genetic variance due to recessive
genes attains a maximum at inbreeding levels of 50 percent and then declines under further
inbreeding as line becomes completely isogenic.

The deleterious effects of inbreeding are of major concern in developing inbred lines
especially those founded with small population size. Various authors (Fisher, 1965; Templeton
and Reed, 1983; Kang and Neustaedt, 1987) have proposed the use of inbreeding to purge the
population of its lethals. Inbreeding can also be used to increase the rate of response to selection
for additive gene effects (Dickerson, 1977). However, this depends on the expected increase in the total variance and selection among sublines, but is limited by generation interval and any consequent reduction in selection intensity or effective population size.

Selection is expected to be less effective in a population of smaller size, except for more effective elimination of rare recessive lethals and semi-lethals which have little influence on performance in crosses in the heterozygous state (Crow, 1952). Selection acts on the genetic variance indirectly by changing family structure and therefore enhancing loss of variation through inbreeding if the population is of limited size (Lush, 1946; Robertson, 1961). In closed populations under selection, there is an additional increase in inbreeding due to small effective population size. As inbreeding accumulates, the genetic variance and thus the rate of response to selection are reduced. Additionally, if directional dominance effects are important, inbreeding reduces the mean phenotypic value of a population, a phenomenon referred to as inbreeding depression (Davenport, 1908; Crow, 1952). The underlying genetic basis of inbreeding depression is still unclear (Mitton, 1993; Crow, 1993). However, there are two hypotheses, the dominance hypothesis and the overdominance hypothesis, that explain inbreeding depression and its converse, heterosis (Crow, 1952). The dominance hypothesis states that inbreeding depression is due to the expression of many recessive genes maintained in populations by mutation-selection balance (Davenport, 1908; Crow, 1952). The overdominance hypothesis argues that inbreeding depression is due to reduction in heterozygote superiority at specific loci (East, 1908; Crow, 1952). In most domestic animal species studied to date, inbreeding has been shown to cause a decline in reproduction and viability (Bowman and Falconer, 1960; Latter and Robertson, 1962; Falconer, 1989; Abplanalp, 1990; Gama and Smith, 1993).
Keller et al. (1990) investigated the importance of different factors affecting response to selection in a closed line. They showed that inbreeding depression could be a major factor in reducing response to selection. When loci combine additively, the change in means from inbreeding is directly proportional to the coefficient of inbreeding (Falconer, 1989). However, if there is epistatic interaction between loci, the relation between the means and inbreeding coefficient is not linear (Crow and Kimura, 1970). The non-linearity is due to the interaction of double or multiple heterozygotes. No other form of interaction affects the linearity, and epistasis without dominance cannot itself cause any inbreeding depression (Falconer, 1989).

To study the effect of rate of inbreeding on inbreeding depression, different mating strategies could be used to generate inbreeding levels among sublines. Consequently, a mating strategy that leads to slower rates of inbreeding should cause less inbreeding depression than a mating strategy which causes higher rates of inbreeding. Mating of close relatives within a line would lead to a greater initial level of inbreeding but to a lower rate of final approach to the limit. Conversely, mating systems of less related individuals would lead to lower initial levels of inbreeding but to a higher final rate of approach to the limit (Shoffner et al., 1953; Robertson, 1964; Robinson and Bray, 1965). In selection experiments, effective population size calculated from the increase in Wright's (1922) inbreeding coefficient is known as inbreeding effective number. Effective population size calculated from the changes in gene frequencies is referred to as the variance effective population size (Crow, 1954).
1.3. EFFECTIVE POPULATION SIZE (NUMBER)

The concept of effective population size was introduced by Wright (1931) as a measure of relating observed numbers and population properties such as increase in homozygosity. Crow (1954) related the change in gene frequency to population size and made the distinction between inbreeding and variance effective population size. Wright's (1931) procedure was based on the probability of homozygosity due to common ancestry and hence became known as the inbreeding effective population size ($N_e$). The amount of allele-frequency drift per generation as measured by its variance was also used to describe the variance effective population size ($N_v$) (Crow, 1954; Kimura and Crow, 1963a). The inbreeding effective population size is closely related to the number of parents since it is based on the probability of two random gametes having to come from the same parents and $N_v$ is more related to the progeny number.

The effective population size ($N_e$) is one of the most widely used concepts in population genetics. The census number ($N$) hardly ever reveals accurately the effects of inbreeding and gene frequency drift. The effective population number is thus a surrogate population number that correctly reflects these effects. The effective population size is the number of individuals that would give rise to the calculated sampling variance or rate of inbreeding as if they are bred in the manner of an idealized population. The ideal population has a constant total number from generation to generation, has random distribution of progeny number, and gametes unite at random. Effective population size has been derived under various models including self-fertilization (Wright, 1931, 1969; Crow, 1954; Crow and Morton, 1955; Latter, 1959; Kimura and Crow, 1963a; Crow and Kimura, 1970; Crow and Denniston, 1988; Caballero and Hill, 1992). This study will be confined mainly to separate-sexed populations which are of
significance to animal breeding.

1.3.1. Inbreeding effective population size

From the standpoint of change in heterozygosity, with self-fertilization excluded, in a completely random union of gametes in a constant population size of $N$ monoecious individuals, where the distribution of progeny is random, $N_{ef}$ is approximated by Wright (1931, 1969) as

$$N_{ef} = N + \frac{1}{2}$$ (1.1)

Equation (1.1) follows the assumptions of an ideal population. Any actual population will depart from such assumptions to some extent. Some causes of departure are nonrandom mating, varying population number, unequal sex ratio, and variation in viability or fertility which result in a non-random distribution of progeny numbers (Crow, 1954). In a monoecious population with non-random distribution of progeny number, $N_{ef}$ is estimated from the rate of inbreeding. Assuming that the $N$ individuals furnish varying number of gametes to the next generation, the mean number, $\mu$, per individual is 2. $N_{ef}$ is given by Wright (1939) as

$$N_{ef} = \frac{4N - 2}{\sigma_k^2 + 2}$$ (1.2)

where $\sigma_k^2$ is the variance in progeny number. When the number of progeny per parent is constant, $\sigma_k^2 = 0$, Equation (1.2) reduces to $N_{ef} = 2N - 1$. The inbreeding effective size is approximately twice the actual census number.
In domestic and laboratory animals, the sexes are often unequally represented among breeding individuals since it is more economical whenever possible to use fewer males than females. Wright (1931) showed that under random mating, $N_{el}$ can be approximated as

$$N_{el} = \frac{4N_{m-2}N_{f-2}}{N_{m-2}N_{f-2}}$$

(1.3)

where $N_m$ is the number of males, $N_f$ the number of females, and $t$ the generation in which inbreeding effect is manifest.

For a dioecious population, Crow and Denniston (1988) have derived an expression for $N_{el}$ taking into consideration the variability in progeny number of both male and female parents. Assuming discrete generations, no selection and no correlation between fertility of parent and its progeny, the following equation holds;

$$\frac{1}{N_{el}} = \frac{\sigma_{mn,mf} + \mu_{mn} \mu_{mf}}{4N_{m,t-2} \mu_{mn} \mu_{mf}} + \frac{\sigma_{fn,ff} + \mu_{fn} \mu_{ff}}{4N_{f,t-2} \mu_{fn} \mu_{ff}}$$

(1.4)

where $\sigma_{mn, mf}$ is the covariance of the number of male and female progeny of a parent of sex $s$ ($s = m$ or $f$), $\mu_{mn}$ and $\mu_{mf}$ are the mean number of sons and daughters of a parent of sex $s$, and $N_{s,t-2}$ is the number in the grandparental generation.

1.3.2. Variance effective population size

Systematic factors (selection, mutation, and migration) tend to carry gene frequency to an equilibrium point and dispersive factors (chance fluctuation in finite population and variations in the magnitude, direction of systematic factors and variation in sampling) cause gene frequency
to scatter from equilibrium (Wright, 1949a, 1951). The result of these two factors is a stochastic process leading to a succession of changes in gene frequency. That part of gene frequency change which is due to sampling variance in a finite population, commonly known as random drift is usually taken as the binomial value, \( q(1-q)/2N_{ev} \), where \( q \) is the frequency of the allele under consideration and \( N_{ev} \) the variance effective population size (Crow and Morton, 1955). Random changes in gene frequency occur through sampling of gametes from parents in the formation of offspring. With two sexes, \( N_{ev} \) can be expressed in many ways. With no viability and fertility differences between families, and progeny number per family are approximately Poisson distributed Kimura and Crow (1963a) have given \( N_{ev} \) to be

\[
\frac{1}{N_{ev}} \approx \frac{1}{4M} + \frac{1}{4F} \tag{1.5}
\]

where \( M \) and \( F \) are the number of males and females. However, for a random mating population of constant size and sex ratio with variation in progeny number, Latter (1959) showed that

\[
\frac{1}{N_{ev}} = \frac{1}{16M} \left[ 2 + \sigma_{mm}^2 + \frac{2M}{F} \text{cov}(mm,mf) + \left( \frac{M}{F} \right)^2 \sigma_{mf}^2 \right] + \frac{1}{16F} \left[ 2 + \left( \frac{F}{M} \right)^2 \sigma_{fm}^2 + \frac{2F}{M} \text{cov}(fm,ff) + \sigma_{ff}^2 \right]
\]

\[
\tag{1.6}
\]

From the male parents, the variances in the number of male and female progeny are \( \sigma_{mm}^2 \) and \( \sigma_{mf}^2 \), respectively, and the covariance between numbers of male and female progeny is \( \text{cov}(mm,mf) \); from female parents, the corresponding quantities are \( \sigma_{fm}^2 \), \( \sigma_{ff}^2 \) and \( \text{cov}(fm,ff) \). Crow and Denniston (1988) pointed out that the formulae of Kimura and Crow (1963a) appear incorrect with separate sexes, because covariance between the number of male and female progeny was neglected. Latter (1959) also considered a case where a negative covariance of
family size is introduced for species such as poultry, in which a fixed total number of eggs may be set or progeny taken, from each family, regardless of sex. Latter (1959) dealt with populations of constant size. For practical estimates of \( N_{ev} \) for species when census data are available, assuming random mating, no selection, and no correlation between fertility of a parent and that of its offspring, Crow and Denniston (1988) have given the variance effective size to be

\[
\frac{1}{N_{ev}} = \frac{1}{4N_s} \left[ \left(1 - \sigma^2_s \right) \left( \frac{1}{\mu_{sm}} + \frac{1}{\mu_{sf}} \right) + \left(1 + \alpha_s \right) \left( \frac{\sigma_{sm}^2}{\mu_{sm}^2} + \frac{2\sigma_{sm} \sigma_{sf}}{\mu_{sm} \mu_{sf}} + \frac{\sigma_{sf}^2}{\mu_{sf}^2} \right) \right]
\]

(1.7)

and

\[
\frac{1}{N_{ev}} = \frac{1}{4N_{evm}} + \frac{1}{4N_{evf}}
\]

(1.8)

where \( \sigma_s \) is the standard deviation in progeny number of parent of sex, \( s \); \( N_s \) the number of individuals of sex \( s \) in generation \( t-1 \); and \( \alpha_s \) the departure from Hardy-Weinberg proportions which is

\[
\alpha_s = \frac{F_t \cdot F_{t+1}}{1 - F_{t+1}}
\]

(1.9)

Assuming that the parents were derived by random mating, Equation (1.9) can be approximated as \( -1/2N_{t-1} \) (Kimura and Crow, 1963a).
Using this approximation in Equation (1.7), $N_{ev}$ becomes

$$
\frac{1}{N_{eva}} = \frac{1}{2(2N_{s} - 1)} \left( \frac{1}{\mu_{sm} \mu_{gf}^2} + \frac{\sigma_{sm}^2 + \sigma_{gf}^2}{\mu_{sm}^2 \mu_{gf}^2 + \mu_{sm}^2 \mu_{gf}^2} \right)
$$

(1.10)

When every parent has exactly the same number of progeny, $\sigma_s^2 = 0$, and $N_{eva} = 2N_t$ when $\alpha_{s1} = 0$. The variance effective population size is exactly twice the number of progeny, which shows that with Hardy-Weinberg proportions in an ideal population, half of the variance is due to segregation from heterozygotes while the rest is caused by unequal progeny number (Kimura and Crow, 1963a; Caballero and Hill, 1992). As $\alpha_{s1}$ approaches unity, $N_{eva}$ becomes infinite, for there is no gene frequency fluctuation possible (Kimura and Crow, 1963a). This suggests that random genetic drift may be controlled by initiating a mating strategy or breeding plan which would shift $\alpha_{s1}$ towards one. Caballero and Hill (1992) showed that Equation (1.7) holds when inbreeding occurs due to selfing. By contrast, it does not hold when inbreeding is due to mating of relatives. They corrected Equation (1.7) with the term $(1 + 3\alpha_s)$ instead of $(1 + \alpha_s)$. In this case $\alpha_s$ should be estimated directly from Equation (1.9). The departure from Hardy-Weinberg proportions is, however, expected to cause a reduction in effective population size because, when mates are related, there is a covariance between their gene frequencies which could increase the genetic drift in the offspring (Caballero and Hill, 1992).

Selection also causes a reduction in $N_{ev}$ (Robertson, 1961; Wray and Thompson, 1990a) because of the variation between families in the trait under selection. The more intense the selection, the greater the magnitude of the reduction in $N_{ev}$ (Robertson, 1961).
1.3.3. Parallelism in genetic drift and inbreeding

It is clear that each effective population number refers to a different reference population, the progeny generation for variance effective population size, and the parent generation (monoecious) and grandparent generation (separate sexes) for inbreeding effective population size. This distinction is useful in deciding on the effective number to be used in different situations. The variance effective number provides an assessment of the amount of allelic frequency currently occurring in the population, and it does not matter how many alleles there are (Crow and Denniston, 1988). If one is interested in conserving genetic variance, it is the most appropriate effective number. The inbreeding effective number is more useful if identity is the property of interest. However, if actual pedigree information is available, direct calculation of inbreeding coefficient is always preferable. When the population size is constant ($\mu_k = 2$), and mating is random, $N_{ad} = N_{ev}$. In both cases, the effective number is $(4N - 2)/(2 + \sigma^2)$, as given by Wright (1939).

Under random mating, Kimura and Crow (1963b) observed that the total genetic drift is proportional to the sum of heterozygotes in all previous generations (or the decline in heterozygosity lags one generation behind genetic drift). However, if mating is not random within a line, decline in heterozygosity may be ahead of or behind the drift (Robertson, 1964). Thus, generating inbreeding levels in different sublines of the same census population size, $N$, a mating strategy may be useful in studying the relationship between the effect of inbreeding and genetic drift on genetic mean, variance of response and inbreeding depression.
1.4. OBJECTIVES OF THE STUDY

Even though much is known about the theoretical consequences of artificial selection, there has not been much empirical data to substantiate them in case of small populations. In most farm animals the generation interval (e.g. 3-4 years in cattle) is so great as to make it impossible to secure conclusive results within a reasonable time. The use of computer simulations has obvious relevance in testing quantitative genetics theories, but it has its own shortcomings. Results obtained from simulations are normally applicable within the assumptions of the models used. It also assumes control of all biological processes, e.g. that animals selected will actually mate and provide the expected number of progeny. Laboratory animals such as *Drosophila* (Clayton *et al.*, 1957; Frankham, 1982, 1989), *Tribolium* (Orozco, 1976), mice (Falconer, 1954; Eisen, 1975) and Japanese quail (Wilson *et al.*, 1961; Marks, 1992) have been used as pilot animals for evaluating predictions from quantitative genetics theory and they have proven to be effective (Frankham, 1989). In animal breeding, despite the large census population size, only a few become part of the breeding population for the next generation. This results in a small effective population size and thus increases the potential effects of genetic drift and inbreeding on the population. Breeders seeking to improve minor poultry species such as tinamou, pheasant, squab etc. have to deal with much smaller foundation populations. Most animal populations in genetic resource conservation programs are in small numbers (Gill and Harland, 1989), and developing effective mating schemes for conserving genetic variance is urgently needed. There is a need therefore to study inbreeding and genetic drift in small populations under artificial selection. Though there are numerous reports on selection experiments (see Falconer, 1989; Hill and Mackay, 1989), there is no documentation on selection for quantitative traits in small
populations under the influence of genetic drift and inbreeding. Performing a long-term selection experiment is beyond the limits of this thesis work. Therefore, experimental aspects of this thesis shall be confined to short-term selection.

The goal of short-term selection is to maximizing gain (Hill, 1985, 1986; Falconer, 1989; López-Fanjul, 1989). The underlying assumptions for short-term selection are that (i) the base population parameters do not change, (ii) the effect of inbreeding is negligible, and (iii) there is no relationship between effects of selection and fitness. These assumptions however, have not been previously documented in literature. These assumptions may hold true for large populations, but in small populations the validity of these assumptions are yet to be tested. It is therefore essential to conduct selections experiment in small populations to evaluate accuracy of selection, inbreeding, genetic drift, variability of response and the association between selection and fitness. Results from such experiments should either validate the assumptions for short-term selection or indicate that an alternative approach be taken for short-term selection in small populations. Results from this study could be applicable in conserving genetic variability in conservation programs.

Japanese quail (Coturnix japonica) was used as a model animal (Wilson et al., 1961; Marks, 1990; Caron et al., 1990) to evaluate experimentally the theories of genetic drift and inbreeding in small populations under artificial selection and results obtain in this studies could be generalized to other small populations.
OBJECTIVES

1. To determine the size of the breeding population required in a short term selection program to reduce genetic drift to a predefined level.

2. To establish a foundation population and estimate genetic parameters for body weight traits, and determine a trait to be used for selection.

3. To study the effects population size on selection response, inbreeding and variability of response in a short-term selection experiment.

4. To use mating strategy to generate different levels of inbreeding in 3 populations of the same census numbers in order to study the relationship between drift and inbreeding, selection response and variability of selection, and strategies to control drift and/or inbreeding.

5. To study the effects of inbreeding on some fitness components and the gene actions controlling the fitness traits.

6. To utilize the results in Objectives 2 - 5 to reappraise short-term selection for small populations.

1.5. ORGANIZATION OF THESIS

This thesis starts with a review on population size and how it is affected by selection, genetic drift and inbreeding. In Chapter 2, the effective population size required to reduce genetic drift to a predefined level was evaluated under alternative breeding schemes. The resulting manuscript has been accepted for publication in *Theoretical and Applied Genetics*. In order to initiate selection experiments, a base population needs to be established. In Chapter 3, a base population was established for the estimation of genetic parameters. A manuscript on the genetic parameters of the base population has been accepted for publication in *Poultry Science*. Based on the parameters estimated, Week 2 body weight was selected for phenotypic (mass) selection. In Chapter 4, phenotypic selection was initiated in a large and a small population in order to
study how population size influences additive genetic variance, inbreeding, and variability and rate of response during artificial selection. Large and small are used to make a distinction between two populations of different sizes. From an animal breeder's point of view, both populations are very small. In Chapter 5, mating strategies were used to generate inbreeding levels among subpopulations in order to study the relationships between rate of inbreeding, rate of response and variability of response in 3 small populations. Restricted maximum likelihood program with EM algorithm used in Chapters 3 to 5 were written by Dr. C. Y. Lin, Agriculture Canada, Ottawa (see Lin, 1988; Lin and McAllister, 1983). In order to study the association between selection and fitness in small populations under selection, some fitness components were studied in the selected populations of Chapters 4 and 5, and is reported on in Chapter 6. Chapter 7 provides a synthesis of Chapters 1 to 6 and offers an alternative to the goal of short-term selection in small populations.

In summary, this thesis addresses how population size, selection and mating strategy affect selection response, variability of response, inbreeding and genetic drift in small populations. The information obtained from this research will be pertinent in the design of optimum breeding schemes for small populations under artificial selection for a quantitative trait.
CHAPTER 2

2. SIZE OF BREEDING POPULATION REQUIRED FOR SELECTION EXPERIMENTS

2.1. ABSTRACT

The minimum population size required for a selection experiment in order to reduce the effect of genetic drift to a predefined level has been studied. The model proposed by Nicholas (1980) was extended to include the measurement error variance in the response variance. Situations where the sex ratio among scored and breeding individuals are unequal are also considered. When the duration of a selection experiment is relatively long, Nicholas' approximation (i.e. assuming the measurement error is negligible relative to drift) is useful in determining the minimum effective population size required. However, the measurement error variance becomes an important source of variation in short-term (≤ 5 generations) selection experiments, and should not be ignored.
2.2. INTRODUCTION

Response to selection for a single trait per unit of time depends on four factors: genetic variability of the trait, intensity of selection, generation interval and accuracy of selection. Effective population size indirectly affects genetic variability, intensity of selection and accuracy of selection. Restriction of breeding population size influences selection differential (Hill, 1976; Meuwissen, 1991a), increases homozygosity within the population (Robertson, 1960; Latter and Robertson, 1962) and affects the utilization of new variation arising from mutation (Robertson, 1960; Hill, 1986). In small populations, random genetic drift is an important source of genetic variation between lines (Hill, 1971), reduces the genetic variance within lines, and increases genetic variance among lines (Avery and Hill, 1977). The variance of the estimate of genetic change in a selected line comprises drift and measurement error variances. Genetic drift is the random changes in gene frequency due to sampling of gametes (Wright, 1949b). The measurement error variance comprises the error variance due to sampling of finite number of breeders from the parental population and the environmental variance (Hill, 1980). The drift effect accumulates with generation, whilst the measurement error variance does not.

Breeding schemes are often discussed solely in terms of responses to selection (Crawford, 1990), with little regard to the effect of selection on genetic drift especially in finite populations, therefore making objective assessment of the success of the schemes difficult. In a selection program, as effective population size decreases, both selection response and the selection limit decrease (Robertson, 1961). Small proportions of selected males and females (i.e. small effective population size) tend to increase rate of genetic change, and its variability so that there is less chance of agreement between the observed and the predicted results (Nicholas, 1980).
Comstock (1977) estimated the minimum population size required to ensure a certain probability of fixation of an allele by assuming value for the size of the allelic effect and the initial frequency. Though this approach is useful in providing an indication as to the minimum population size required to exhaust the genetic variance present in the base population, it has limited practical applications. In fact, the actual information on the distribution of allele effects and frequencies for metric characters is never known.

Nicholas (1980) determined the effective population size required to reduce drift to a predefined level in a selection program. His choice of population size was based on coefficient of variation of selection response (CV(R)) as a measure of random genetic drift. In search of a simple model Nicholas (1980) assumed that the measurement error is negligible as compared to the drift variance. However, when heritability of the trait under selection is low, environmental correlation among full sib is high, and the selection program spans a small number of generations, measurement error becomes a significant component of the variance of selection response (Hill, 1972a) and cannot be completely ignored except in long-term selection experiments.

The objective of this study was to extend Nicholas' (1980) model to include the measurement error in determining effective population size required to reduce genetic drift to a predefined level and to evaluate its implication for both short and long term selection experiments. The case of unequal sex numbers in both the scored and selected groups would be incorporated into the model, and how they affect the population size required for selection experiments will be examined.
2.3. MODEL

Consider a selection line derived from a large base population and undergoing artificial directional selection with discrete generations for a quantitative trait controlled only by additive genes and having additive genetic variance $\sigma_a^2$, phenotypic variance $\sigma_p^2$ and heritability, $h^2$. Consider that $M$ males and $F$ females ($F = \alpha M$) are scored every generation ($M + F = T = \text{a constant}$) and from these, $m$ males and $f$ females ($f = \beta m$) are selected. The proportions selected in each sex are then $p_m = m/M$ and $p_f = f/F$, giving rise to selection intensity $i_m$ and $i_f$, respectively. In a population so defined, the effective population size, $N_e$ is given by $N_e = 4mf/(m+f)$. The drift variance ($\sigma_d^2$) in a population with two sexes over $t$ generations was approximated by Hill (1972a) as,

$$\sigma_d^2 = \frac{t\sigma_a^2}{N_e} \tag{2.1}$$

where $\sigma_a^2$ is the additive genetic variance, and $N_e$ the effective population size. For a nested full sib design, the measurement (of genetic mean performance) error variance was given by Hill (1980) as,

$$\sigma_e^2 = \frac{\sigma_p^2}{f} \left[ \frac{c^2}{f} + \frac{(1 - c^2 - h^2/2)}{T} \right]$$

where $h^2$ is the heritability of the trait under selection, $c^2$ the environmental correlation among full sibs, $f$ the number of females selected, and $T$ the total number of individuals scored. In terms of effective population size the measurement error variance can be expressed as,

$$\sigma_e^2 = \frac{4\sigma_p^2}{N_e(1+\beta)} \left[ \frac{\beta p_m}{1+\alpha} (1 - c^2 - h^2/2) \right] \tag{2.2}$$
When \( \alpha = \beta = 1 \), and \( p = p_a = p_r \), \( \sigma_e^2 \) reduced to \( \sigma_r^2/N_e[2c^2 + p(1 - c^2 - h^2/2)] \) (Hill, 1980).

The measurement error variance contains the error variance due to the sampling of a finite number of offspring from their parents and also the environmental variance. The derivation of Equation (2.2) is given in Appendix 1.

2.4. CRITERIA FOR ANALYSIS

The coefficient of variation of response, \( CV(R) \) is defined as a ratio of the standard deviation of the response to its expectation, \( CV(R) = SD(R)/E(R) \). This parameter can be used as a criterion for determining the size of a breeding population required in a selection experiment, and to compare the relative results achieved from various selection schemes (Nicholas, 1980).

2.4.1. Case 1: Selection with a control population

If \( m \) males and \( f \) females are selected as parents from \( M \) males and \( F \) females scored respectively in the selection line, then drift variance is defined as in Equation (2.1) and the measurement error is the same as in Equation (2.2). Similarly, over \( t \) generations the drift variance and measurement error variance in a contemporaneous control line of size, \( J_c \) can be written as \( \sigma_e^2/J_c \) and \([4\sigma_r/J_c(1+\beta')][c^2+(\beta p_m'/(1+\alpha'))(1-c^2-h^2/2)] \), respectively where \( \alpha' \) and \( \beta' \) are the sex ratio of the scored and selected groups of the control line, respectively, and \( p_m' \) is the proportion of males selected in the control line.
Let $\bar{X}_t$ and $\bar{C}_t$ be the phenotypic means of the selection and control lines, respectively, at generation $t$. Response to $t$ generations of selection is estimated as,

$$\hat{R} = \bar{X}_t - \bar{C}_t \quad (2.3)$$

Assuming no covariance between the selection line and its control, the variance of the estimate of response, $\sigma_R^2$ is given by,

$$\sigma_R^2 = \sigma_{dx}^2 + \sigma_{dc}^2 + \sigma_{ex}^2 + \sigma_{ec}^2 \quad (2.4)$$

where $\sigma_{dx}^2$ and $\sigma_{dc}^2$ are the drift variances of selection and control lines, and $\sigma_{ex}^2$ and $\sigma_{ec}^2$ are the measurement error variances in selection and control lines.

If $\beta = \beta'$ and $p_m = p_m'$, then substituting Equations (2.1) and (2.2) and the appropriate values of the drift and measurement error variance of the control line into Equation (2.4) gives,

$$\sigma_R^2 = \frac{\sigma^2}{N_e} \left( \frac{1}{\alpha x} + \frac{1}{J_e} \right) + \frac{4\sigma_p^2}{1 + \beta} \left[ c^2 + \frac{\beta p_m}{1 + \alpha} \left( 1 - c^2 - h^2/2 \right) \right] \left( \frac{1}{N_e} + \frac{1}{J_e} \right) \quad (2.5)$$

If the selection and control lines have the same number of males and females selected as parents, Equation (2.5) reduces to

$$\sigma_R^2 = \frac{2\sigma^2}{N_e} \left[ 1 + \frac{4}{(1+\beta)h^2} \left( c^2 + \frac{\beta p_m}{1 + \alpha} \left( 1 - c^2 - h^2/2 \right) \right) \right] \quad (2.6)$$

Expression (2.6) ignores the decline in within-line variance because it is small relative to changes due to genetic drift. Disregarding any linkage disequilibrium and gene frequency change which
affects the linearity of response in mass selection of $t$ generations, the expected response to
selection $E(R_i)$ is given by

$$E(R_i) = tih\sigma_a$$

(2.7)

where $i$ is the standardized selection differential. From Equations (2.6) and (2.7), the coefficient
of variation of response is,

$$CV(R) = \sqrt{\frac{2\sigma_a^2}{N_e}} t h \left[ \frac{4}{(1+\beta)h^2} \left( c^2 + \frac{\beta p_m (1-c^2-h^2/2)}{1+\alpha} \right) \right]$$

(2.8)

Equation (2.8) can be rearranged as,

$$CV(R) = \sqrt{\frac{2\sigma_a^2}{N_e}} t h \left[ \frac{4}{(1+\beta)h^2} \left( c^2 + \frac{\beta p_m (1-c^2-h^2/2)}{1+\alpha} \right) \right]$$

(2.9)

If $\alpha = \beta = 1$ and $p_m = p_t = p$, Equation (2.9) reduces to $\sqrt{2}$ times Equation (13) of Hill
(1980). The difference by $\sqrt{2}$ is because Hill considered $\sigma_a^2$ and $\sigma_e^2$ of the selected line only.

When $\alpha=1$, $t=5$ and $c^2=.1$, the corresponding $N_e$ under different combinations of $CV(R_i)$, $h^2$,
$\beta$ and $i$ values were arithmetically determined and are shown in Table 2.
TABLE 2.1. Effects of CV(R), h², β and i on $N_e$ required (when $\alpha = 1$, $t=5$ and $c^2 = .1$).

<table>
<thead>
<tr>
<th>CV(R)</th>
<th>h²</th>
<th>β</th>
<th>i</th>
<th>$N_e$</th>
</tr>
</thead>
<tbody>
<tr>
<td>5%</td>
<td>.25</td>
<td>1</td>
<td>1.400</td>
<td>399</td>
</tr>
<tr>
<td></td>
<td>.25</td>
<td>1</td>
<td>1.159</td>
<td>582</td>
</tr>
<tr>
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<td>.25</td>
<td>5</td>
<td>1.400</td>
<td>377</td>
</tr>
<tr>
<td></td>
<td>.25</td>
<td>5</td>
<td>1.159</td>
<td>551</td>
</tr>
<tr>
<td></td>
<td>.40</td>
<td>1</td>
<td>1.400</td>
<td>232</td>
</tr>
<tr>
<td></td>
<td>.40</td>
<td>1</td>
<td>1.159</td>
<td>338</td>
</tr>
<tr>
<td></td>
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<td>5</td>
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<td>206</td>
</tr>
<tr>
<td></td>
<td>.40</td>
<td>5</td>
<td>1.159</td>
<td>300</td>
</tr>
<tr>
<td>20%</td>
<td>.25</td>
<td>1</td>
<td>1.400</td>
<td>25</td>
</tr>
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<td>1.400</td>
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<tr>
<td></td>
<td>.40</td>
<td>5</td>
<td>1.159</td>
<td>19</td>
</tr>
</tbody>
</table>
2.4.2. Case 2: Selection without a control population

When the objective is to compare alternative selection schemes for improving the same trait, selection experiments are often conducted without a control. However, the importance of variance in common environmental effects among generations must be considered. The effects common to individuals within a generation are randomly and independently distributed with mean zero and variance $\sigma_e^2$ which becomes a part of error variance in the selected line. Consequently, the error variance is

$$
\sigma_e^2 = \frac{4\sigma_p^2}{N_e(1+\beta)} \left[ c^2 + \frac{\beta p_m(1-c^2-h^2/2)}{1+\alpha} \right] + \sigma_c^2 \quad (2.10)
$$

In the absence of a control, the observed response is,

$$
\hat{R} = \bar{X}_r - \bar{X}_0 \quad (2.11)
$$

where $\bar{X}_0$ is the phenotypic mean of base population. Expected variance of $R$ is,

$$
V(R) = \sigma_{dx}^2 + 2\sigma_{ex}^2 \quad (2.12)
$$

Substituting Equations (2.1) and (2.10) into Equation (2.12), leads to,

$$
V(R) = \frac{\sigma_a^2}{N_s} \left[ t + \frac{8}{(1+\beta)h^2} \left( c^2 + \frac{\beta p_m(1-c^2-h^2/2)}{1+\alpha} \right) \right] + 2\sigma_c^2 \quad (2.13)
$$

Unlike the drift variance, $\sigma_e^2$ does not accumulate, and may not be a major source of error in the long term, but certainly is of concern in short term experiments. The magnitude of $\sigma_e^2$ cannot
be predicted \textit{a priori}, however, it can be estimated from selection experiments (Hill 1972b). Once it is determined, actual results achieved from selection experiments with or without control can be compared in terms of CV(R).

2.4.3. Case 3: Divergent selection

Divergent selection has often been used as an alternative to running a selection experiment with a control. One line is selected for high value (H) of the trait and another contemporaneous line selected for low value (L). Let $\overline{X}_H$ and $\overline{X}_L$ represent the phenotypic means for the high and low selection lines, respectively after $t$ generations of selection. The response to divergent selection is

\begin{equation}
R = \overline{X}_H - \overline{X}_L
\end{equation}

\begin{equation}
V(R) = 2\sigma^2 + 2\sigma^2_{ex}
\end{equation}

For a short term experiment, symmetry of response in a two-way selection can be assumed. Therefore,

\begin{equation}
E(R) = 2\sigma_a
\end{equation}

Thus, the coefficient of variation of response in Case 3 is,

\begin{equation}
CV(R) = \frac{1}{ih\sqrt{2N_t}} \left[ 1 + \frac{4}{\kappa (1+\beta)h^2} \left( c^2 + \frac{\beta p_m}{1+\alpha} (1-c^2-h^2/2) \right) \right]
\end{equation}
which is one half of the coefficient of variation for selection with a control as shown in Equation (2.9).

2.5. DISCUSSION

The assumptions for the derivation of CV(Rs) are that the number of individuals scored and the proportion selected are the same for both sexes every generation. This situation is rare in practical animal breeding although it is commonly found in laboratory experiments. In deriving Equation (2.9) the number of parents in both selection and control lines was assumed to be the same, but CV(Rs) in a more general case could be evaluated by substituting the most general formulae for $\sigma^2_d$ and $\sigma^2_e$ directly into Equation (2.4). The effective population size can be expressed as $N_e = 4\beta m / (1+\beta)$. The required number of breeding males of the selected line is then $m = N_e (1+\beta) / 4\beta$ and $f = \beta m$. To determine the size of a selection experiment with a control, a predefined value for CV(Rs) needs to be set. For example, taking CV(Rs) to be 20% (i.e., selection response five times as great as its standard deviation), and considering a specific case where $p_m = 10\%$, $\alpha = 1$, $\beta = 3$, $h^2 = 0.25$, $p_r = \beta p_m = 30\%$, $i = 1.4$, and $c^2 = 0.1$, and substituting all these terms into Equation (2.9), it turns out that an effective population size of 43 for 3 generations and 24 for 5 generations are required. By ignoring the measurement error variance (Nicholas, 1980), $N_e$ would have been 34 and 20 for 3 and 5 generation selection experiments, respectively. In this case, Nicholas' approximation is 20% and 17% less accurate for 3 and 5 generations, respectively. The decision to incorporate the measurement error variance into the model or use Nicholas's (1980) approximation should be based on the number of generations. Since the measurement error is independent across generations, the measurement
error variance is $1/t$ times in any generation $(t)$. Therefore as $t$ increases, the measurement error becomes insignificant as compared to the drift variance. Under such conditions, Nicholas' approximation is useful. However, not all selection experiments span large numbers of generations. In selection experiments where $t$ is small, the contribution of the measurement error cannot be ignored. There is no fixed definition for short or long term. However, up to 5 generations can be taken as short term. The degree to which Nicholas' approximation underestimate population size required for short-term selection program is proportional to the value of $c^2$. Also the underestimation is greater when the number of individuals recorded in each family and $h^2$ are small (Hill, 1972a). Under such conditions, it would be better to use the more complete equations rather than Nicholas's approximation. Also when $t$ is small, variations in $\alpha$ and $\beta$ have influence on population size.

As shown in Table 2, the $N_e$ required for a selection program is much larger when $CV(R_e)$ is set at 5% than at 20%. The required value of $CV(R_e)$ is more important in deciding the size of breeding population as compared to $h^2$, $\beta$ or $i$. It can be seen from Equations (2.9) and (2.17) that $CV(R_e)$ is inversely related to selection intensity ($i$), heritability ($h^2$), effective population size ($N_e$), and generation number ($t$). Given a predefined value of $CV(R_e)$, the number of breeding animals required is smaller for high selection intensity, a highly heritable trait, or long term selection than for low selection intensity, a lowly heritable trait or short term selection. These relationships were reflected in Table 2 which was derived based on Equation (2.9).

In this study the effect of selection on drift variance was not accounted for (i.e. assuming $N_e$ is the same every generation). Drift variance per generation is reduced during selection (Meuwissen, 1991b), and the rate of decline of drift variance depends on the number of loci
controlling the selected trait. Therefore, effective population sizes determined from Equations (2.9) and (2.17) overpredicted the drift variance, and thus led to conservative estimates of the required population sizes.

Directional selection acts on the genetic variance first by inducing linkage disequilibrium and secondly by changing gene frequencies which also causes changes in genetic variance (Bulmer, 1980). Selection also acts on the genetic variance by changing the family structure and therefore enhancing loss of variation through inbreeding if the population size is limited (Robertson, 1961). It was also assumed that the heritability of a trait is known a priori without error and the standardized selection differential, $i$ does not change over generations. However, with finite population size, selection differentials are altered (Hill, 1985).

In the short term, it was assumed that the parameters estimated in the base population do not change. This assumption is not true. Linkage disequilibrium, inbreeding depression and changing family structure should be accounted for in a more complete model. However, the model used in this study is able to provide useful indications of how large selection experiments need to be.
CHAPTER 3

3. ESTIMATION OF GENETIC PARAMETERS FOR BODY WEIGHT TRAITS IN JAPANESE QUAIL

3.1. ABSTRACT

Records of 1,509 Japanese quail were used to estimate heritabilities and genetic correlations based on restricted maximum likelihood method with an animal model (AM). The AM included fixed effects of hatch and sex, and random effect of additive genetic value of the bird. Heritabilities estimated for body weights at hatch, 7, 14, 21, and 28 days of age were .57, .52, .45, .48 and .49, respectively. Genetic correlations of .75 ~ .88 among body weights at 14, 21 and 28 days of age indicate the possibility of improving body weight at 28 days of age by selecting for body weight at either 14 or 21 days of age.
3.2. INTRODUCTION

Japanese quail (*Coturnix japonica*) have been used as a pilot animal for poultry genetic research because they are small and less expensive to maintain than chickens and turkeys, have a short generation interval, and show genetic variation for growth traits in most populations (Wilson *et al*., 1961; Marks, 1990). More recently, Japanese quail have been produced commercially in North America and have enjoyed increasing popularity as a form of poultry meat and eggs (Caron *et al*., 1990). However, quail breeding methods for improving economic traits are lacking and only few estimates of heritability for body weight and weight gain are available (Collins *et al*., 1968; Marks and Lepore, 1968; Sefton and Siegel, 1974; Narayan, 1976). Heritability estimates for body weight and weight gain in Japanese quail vary considerably. Reliable estimates of genetic parameters (heritability and genetic correlation) are necessary for efficient design of breeding experiments and for prediction of response to direct or indirect selection.

Traditionally, poultry breeders have used analysis of variance (ANOVA) procedures (Henderson, 1953) to estimate genetic parameters. Henderson's (1953) Methods 1 and 2 are adequate when data are balanced (Searle, 1971). In practice, data arising from livestock and poultry breeding programs are usually unbalanced and methods analogous to ANOVA have also been developed for unbalanced data. As a result, Henderson's (1953) Method 3 of "fitting constants" has been used extensively. Its use has been enhanced by the availability of a general least-squares computer program designed towards applications in animal breeding (Harvey, 1960, 1977). However, there is an unresolved difficulty with the fitting constants method of estimating variances. It can yield more equations than there are components to be estimated, and it provides
no guidance as to which equations should be used (Searle, 1971).

Another disadvantage of ANOVA-type methods of analysis is that they are based on the assumption of random sampling and consequently the resulting estimates are biased by selection (Meyer, 1989). Furthermore, estimates may lie outside the parameter space (i.e., heritability less than 0 or greater than 1 and correlation estimates may be less than -1 or greater than +1). On the contrary, the maximum likelihood (ML) method (Hartley and Rao, 1967) of estimating variance components maximizes the likelihood function in the parameter space. Maximum likelihood estimates are consistent, asymptotically normal and efficient (Harville, 1977) and account for selection (Kennedy, 1981). However, one disadvantage of ML estimation in a mixed model is that fixed effects are treated as if they are known, i.e., the loss in degrees of freedom due to fitting these effects is ignored. A modified ML procedure, restricted maximum likelihood (REML) (Patterson and Thompson, 1971) overcomes this problem by maximizing only that part of the likelihood that is independent of the fixed effects.

Over the past decade the REML method has been used extensively for parameter estimation and genetic evaluation especially under the so-called animal model (AM) (Henderson, 1984; Kennedy et al., 1988). The AM estimates the additive genetic merit for animals with or without records incorporating all known relationship information in the analysis. With the AM, the genetic variance is estimated as the variance of animals' additive genetic merit instead of four times the covariance between half-sibs, two times the covariance between full-sibs, or two times the covariance between parents and offspring (Meyer, 1989). REML approach has been used for estimating heritabilities in egg layers (Aggrey, 1990), broilers (Wang, 1992) and turkey (Smith and Savage, 1992) but not in quail.
The objective of this study was to estimate genetic parameters for growth traits in Japanese quail using an animal model.

3.3. MATERIALS AND METHODS

3.3.1. Experimental Population

Forty males and 120 females of Japanese quail of UBC-QF strain (Bitgood and Somes, 1994) were obtained from the Quail Genetic Resource Centre (QGRC) of the University of British Columbia to establish a foundation population. UBC-QF was originally imported from California (Pharaoh line) to the University of Laval, Québec, Canada in 1976. The line was selected for 45 day body weight for 20 generations (Caron et al., 1990). Thereafter, selection was discontinued and the line was propagated by random mating for about 12 generations before the line was acquired by QGRC.

For this study three females were randomly assigned to a male in a breeding cage. Eggs from each hen have a specific shape and color pattern, which provide a means of pedigree identification. Pedigreed eggs were saved and stored at 10 °C for 14 days before incubation. Incubated eggs were transferred in pedigree baskets to a hatcher on Day 15 of incubation. A total of 1,690 chicks were removed from the hatcher on the 18th day, wing-banded, weighed, and assigned to community cages with wood-shavings floors. Chicks were fed a 26% protein turkey starter diet. Feed and water were provided for ad libitum consumption with light regimen of 10 h light and 14 h darkness. Heat was provided by infrared heat lamps placed 45 cm above the floor of the pen. There were two hatches at an interval of 14 days. The initial brooding
temperature of 37 °C was gradually reduced to 25 °C after 14 days. At this age the quail were transferred to wire floors, where they remained until 28 days. There was 2% mortality from hatching through Day 28.

Measurements

Individual body weights were recorded at hatching (Day 0) and every 7 days till 28 days of age. Weights were obtained to the nearest .1 g. Sex was determined at 21 days of age by plumage color. Dams that either did not lay or had no chicks at hatching or chicks that lost their wing-bands before sexing (7.5%) were excluded. However, all males were represented by offspring. After data editing, a total of 1,509 chicks of 40 sires and 100 dams was available for analysis.

3.3.2. Model

The AM used to estimate variance components for body weights at different ages and weight gains included a fixed effects of hatch and sex, a random effect of direct additive genetic value of each bird (u), and residual environmental effect (e). The AM in matrix notation is:

\[ y = Xb + Zu + e \]  

(3.1)

where \( y \) is a vector of observed body weight or weight gain of birds; \( X \) is the incidence matrix for fixed effects; \( b \) is a vector of fixed effects; \( Z \) is the incidence matrix for direct additive genetic effects; \( u \) is the vector of the direct additive genetic effects, and \( e \) is the vector of random residual errors. The assumptions of the AM are that, animals in the base population
were (i) randomly sampled, and (ii) unrelated, and (iii) body weight/weight gain is determined by an infinite number of additive and unlinked loci, (iv) the model is correct, (v) the variance is known at least to proportionality, and (vi) the random effects have multivariate normal distribution.

The random effects were assumed to be normally distributed with means zero and variances:

\[
V \begin{bmatrix} u_e \\ e \end{bmatrix} = \begin{bmatrix} \Lambda \sigma_a^2 & 0 \\ 0 & \Lambda \sigma_e^2 \end{bmatrix}
\]

The relationship matrix, \( A \), includes all additive genetic relationships among birds used in the analysis and \( I \) is an identity matrix. The mixed model equations for model (3.1) were of the form:

\[
\begin{bmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1} \lambda \end{bmatrix} \begin{bmatrix} b \\ u \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \end{bmatrix}
\]

where \( A^{-1} \) is the inverse of the numerator relationship matrix (Henderson, 1976) and \( \lambda = \sigma_a^2 / \sigma_e^2 = (1-h^2)/h^2 \). A univariate analysis was used to estimate additive genetic variance (\( \sigma_a^2 \)), error variance (\( \sigma_e^2 \)), phenotypic variance (\( \sigma_p^2 \)), heritability (\( h^2 \)), and genetic (\( r_g \)) and phenotypic correlations (\( r_p \)) between traits. Estimation of standard errors failed. Standard error for heritability estimates were therefore obtained from a table of standard error given by Klein et al.,
Compared to other studies, e.g. Winkelman and Peterson (1994a,b) standard errors obtained from the table provided by Klein et al. (1973) were low. Covariance component between traits i and j was obtained as:

\[ \text{Cov}_{ij} = \frac{(\sigma_k^2 - \sigma_i^2 - \sigma_j^2)}{2} \]  

where \( k \) is formed by summing the values of traits i and j. ANOVA procedure were used to estimate sire (\( \sigma_s^2 \)), dam (\( \sigma_d^2 \)) and error (\( \sigma_e^2 \)) components of variance using Henderson’s Method.

3. Results obtained from the ANOVA procedure are presented in Appendix 2.

3.4. RESULTS

Overall means, standard deviations, coefficients of variation, and heritability for body weights and weight gains are presented in Table 3.1. Coefficient of variation for body weight was about 10% at Day 0 (hatch) and about 8% at 28 days of age and ranged from 10 to 14% for weight gain. Heritability estimates decreased from day of hatch till Week 2, then increased hereafter. Genetic and phenotypic correlations among body weights and between weight gains are presented in Tables 3.2 and 3.3, respectively. Genetic correlations among body weights ranged from .14 to .88. Phenotypic correlations among body weights were between .32 and .75. Genetic correlations among the different weight gains ranged from -.45 to .49, and phenotypic correlations among weight gains were between .09 and .37.
TABLE 3.1. Means (x), standard deviation (SD), coefficients of variation (CV) and heritability ($h^2$) for body weight and weight gain at different ages.

<table>
<thead>
<tr>
<th>Trait</th>
<th>x ± SD</th>
<th>CV</th>
<th>$h^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body weight</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 d</td>
<td>7.9 ± .8</td>
<td>9.5</td>
<td>.57</td>
</tr>
<tr>
<td>7 d</td>
<td>36.2 ±3.3</td>
<td>8.9</td>
<td>.52</td>
</tr>
<tr>
<td>14 d</td>
<td>82.3 ±7.2</td>
<td>8.8</td>
<td>.45</td>
</tr>
<tr>
<td>21 d</td>
<td>129.4 ±10.2</td>
<td>7.9</td>
<td>.48</td>
</tr>
<tr>
<td>28 d</td>
<td>179.3 ±13.4</td>
<td>7.5</td>
<td>.49</td>
</tr>
<tr>
<td>Weight gain</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 to 7 d</td>
<td>28.3 ±2.9</td>
<td>10.2</td>
<td>.17</td>
</tr>
<tr>
<td>8 to 14 d</td>
<td>46.2 ±4.8</td>
<td>10.4</td>
<td>.42</td>
</tr>
<tr>
<td>15 to 21 d</td>
<td>46.8 ±6.9</td>
<td>14.7</td>
<td>.33</td>
</tr>
<tr>
<td>22 to 28 d</td>
<td>50.1 ±7.1</td>
<td>14.1</td>
<td>.45</td>
</tr>
</tbody>
</table>

Standard errors of heritabilities ranged from .02 to .05 (Klein et al., 1973)
TABLE 3.2. Genetic (above diagonal) and phenotypic (below diagonal) correlations among body weights at various ages

<table>
<thead>
<tr>
<th>Age (day)</th>
<th>0</th>
<th>7</th>
<th>14</th>
<th>21</th>
<th>28</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td></td>
<td>.69</td>
<td>.30</td>
<td>.79</td>
<td>.14</td>
</tr>
<tr>
<td>7</td>
<td>.56</td>
<td></td>
<td>.64</td>
<td>.50</td>
<td>.45</td>
</tr>
<tr>
<td>14</td>
<td>.42</td>
<td>.67</td>
<td></td>
<td>.75</td>
<td>.76</td>
</tr>
<tr>
<td>21</td>
<td>.37</td>
<td>.64</td>
<td>.74</td>
<td></td>
<td>.88</td>
</tr>
<tr>
<td>28</td>
<td>.32</td>
<td>.58</td>
<td>.73</td>
<td>.75</td>
<td></td>
</tr>
</tbody>
</table>
TABLE 3.3. Genetic (above diagonal) and phenotypic (below diagonal) correlations among weight gains to 28 days of age

<table>
<thead>
<tr>
<th>Age (day)</th>
<th>Age interval (day)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 - 7</td>
<td>8 - 14</td>
<td>15 - 21</td>
<td>22 - 28</td>
</tr>
<tr>
<td>0 - 7</td>
<td></td>
<td>.45</td>
<td>-.34</td>
<td>-.16</td>
</tr>
<tr>
<td>8 - 14</td>
<td>.37</td>
<td></td>
<td>.09</td>
<td>.32</td>
</tr>
<tr>
<td>15 - 21</td>
<td>.23</td>
<td>.13</td>
<td></td>
<td>.09</td>
</tr>
<tr>
<td>22 - 28</td>
<td>.10</td>
<td>.26</td>
<td>.09</td>
<td></td>
</tr>
</tbody>
</table>
3.5. DISCUSSION

Body weight at hatch had a $h^2$ of .57. This $h^2$ is lower than the estimate of .81 reported by Narayan (1976). Since Narayan's (1976) estimate was based on full-sib component of variance, it had a confounding effect of common environment and dominance genetic variance. Common environmental effects are to some extent the consequence of genetic variation of some characters of the dams. Maternal environment affects chick growth in two stages, namely the preovipositional and the postovipositional maternal effect. The postovipositional effect can be divided into prehatch (incubation) and posthatch effects. In this study the posthatch maternal influence on chick growth was not important because chicks were raised independently of the dams. Therefore, the common environmental effects that may possibly affect chick growth are preovipositional maternal components, which are mainly oviductal factors such as egg size, egg weight, shell quality, and yolk composition (Aggrey and Cheng, 1993). Shanawany (1987) reported a high correlation ($r_p = .89$) of egg weight with hatch weight in quail, suggesting an influence of maternal effects on hatch weight. However, in broilers, Pinchasov (1991) observed that the initial high correlation between egg weight and hatch weight declined with age.

Heritability estimates for body weights were moderate at all ages, suggesting adequate additive genetic variation. The quail population used had previously been selected for 45 day body weight and since relationships in the population were not known, they were not fully accounted for. Heritability estimates for weekly body weight reported by Sefton and Siegel (1974) fluctuated. In addition, some of their estimates were outside the parameter space (i.e., $h^2$ less than 0 or greater than 1), and have no application.
Heritability estimates for weekly gains were moderate. Heritability estimates for body weights at 14, 21 and 28 days of age were .45, .48 and .49, respectively, suggesting that selection would be effective in improving 14-, 21- and 28-day body weights.

Phenotypic correlations between body weights at various ages and among weight gains were positive. Genetic correlations among the traits studied did not show any trend. The conventional univariate analysis calculates simple correlation between two traits at a time (pairwise estimation) and disregards other traits and the correlations of them with the two traits under study (Lin and Lee, 1986). Genetic correlations estimated this way are not REML estimates, the properties (e.g. unbiasedness) of such methodology are not known. Bivariate analysis of correlation is preferable to univariate analysis especially when the data comes from a selection experiment. However, in the absence of selection and missing values, differences between bivariate analysis and pairwise estimation of correlation may be negligible (C.Y. Lin, personal communication). Genetic correlations ($r_g$) are important for determining the genetic relationships between body weights and among weight gains. The effect of preovipositional maternal effects may influence this relationship. Preovipositional maternal effects associated with the first week gain may be the cause of negative genetic correlations with later periods. Negative genetic correlations were also reported by Sefton and Siegel (1974) between Day 1 body weight (which is also influenced by egg weight) and weekly body weights from 35 to 56 days of age. Many of the positive genetic correlation reported by Sefton and Siegel (1974) and Narayan (1976) were either close to or greater than 1, indicating that non-additive genetic effects and common environmental effects present in full-sib families had made these correlation estimates unrealistic. This is one reason why REML is better than ANOVA-type analysis in
preventing estimates from getting out of parameter space. Genetic correlation estimates of .75 – .88 among body weights at 14, 21 and 28 days of age indicate the possibility of improving body weight at 28 days of age by selecting at either 14 or 21 days of age.
CHAPTER 4

4. EFFECTS OF POPULATION SIZE ON RESPONSE TO SELECTION, VARIABILITY OF RESPONSE AND INBREEDING IN A SHORT-TERM SELECTION EXPERIMENT.

4.1. ABSTRACT

The effect of population size on the mean genetic gain, variability of response and inbreeding were examined for a 3 generation phenotypic (mass) selection experiment. Effective population sizes of 12 (Large) and 6 (Small) per replicate were evaluated at the same selection intensity. The selection criterion was Week 2 body weight. Selection response was higher in the large population than in the small population. Inbreeding and variability of response were however, higher in the small population as compared to the large population. Estimates of genetic gain at Generation 3 were 10.67 and 8.89 grams, respectively in the large and small populations. Reduced apparent additive genetic variance, inbreeding depression and genetic drift reduced selection response and increased variability of response in the small population. In small populations however, an optimum combination of response to selection and inbreeding may be a useful goal in the short-term selection than maximizing response to selection.
4.2. INTRODUCTION

With the development of mass selection theory, its application for predicting genetic changes in a quantitative character has been widely made by plant and animal breeders. Genetic gain depends on the heritability of the trait under selection, intensity of selection and phenotypic standard deviation of the trait (Falconer, 1989). In the short term, population size influences selection differential, through inbreeding and reduction in genetic variance from genetic drift. Inbreeding also causes a reduction in the additive genetic variance (Gomez-Raya and Burnside, 1990). Long term response is also affected by change of variance through changes in gene frequency and fixation of genes and by new variation arising from mutation subsequent to the start of the selection program (Hill, 1985).

Selection theory is usually based on infinite sample size (Falconer, 1989). In practice, artificial selection is always conducted with finite number of individuals. In large populations, both simulation and experimental studies have demonstrated that response to selection could be predicted in short-term selection using base population parameters (Hill, 1985, 1986; Nicholas, 1987; Lopéz-Fanjul, 1989; Marks, 1990, 1992; Chambers, 1990). However, in most laboratory and farm animals, selection is done in small populations (Hill and Keightley, 1988) and using base population parameter to predict response to selection beyond one generation of selection may not be appropriate. Robertson (1967) indicated that the most important topic which requires a fresh approach is the role of population size in artificial selection.

Frankham et al. (1968) and Hanrahan et al. (1973) reported the effect of population size on response to selection. Though results from both studies showed that response to selection was
greater in large populations than in small populations, they did not provide possible mechanisms to explain their results. In addition they did not consider variability of response, which is considered as an indicator of risk of breeding plans (Meuwissen, 1991b). Their analyses were mostly concerned with estimation of realized heritability. Variability of response to selection is relevant for testing possible departures from expectation, comparing selection schemes, estimating genetic parameters of the base population and checking response in populations (Hill, 1977).

Parameters in a population under selection are not static. Genetic drift accumulates in a particular generation as a result of random deviations in all previous generations (Sorensen and Kennedy, 1983) and the variance of genetic means increases each generation as means of different generations become correlated. Directional selection also causes linkage disequilibrium which leads to a reduction in the additive genetic variance within lines (Bulmer, 1971). The cumulative effect of selection, genetic drift and inbreeding may yield a mean response less than predicted. At present, there is a paucity of experimentation dealing with changes in population parameters in small populations and how they affect mean response and variability of response. Such information is pertinent in understanding how factors which affect changes in genetic mean behave in small populations under selection, and their importance in designing an efficient breeding program.

The objective of this study was to investigate the effects of population size on selection response, inbreeding and variability of response. Changes in population parameters under selection was also examined and utilized in the evaluation of breeding strategies and analysis of selection experiments in small populations.
4.3. MATERIALS AND METHODS

4.3.1. Experimental Design

From the population described in Chapter 3, two treatment lines (Large and Small) were established. Large and Small are denoted by L and S, respectively. The L lines consisted of 2 selection lines (LS) and 2 control lines (LC). The lines were established such that no two individuals within a line were related by descent. Phenotypic selection was conducted in the selected lines. Each generation, 4 of 40 males and 12 of 40 females were selected on Week 2 body weight in each of the LS lines. In the LC lines, 4 males and 12 females were randomly selected per line. Each male was randomly mated to 3 females in all the lines. The S lines also consisted of 2 selection lines (SS) and 2 control lines (SC). The selection and mating criteria in the S lines were similar to those of the L lines except that 2 males and 6 females were selected from 20 birds of each sex per line. An attempt was made to maintain a selection intensity of 10% in males and 30% in females in both LS and SS lines. Selection intensity was obtained from mathematical tables (Becker, 1992) and selection differential was the mean difference between the population and the selected parents weighted by the number of progeny. If a selected bird died before it was bred it was replaced by the next highest ranking bird. All the lines were propagated for 3 generations with a generation interval of about 4 months. Replicates were combined during analysis. There were no interbreeding among replicates. The L and S lines comprised of 320 (selected and control) and 160 (selected and control) individuals, respectively at each generation. Birds were kept and managed under similar conditions as described in Chapter 3.
4.3.2. Estimation of genetic parameters

The model used was

\[ Y_{ijk} = \mu + g_i + S_j + m_{ijk} + bF_{ijk} + e_{ijk} \]  \hspace{1cm} (4.1)

where \( Y_{ijk} \) is Week 2 body weight of a bird, \( \mu \) is the population mean, \( g_i \) is the fixed effect of the \( i^{th} \) generation \((i=0,\ldots,t)\), \( S_j \) is the fixed effect of the \( j^{th} \) sex \((j=1,2)\), \( m_{ijk} \) is the additive genetic effect of the \( ijk^{th} \) bird, \( b \) is the regression coefficient of the body weight of the \( ijk^{th} \) bird on its inbreeding coefficient \((F_{ijk})\) and is used as a measure of inbreeding depression of Week 2 body weight, and \( e_{ijk} \) is the random residual. Inbreeding coefficient of individual birds \((F_{ijk})\) were computed using an algorithm of Quaas (1976). Week 2 body weight was regressed on the individual's inbreeding coefficient to test whether the regression coefficient (inbreeding depression) was significantly different from zero. Separate analysis were done for the L and S lines. A total of 1,344 and 672 individual were used to estimate heritability of the base population in the L and S lines, respectively. (These included individuals from the base population (with no records) and generations 0 through 3).

In matrix notation, Equation (4.1) can be represented as

\[ y = Xb + Za + e \]  \hspace{1cm} (4.2)

where \( y \) is a vector of Week 2 body weights, \( b \), a vector of fixed effects, \( a \), a vector of random effects, \( e \), a vector of random residual errors, \( X \) and \( Z \) are known incidence matrices associated with vectors \( b \) and \( a \). The random effects were assumed to be normally distributed with expectations zero and variances as given in Equation (3.2) For a single record on a single trait, the mixed model equation (MME) can be written as in Equation (3.3).
Sixty-four animals of the 140 animals in the base population described in Chapter 3, constituted a new base population for the L lines. The S lines had 32 animals of the 140 animals as its new base population. At each generation, 384 (320 scored plus 64 parents) individuals were used to estimate additive genetic variance in the L lines. Similarly, 192 (160 scored plus 32 parents) individuals were also used to estimate additive genetic variance at each generation in the S lines. Parents in the base populations of both L and S lines were unrelated. Additive genetic variance estimated at each generation in the L and S lines would be referred to as apparent additive genetic variance because their respective base populations (L and S) were sampled from a sample (base population in Chapter 3). Restricted maximum likelihood (REML) $h^2$ was estimated for the base populations and predictions of additive genetic effects in the L and S lines were carried out using the model in Equation (4.1). Standard error for REML heritability estimates were obtained from a table of standard error given by Klein et al., (1973). Realized heritability ($h_r^2$) was estimated as ratio of cumulative realized response to the cumulative selection differential.
4.3.3. Estimation of Selection Response and Genetic Gain (Trend)

Predicted Response

Response to selection was predicted (Falconer, 1989) by

\[ R = ih^2 \sigma_p \] (4.3)

where \( R \) is the predicted response; \( i \) is the selection differential in standard units; \( h^2 \) is the heritability of the trait under selection; and \( \sigma_p \) is the phenotypic standard deviation. Equation (4.5) was used to predict response to selection at generation \( t \) ignoring the decline in genetic variance.

Realized Response

Realized response at generation \( t \), \( Y_t \), was estimated as a deviation of the mean phenotypic value of the selected lines from control lines for both L and S population sizes.

\[ Y_t = \frac{\sum Y_{sk}/n_{t_s}}{\sum Y_{ck}/n_{t_c}} - \sum Y_{sk}/n_{t_s} \] (4.4)

where \( s \) and \( c \) denote selection and control lines, respectively, and \( n_t \) is the number of birds in \( i^{th} \) line.

Genetic gain

Genetic mean at generation \( t \) was estimated as average breeding values obtained from solutions to the mixed-model equations.

\[ \bar{m}_t = \sum_{jk} m_{jk}/n_t \] (4.5)
where $n_i$ is the total number of birds in $i^{th}$ line. Genetic gain ($\Delta G$) at generation $t$, was estimated as

$$\Delta G_t = \bar{m}_i - \bar{m}_e$$

(4.6)

4.3.4. Estimation of Variability of Response

Coefficient of variation of response, $CV(R_i)$ defined as the ratio of standard deviation of response to phenotypic response (Hill, 1980; Nicholas, 1980, 1987) was used as a measure of genetic drift. Variance among replicated lines were estimated using the additive relationship matrix as described by Sorensen and Kennedy (1983). Sorensen and Kennedy (1983) have given the variance of response at generation $t$ to be

$$Var(\bar{Y}_p) = 2\bar{F}_{t-1}\sigma_a^2 + \left(1 - \bar{F}_{t-1}\right)\sigma_a^2 + \sigma_e^2 / M$$

(4.7)

where $\sigma_a^2$ and $\sigma_e^2$ are the additive genetic and environmental variances, respectively and $F$ the inbreeding coefficient, and $M$ the number of individuals scored. The first term in Equation (4.9) is the drift variance, the second term is the variance of sampling finite number of breeders from the parental population. The variance of the response was estimated as,

$$Var(\bar{Y}_p) = Var(Y_{a_i}) + Var(Y_{e_i})$$

(4.8)

Coefficient of variation of response, $CV(R_i)$ for each population at generation $t$ was estimated as

$$CV(R_i) = \sigma_r / \bar{Y}_t$$

(4.9)
4.3.5. Estimation of Effective population size

The effective population size \( N_e \) at Generation 0 is defined as,

\[
N_e = \frac{4mf}{m + f}
\]  
(4.10)

where \( m \) and \( f \) are the number of males and females selected to breed. Inbreeding effective population size \( N_{el} \) is given by Falconer (1989) as

\[
\frac{1}{2N_{el}} = \Delta F = \frac{F_t - F_{t-1}}{1 - F_{t-1}}
\]  
(4.11)

where \( \Delta F \) is the rate of inbreeding per generation (t), and \( F \) the inbreeding coefficient.

Effective population size was calculated in only one replicate in both the LS and SS lines.
4.4. RESULTS

Table 4.1 shows the apparent additive genetic variance, cumulative selection differential, cumulative predicted response, cumulative realized response, and realized heritability at generation t of selection. Apparent additive genetic variance declined each generation in both the Large (L) and Small (S) populations. The realized response in both the L and S populations were similar at generation 1. At generations 2 and 3, realized responses in both L and S lines were lower than their respective predicted responses. The L lines realized a greater amount of the predicted response than in the S lines. Realized responses were greater in the L lines than the S lines at generations 2 and 3. Apparent additive genetic variance declined in both the L and S lines as the number of generations increased. Realized heritability declined in both the L and S populations as the number of generations increased. Genetic gain, variability of response, $\sigma_R$, coefficient of variation of response, $\text{CV}(R)$, and inbreeding coefficient, $F$, for both the L and S lines are presented in Table 4.2. Genetic gain, $\sigma_R$ and $F$ increased with generation in both L and S lines. The estimated effective population size ($N_e$) based on the number of mated males ($m$) and females ($f$) was larger than that ($N_{qe}$) based on the rate of change of inbreeding ($\Delta F$). The effective population size was larger in the L lines than in the S lines. Inbreeding caused inbreeding depression in Week 2 body weight. Inbreeding depression was 1% per 10% increase ($P \leq 0.05$) in the L lines as compared to 2% per 10% increase ($P \leq 0.05$) in inbreeding in the S lines (Table 4.2). Coefficient of variation of response declined as the number of generations increased in the L lines. However, in the S lines, $\text{CV}(R)$ declined from generation 1 to 2 but did not change at generation 3. Genetic gain, $\sigma_R$ and $\text{CV}(R)$ were similar for both L and S lines in
generation 1. In generations 2 and 3, ΔG was larger in the L lines compared to the S lines, but $\sigma_R$, CV(R), and $F$ were larger in the S lines compared to the L lines. Data on means and standard deviations of Week 2 body weight of the different treatment lines and replicates are present in Appendix 3.
TABLE 4.1. Estimates of apparent additive genetic variance ($\sigma_a^2$) selection differential, response to selection and realized heritability ($h_R^2$) for three generations (t) of selection in Large (L) and Small (S) Japanese quail populations.

<table>
<thead>
<tr>
<th>t</th>
<th>L</th>
<th>S</th>
<th>L</th>
<th>S</th>
<th>L</th>
<th>S</th>
<th>L</th>
<th>S</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>19.17</td>
<td>20.64</td>
<td>18.21</td>
<td>16.08</td>
<td>17.75</td>
<td>16.14</td>
<td>16.43</td>
<td>15.13</td>
</tr>
<tr>
<td>1</td>
<td>9.96</td>
<td>9.44</td>
<td>17.89</td>
<td>17.04</td>
<td>25.89</td>
<td>22.94</td>
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<td></td>
</tr>
<tr>
<td>2</td>
<td>4.28</td>
<td>4.16</td>
<td>8.56</td>
<td>8.32</td>
<td>12.84</td>
<td>12.48</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>4.32</td>
<td>4.16</td>
<td>7.23</td>
<td>6.70</td>
<td>10.46</td>
<td>8.89</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$h_R^2$</td>
<td>.43</td>
<td>.44</td>
<td>.40</td>
<td>.39</td>
<td>.40</td>
<td>.38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 384 records (320 scored plus 64 parents) were used at each generation in the L lines; 192 records (160 scored plus 32 parents) were used at each generation in the S lines.

2 1344 records (1280 scored plus 64 parents) were used in the L lines; 672 records (640 scored plus 32 parents) were used in the S lines.

1 384 records (320 scored plus 64 parents) were used at each generation in the L lines; 192 records (160 scored plus 32 parents) were used at each generation in the S lines.

2 1344 records (1280 scored plus 64 parents) were used in the L lines; 672 records (640 scored plus 32 parents) were used in the S lines.
TABLE 4.2. Estimates of genetic gain (ΔG), variability of response (σ_r), coefficient of variation of response, CV(R), and inbreeding (F) for three generations (t) of selection in Large (L) and Small (S) Japanese quail populations.

<table>
<thead>
<tr>
<th>t</th>
<th>L</th>
<th></th>
<th></th>
<th></th>
<th>S</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>ΔG</td>
<td>σ_r</td>
<td>CV(R)</td>
<td>F</td>
<td>ΔG</td>
<td>σ_r</td>
<td>CV(R)</td>
</tr>
<tr>
<td>(g)</td>
<td>(g)</td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>1</td>
<td>3.78</td>
<td>2.22</td>
<td>.00</td>
<td>3.79</td>
<td>2.14</td>
<td>.00</td>
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</tr>
<tr>
<td>2</td>
<td>6.90</td>
<td>2.57</td>
<td>.36</td>
<td>6.04</td>
<td>2.86</td>
<td>.43</td>
<td>.05</td>
</tr>
<tr>
<td>3</td>
<td>10.67</td>
<td>2.85</td>
<td>.27</td>
<td>8.81</td>
<td>3.84</td>
<td>.43</td>
<td>.14</td>
</tr>
</tbody>
</table>

\[1\] Nei/N_e = 12.00
\[2\] Neq/N_e = 10.21
\[3\] Neq/N_0 = .85
\[4\] Inbreeding depression = .01

\[1\] Estimated in one replicate of the selection line at Generation 0.
\[2\] Estimated in one replicate of the selection line at Generation 3.
\[3\] Regression slope significantly different from 0 at \( P \leq .05 \).
4.5. DISCUSSION

4.5.1. Effect of population size on selection response

The phenotypic and genetic means of the control lines in both populations remained relatively stable. Apparent additive genetic variance declined at each generation. Apparent additive genetic variances estimated at generations 1 to 3 are biased because the parents of these birds at each generation were not sampled at random and the relationships among the parents were not considered. Though the apparent additive genetic variances are biased they still provide the magnitude and trend of the additive genetic variance in the different treatment lines. Decline in apparent additive genetic variance during the first generation of selection was due to the intrinsic effect of selection rather than drift when the trait under selection is affected by many additive loci (Bulmer, 1971). Directional selection in quantitative traits generates gametic disequilibrium (Bulmer, 1971) which results in a decrease in additive genetic variance. Predicted response to selection was observed with high degree of accuracy for the first generation of selection regardless of the population size. Response to selection was higher in the large population than in the small population. Frankham et al., (1968) and Hanrahan et al., (1973) also observed similar responses in large and small populations in short-term experiments.

After the first generation of selection, selection response based on theoretical prediction equation was biased upward (see Table 4.1). The magnitude of the bias depends on how additive genetic variance, accuracy and selection intensity are changing during selection (Gomez-Raya and Burnside, 1990). At generation 3, the realized response was 28% less than predicted in the small population compared to 19% in the large population. This is an indication of how genetic parameters in the base population are changing in the small and large populations. Realized
heritability from the first generation of selection provides an unbiased estimate of the base population. The use of realized heritability estimated from cumulated response to selection beyond the first generation is biased and should not be used. Furthermore, response to selection is associated with gene frequency changes (Falconer, 1989). In short-term selection, changes in gene frequency may be insignificant in the large population, but might be of importance in the small population. Decline in apparent additive genetic variance coupled with possible changes in gene frequencies may be responsible for the smaller response observed in the small population as compared to the large population. Using complete pedigree information and data from all generations, the model in Equation (4.1) was used to estimate the base population heritability. However, the REML estimate of h² was not identical to the estimate of .45 reported in Chapter 3. This may be due to sampling effect, because only a small sample of the base population animals (140) became part of the large (64) and small (32) populations in this analyses. Even though predictions from short-term selection are expected to be fairly accurate regardless of population size (Hill, 1985, 1986), results from this experiment demonstrates clearly that the response observed in short-term selection experiments beyond the first generation of selection depend on population size.

4.5.2. Effect of population size on inbreeding

Inbreeding became evident in generation 2. The rate of inbreeding is inversely related to effective population size (Falconer, 1989). Inbreeding caused a reduction in effective population size in both the large and small populations. As shown in one replicate (selection line) in both the large and small populations, \( N_a \) was larger in the large population than in the small
population. Inbreeding reduced the additive genetic variance. Since inbreeding is a function of population size, heritability after one generation of selection should also be a function of population size. Inbreeding resulted in inbreeding depression in Week 2 body weight in both the small and large populations. The change in mean value on inbreeding is a consequence of dominance at the loci concerned with the trait (Week 2 body weight). The joint effects of dominance and variance of gene frequency change at each loci (genetic drift) causes a deviation from the expected gain (Kojima, 1961). Treating inbreeding coefficient as a covariate in the model may not be reliable when depression also depends on dominance relationships (Smith and Mäki-Tanila, 1990). In future, dominance genetic variance should be considered in developing models for analysis.

4.5.3. Effect of population size on variability of response

Increasing levels of inbreeding and the existence of dominance variance also caused the variance of response to increase. This may also explain why the large variability of response was observed in the small population as compared to the large population. Variability of response is one of the main reasons why realized response deviates from predicted. Variability of response was inversely related to the effective population size (Hill, 1980; Nicholas, 1980), so the large standard deviation of response in the S lines compared to the L lines confirms theoretical expectations. The drift variance of response per generation, $CV(R)$, declined from 36% in generation 2 to 27% in generation 3 in the L lines, but remained the same (43%) in the S lines.
4.5.4. General discussion

It is usually argued that means and variance of response can be predicted from short-term experiments (≤ 5 generations) (López-Fanjul, 1989; Hill, 1985, 1986). Results from this experiment shows that this is only valid for one generation of selection. Estimating genetic parameters using a very small sample of the base population animals would most likely yield parameters which may not reflect the true base population parameters. Individuals become related by ancestry, and inbreeding builds up which causes a decline in the additive genetic variance and inbreeding effective population size. Selection response in Generation 3 suggests that prediction using base population parameters in short-term selection may be useful in relatively large populations but not in small populations. Frankham et al. (1968) and Hanrahan et al. (1973) estimated realized heritability under the assumption that the response to selection per generation is linear. Results from this experiment show that such an assumption in small populations leads to biased estimates and should be discouraged. Predicting variability of response is useful in designing selection experiments to assess possible departures from expectations. The present study suggests that selection experiments of more than one generation is more efficient from the variance stand point but give biased estimates of the base population parameters. The degree of bias is inversely related to the population size.

4.5.5. Conclusion

Criteria for comparing selection schemes for different population sizes such as dealt with in this research could be used as the bases for formulating optimum breeding strategy for small populations. This experiment showed that inbreeding caused a decline in the apparent additive
genetic variance, and also inbreeding depression in Week 2 body weight. Therefore, to limit the rate of inbreeding in small populations, the use of only one male per full-sib family was suggested by Nicholas and Smith (1983). Such restrictions may reduce selection response but will slow down inbreeding. A criterion for the optimum combination of response to selection and inbreeding may be useful for small populations rather than maximizing response to selection which is often the goal of most short-term selection experiments. An alternative may be to maximize response to selection regardless of inbreeding, in two or more sublines and intercross the sublines periodically to start a new subpopulation (Wright, 1939; Crow, 1952; Dickerson, 1977). This approach may not result in maximum response in the whole population (Smith and Quinton, 1993) but would take advantage of genetic diversity among the sublines for improvement and control inbreeding and genetic drift in small populations.
CHAPTER 5

5. EFFECT OF MATING SYSTEMS ON RESPONSE TO SELECTION, VARIABILITY OF RESPONSE AND INBREEDING IN SHORT-TERM SELECTION IN SMALL POPULATIONS.

5.1. ABSTRACT

A selection experiment involving 3 mating strategies was conducted in order to evaluate the efficiency of selection, and ways to reduce genetic drift and inbreeding in small populations. The mating strategies were random (RM), minimum coancestry (MN) and maximum coancestry (MX) mating. The selection criterion was Week 2 body weight and selection intensity was the same under all the mating strategies. The effective population size in one replicate under each mating strategy was 16 at Generation 0. Genetic gain at Generation 3 were 7.03, 7.36 and 6.62 and inbreeding levels were 6%, 4% and 12% in the RM, MN and MX lines, respectively. After 3 generations of selection, inbreeding effective population size declined by 62% in the MX lines. In the MN lines, inbreeding effective population size increased by 16%. A substantial reduction of inbreeding was found with the use of the MN mating strategy. The reduction was due to an increase in the effective population size. Practising MN mating over RM mating would be useful in achieving higher genetic gain with limited inbreeding in short-term selection as far as the level of inbreeding is lower than what would be expected under random mating.
5.2. INTRODUCTION

Prediction of selection response is essential in evaluating selection methods and economic returns from a selection scheme, and comparing different selection strategies. The traditional approach for evaluating response to selection was developed for a population of infinite size (Falconer, 1989) and predictions are not always accurate if the population size is limited (Verrier et al., 1991). In finite populations, linkage disequilibrium, genetic drift and inbreeding would cause realized response to be less than that predicted with models developed for infinite populations (Bulmer, 1971; Robertson, 1961). Experimental results from Chapter 4 show that bias in prediction is more pronounced in small populations than in large ones. In animal breeding, despite the large number of individuals scored, only a few are selected to breed for the next generation. This results in a small effective population size, thereby increasing the chance of drift and inbreeding. Furthermore, breeders seeking to improve minor or rare breeds have no choice but to deal with small foundation population. Therefore, any strategy that minimizes the effects of inbreeding and genetic drift would be beneficial in increasing selection response in small populations.

Genetic drift and inbreeding are both inversely related to the effective population size (Crow, 1954). They have related but distinctive effects and a system that minimizes one of these processes does not necessarily minimize the other (Kimura and Crow, 1963b). Theoretical studies by Kimura and Crow (1963b) suggested that practising non-random mating of individuals on the basis of their relationship to each other may either reduce or increase genetic drift. Hill (1972a) also suggested that in breeding schemes where there is maximum avoidance of mating relatives, heterozygosity may increase over that expected from random mating, and consequently drift may
Attempts have been made in the past to reduce inbreeding and/or drift in small populations under selection. Some of the strategies pursued were reducing selection intensity and ignoring family information or practising weighted selection (Toro and Perez-Enciso, 1990, Toro et al., 1988). An approach focusing on mating strategies is proposed now. Mating strategy could be used to modify gene and genotypic frequencies. Avoidance of close relatives could decrease the rate of inbreeding in the short term. Conversely, mating of closely related individuals may lead to increased rate of inbreeding.

The objective of this study was to investigate the merit of mating systems with regard to selection response, variance of response and inbreeding in a short-term selection experiment in small populations. Evaluation of mating systems would improve the efficiency of selection and strategies to reduce drift and/or inbreeding in small populations under artificial selection.
5.3. MATERIALS AND METHODS

5.3.1. Experimental Design

From the base population described in Chapter 3, four treatment lines, each replicated, were established with the same number (64) of equal sex ratio. Three treatment lines were selected for Week 2 body weight under 3 mating strategies, namely; minimum coancestry mating (MN), maximum coancestry mating (MX) and random mating (RM). In other words

MN: Least related individuals within the selected group are mated.

MX: Most related individuals within the selected group are mated.

RM: Individuals within the selected group are mated at random.

Phenotypic selection was conducted in the MN, MX and RM lines. At each generation 8 males and 8 females in each replicate were selected on Week 2 body weight. The fourth treatment line was used as a control where 8 males and 8 females were randomly selected and bred. The control line was used in the evaluation of selection response for the mating strategies (see Equations 4.4 - 4.6). Coancestry between 2 individuals X and Y, \((r_{xy})\), is the probability that a random gene of a given locus from individual X is identical by descent to a random gene of that locus in individual Y (Malécot, 1969). Theoretical selection intensity was obtained from mathematical tables (Becker, 1992) and selection differentials were determined by the mean difference between the population and the selected parents weighted by the number of progeny.

If a selected bird died before it was bred, it was replaced by the next highest ranking bird. All the lines were propagated for 3 generations with a generation interval of about 4 months. Birds were kept and managed under similar conditions as described in Chapter 3. There were no interbreeding among replicates. Replicates were combined during analysis. Three hundred and
twenty (64 base population animals included) animals were used per mating strategy every generation to estimate apparent additive genetic variance.

5.3.2. Estimation of genetic parameters

Refer to sections 4.3.3 to 4.3.6 in Chapter 4. Variance of response was estimated in the selection lines only. Separate analysis were done for each mating strategy.

5.4. RESULTS

Table 5.1 shows apparent additive genetic variance, cumulative selection differential, cumulative response, realized heritability for 3 generations under the 3 mating strategies. Apparent additive genetic variance declined each generation in all the selected lines. Realized responses under all the mating strategies were similar after one generation of selection and were also close to the predicted response. However, after the first generation of selection the MN lines showed the greatest response followed by the RM lines and the MX lines. There was a decreasing trend in the realized heritability as the number of generations increased. The inbreeding effective population size reduced in the RM and MX lines, but increased in the MN lines. The inbreeding effective population size was larger in the RM lines than in the MX lines. Genetic gain (trend), standard deviation of response, coefficient of variation of response, and inbreeding are presented in Table 5.2. Cumulative genetic trend followed the same pattern as the phenotypic response to selection. The variability of response increased at each subsequent generation of selection. Variability of response was largest in the MX lines, with the MN lines...
having the least variability. The variability of response per generation measured in terms of the coefficient of variation followed a similar pattern as the standard deviation of variation of response. Inbreeding became evident at generation 2. In generation 3, inbreeding level in the MX lines was 3 times that of the MN lines. Inbreeding calculated in the RM lines was between the MN and MX lines. The effect of inbreeding on body weight (i.e., inbreeding depression) is given in Table 5.2. Inbreeding affected body weight differently under the 3 mating strategies. Inbreeding depression was 2% per 10% increase (P≤.05) in inbreeding in the RM lines, and 3% per 10% increase (P≤.05) in inbreeding in the MX lines. Inbreeding had no effect on Week 2 body weight (P>.05) in the MN lines. Data on means and standard deviations of Week 2 body weight under of the different treatment lines and replicates are presented in Appendix 4.
TABLE 5.1. Estimates of apparent additive genetic variance ($\sigma_a^2$) selection differential, response to selection and realized heritability ($h_r^2$) for three generations of selection in Japanese quail populations under three mating strategies

<table>
<thead>
<tr>
<th>Generation</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma_a^2$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>15.35</td>
<td>10.92</td>
<td>10.18</td>
<td>9.88</td>
</tr>
<tr>
<td>MN</td>
<td>18.23</td>
<td>15.54</td>
<td>15.01</td>
<td>13.34</td>
</tr>
<tr>
<td>MX</td>
<td>16.19</td>
<td>13.95</td>
<td>11.62</td>
<td>11.31</td>
</tr>
<tr>
<td>Cumulative differential</td>
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</tr>
<tr>
<td>RM</td>
<td>8.88</td>
<td>16.99</td>
<td>24.50</td>
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</tr>
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<td>MN</td>
<td>8.94</td>
<td>18.00</td>
<td>28.06</td>
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<tr>
<td>MX</td>
<td>8.92</td>
<td>17.21</td>
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<tr>
<td>Predicted response (g)</td>
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</tr>
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<td>7.03</td>
<td>10.54</td>
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</tr>
<tr>
<td>MN</td>
<td>3.51</td>
<td>7.03</td>
<td>10.54</td>
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</tr>
<tr>
<td>MX</td>
<td>3.51</td>
<td>7.03</td>
<td>10.54</td>
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<tr>
<td>Realized response (g)</td>
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<tr>
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<td>5.97</td>
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<td>$h_r^2$</td>
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<td>RM</td>
<td>.38</td>
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<tr>
<td>MN</td>
<td>.40</td>
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<td>$^3$REML $h^2$</td>
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<tr>
<td>MX</td>
<td>.34±.09</td>
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</tr>
</tbody>
</table>

$^1$RM=random mating; MN=minimum coancestry mating; MX=maximum coancestry mating.
$^2$320 records (256 scored plus 64 parents) were used at each generation.
$^3$1088 records (1024 scored plus 64 parents) were used.
<table>
<thead>
<tr>
<th>Generation</th>
<th>ΔG</th>
<th>σ&lt;sub&gt;R&lt;/sub&gt;</th>
<th>CV(R&lt;sub&gt;R&lt;/sub&gt;)</th>
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<tr>
<td><strong>Generation 1</strong></td>
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</tr>
<tr>
<td>RM</td>
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3<sup>N<sub>e</sub></sup>

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<tr>
<td>MX</td>
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3<sup>N<sub>e</sub>/N<sub>c</sub></sup>

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<th>ΔG</th>
<th>σ&lt;sub&gt;R&lt;/sub&gt;</th>
<th>CV(R&lt;sub&gt;R&lt;/sub&gt;)</th>
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<tbody>
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<td></td>
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<td>RM</td>
<td>.76</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>MN</td>
<td>1.16</td>
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<tr>
<td>MX</td>
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Inbreeding depression

<table>
<thead>
<tr>
<th>Generation</th>
<th>ΔG</th>
<th>σ&lt;sub&gt;R&lt;/sub&gt;</th>
<th>CV(R&lt;sub&gt;R&lt;/sub&gt;)</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Inbreeding depression</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RM</td>
<td>.02&lt;sup&gt;4&lt;/sup&gt;</td>
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<td></td>
<td></td>
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<tr>
<td>MN</td>
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</tr>
<tr>
<td>MX</td>
<td>.03&lt;sup&gt;4&lt;/sup&gt;</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

<sup>1</sup>RM = random mating; MN = minimum coancestry mating; MX = maximum coancestry mating.
<sup>2</sup>Calculated in one replicate at Generation 0.
<sup>3</sup>Calculated in one replicate at Generation 3.
<sup>4</sup>Regression slope significantly different from 0 at P<.05.
5.5. DISCUSSION

5.5.1. Effect of mating system on selection response

Response to selection after the first generation of selection was similar under the 3 mating strategies. Therefore, realized heritability from the first generation of selection under the 3 mating systems were unbiased estimates of the heritability in the respective base populations. REML estimates of the base populations heritability utilized complete pedigree information and data from all generations. Sixty-four of the 140 animals which constituted the base population in Chapter 3 were used in the REML analysis using the model given in Equation (4.1). Sampling may have had an effect on the REML estimates. Sampling a small number of animals for each mating strategy may be responsible for the differences in the additive genetic variance in Generation 0. This indicate that sampling very small number of base population animals may result in unreliable estimates of the base population genetic parameters. After the first generation of selection, apparent additive genetic variance declined as a result of both gametic disequilibrium, reduced accuracy of selection and inbreeding. Apparent additive genetic variance declined at each generation. Apparent additive genetic variances estimated at generations 1 to 3 are biased because the parents of these birds at each generation were not sampled at random and the relationships among the parents were not considered. The MN lines had lower inbreeding levels and larger response to selection as compared to RM lines. Selection response among the 3 mating strategies showed a trend at Generation 3, but difference among mating strategies were not evident. Selecting for 5 or more generations may yield definite and conclusive results.
5.5.2. Effect of mating system on inbreeding

In this study, individuals in generation 0 within the lines were unrelated, thus resulting in zero inbreeding after the first generation of selection. Inbreeding level was 3 times higher in the MX lines than in the MN lines in generation 3. Inbreeding in the MN lines (4%), was lower than the expected inbreeding level (5%) of a random mating unselected population of the same population size. This implies that the inbreeding effective population size increased. The converse was observed in the MX lines. Inbreeding depression was 3% per 10% increase in inbreeding in the MX lines compared to 2% in the RM lines. The existence of inbreeding depression indicates that Week 2 body weight is also affected by dominance effects (Falconer, 1989). When genotypic value at different loci within an animal become positively correlated as a result of inbreeding, increased dominance variance results (Johansson et al., 1993). As mentioned in Chapter 4, inbreeding depression was accounted for by treating inbreeding coefficient as a covariate in the model presented in Equation (4.1). Such an approach is only a rough approximation of the dominance effect because the effect of inbreeding on the genetic covariance matrix was not accounted for (Smith and Mäki-Tanila, 1990). Future research should take into account dominance genetic variation.

5.5.3. Effect of mating system on variability of response

Both variability and inbreeding are important criteria for the selection of the best breeding plan. Variability of selection response can be used as an indicator of risk of breeding plans (Meuwissen, 1991b). In the present experiment variability increased with the number of
generations, but the variability per generation, CV(R), declined slightly from generation 2 to 3. Variability of response is affected by both inbreeding and additive genetic variance (Equation 4.9). Inbreeding depression reduced the genetic gain. Inbreeding level was lower in the MN lines than in the RM lines in generations 1 and 2 and thus explains why variability of response was lower in the MN lines as compared to the RM lines in generations 1 and 2.

At Generation 3, N_{af} declined by about 62% in the MX lines. In the MN lines however, N_{af} increased by 16%. The variance of response of a selection experiment therefore become a trade off between inbreeding and additive genetic variance. In the MX lines, the decline in heterozygosity, measured in terms of inbreeding was greater than the rate of decline in additive genetic variance thereby resulting in a large variability of realized response. When the decline in heterozygosity is greater than what is expected in random mating population, as was observed in the MX lines, the coefficient of variation of response may not be an appropriate criteria for assessing drift because of the large increase in the variance of response. The converse is true in the MN lines. Using the factor 1 - F_{i} to assess drift may be more appropriate.

Using 1 - F_{i} as an indicator of drift implies that mating systems which build up high levels of inbreeding have reduced drift, and vice versa. The questions as to whether to control drift or inbreeding is subject to debate. When the trait under selection is affected by inbreeding depression, a trade off among rate of inbreeding, drift, genetic gain and variance of response could be a useful criteria for choosing the best selection scheme. The present results show that practising minimum coancestry mating over random mating can alleviate small populations from inbreeding depression.
5.5.4. **Short-term breeding goal for small populations**

The choice of a breeding plan depends on the time horizon of the selection experiment and the breeding goal. Hill (1985, 1986) argued that the importance of population size in selection depends on the time horizon in which the breeder operates, and that in the short term selection should be as intense as possible to achieve maximum response. Hill's approach for short term selection assumes that inbreeding depression in the selected trait is negligible and selection would have no substantial repercussions on the reproductive performance of the population. These assumptions may hold true in large populations but definitely not in small populations. In this experiment inbreeding depression in Week 2 body weight was significant (Table 5.2) and should be considered as an important factor in defining the breeding goal for small populations, even in the short term. Information about the association between the trait under selection and fitness characteristics of the population is also important in designing the appropriate breeding strategy. Although information about the correlation between selected traits and reproductive capacity cannot be known *a priori*, a rough estimate is necessary because the reproductive capacity of the population should be able to support the breeding strategy of choice.
CHAPTER 6

6. EFFECTS OF RATE OF INBREEDING ON INBREEDING DEPRESSION IN SOME FITNESS TRAITS IN SMALL POPULATIONS UNDER ARTIFICIAL SELECTION

6.1. ABSTRACT

The effects of inbreeding on fertility, hatchability and embryonic mortality were studied in two experiments, each under artificial selection for Week 2 body weight for 3 generations. Experiment I comprised a large and small population sizes with effective population sizes of 12 and 6 per replicate, respectively. Experiment II consisted of 4 lines each with an effective population size of 16 per replicate under 3 mating strategies, namely, random mating (RM), minimum coancestry mating (MN), and maximum coancestry mating (MX). The fourth line was a random bred control. The effects of inbreeding were the same for the large and small sizes in Experiment I at the same level of inbreeding. Ten percent increase in the embryo's inbreeding caused 10% reduction in fertility in both experiments. Ten percent increase in the embryo's inbreeding caused about 10% reduction in hatchability in Experiment I. In Experiment II, 10% increase in inbreeding reduced hatchability by 12% in the MN and RM lines, and about 15% reduction in the MX lines. The reduction in hatchability in both Experiments I and II were caused by an increase in early embryonic mortality. Early embryonic death increased at the expense of late embryonic death and pip (piercing the egg shell with the beak). Severity of inbreeding depression appeared to be similar under random mating regardless of populating size. Inbreeding depression appeared to be more severe under maximum coancestry mating compared
to random mating.
6.2. INTRODUCTION

From a theoretical study Hill (1985, 1986), concluded that the importance of population size in a selection program depends on the horizon in which the breeder operates. Hill further stated that in the short term, population size matters little and selection should be as intense as possible. As mentioned in Chapter 5, Hill's approach for short term selection assumes that inbreeding depression on the trait under selection is negligible and there is no repercussions of selection on the reproductive performance of the population. These assumptions may be true for large populations, but definitely not in small populations. In small populations inbreeding builds up at a faster rate than in large populations, therefore the detrimental effects of inbreeding are expected to be more severe in small populations than in large ones. The detrimental effects of inbreeding referred to as inbreeding depression are commonly recognized by reduced reproductive performance and viability (Latter and Robertson, 1962; Nordskog and Cheng, 1988).

In Japanese quail, reproductive characters such as fertility, hatchability and viability are affected by inbreeding (Sittman et al., 1966; Kulenkamp et al., 1973; MacNeil et al., 1984; Sato et al., 1984a). Most of these studies were conducted in unselected populations under different mating strategies and reports on inbreeding depression in quail as a result of selection are few. Fertility and hatch of fertile eggs are complex physiological traits which may be considered as major components of fitness (Crittenden et al., 1957). Fertility is solely a trait of the parents (Bernier et al., 1951), but hatch of fertile eggs is a complex trait made up of two components. The first is the ability of the embryo to survive, and second is the contribution of the dam to the
extra-embryonic portion of the egg which provides the environment for embryonic development (Abplanalp and Kosin, 1953).

In order to formulate an appropriate breeding goal for small populations under selection, information on the consequences of selection on reproductive performance of the population is also required because the reproductive performance of the population should be able to support the breeding goal of choice. The objective of this study was to characterize the levels of inbreeding in two Japanese quail populations under selection for body weight at generation 3 and determine how inbreeding affects fertility, hatchability and embryonic mortality. The two experiments I and II are described in Chapters 4 and 5, respectively.
6.3. MATERIALS AND METHODS

6.3.1. Experimental population

Two Japanese quail populations designated I and II were studied. Experiment I comprises the L (Large) and S (Small) lines described in Chapter 4. Experiment II comprises 4 lines under 3 mating strategies (random, minimum coancestry and maximum coancestry) as described in Chapter 5. Each treatment is replicated. Description of treatments are given in Table 6.1. Individuals selected to be parents for generation 3 progeny were mated at Week 12. Management practices were similar to those described in Chapter 3.

TABLE 6.1. Description of population structure, size and breeding scheme

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Line(^1)</th>
<th>Size</th>
<th>Breeding Structure</th>
<th>Mating Scheme</th>
<th>Selected/ Unselected</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>LS</td>
<td>40♂:40♀</td>
<td>4♂:12♀</td>
<td>Random</td>
<td>Selected</td>
</tr>
<tr>
<td></td>
<td>LC</td>
<td>40♂:40♀</td>
<td>4♂:12♀</td>
<td>Random</td>
<td>Unselected</td>
</tr>
<tr>
<td></td>
<td>SS</td>
<td>20♂:20♀</td>
<td>2♂:6♀</td>
<td>Random</td>
<td>Selected</td>
</tr>
<tr>
<td></td>
<td>SC</td>
<td>20♂:20♀</td>
<td>2♂:6♀</td>
<td>Random</td>
<td>Unselected</td>
</tr>
<tr>
<td>II</td>
<td>RM</td>
<td>32♂:32♀</td>
<td>8♂:8♀</td>
<td>Random</td>
<td>Selected</td>
</tr>
<tr>
<td></td>
<td>MN</td>
<td>32♂:32♀</td>
<td>8♂:8♀</td>
<td>Minimum coancestry</td>
<td>Selected</td>
</tr>
<tr>
<td></td>
<td>MX</td>
<td>32♂:32♀</td>
<td>8♂:8♀</td>
<td>Maximum coancestry</td>
<td>Selected</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>32♂:32♀</td>
<td>8♂:8♀</td>
<td>Random</td>
<td>Unselected</td>
</tr>
</tbody>
</table>

\(^1\)LS=Large selected; LC=Large control; SS=Small selected; SC=Small control; RM=random mating; MN=minimum coancestry; MX=maximum coancestry; C=Control
6.3.2. Data collection

Eggs from each dam were collected over a 21 day period and stored at 10°C before incubation. Incubated eggs were transferred in family baskets to a hatcher at Day 15 of incubation. The hatch was taken out on Day 18 and unhatched eggs were stored overnight at 4°C. Chicks were raised under the same conditions as described in Chapter 3. The unhatched eggs were examined macroscopically and broken on Day 19 to determine fertility, infertility, early- and late- embryonic death, and pips. Fertility was calculated as the number of fertile eggs over the total number of eggs laid. The number of fertile eggs was determined as the total number of chicks hatched on the 18th day of incubation and the number of unhatched eggs judged to be fertile on the 19th day of examination. Hatchability was expressed as the number of hatched chicks over the number of fertile eggs. Embryonic mortality was determined as early (feather germs not visible) i.e. less than approximately 8 days, or late (feather germs are visible) i.e. greater than approximately 8 days (Padgett and Ivey, 1960). Pip (piercing the egg shell with the beak) was determined by examining the unhatched egg for any crack in the shell resulting from the beak of an 18 day old embryo. Each component of embryonic mortality was expressed as a percentage of the total embryonic mortality. Post-hatch survival was not considered in this investigation because about 15% of chicks which died lost their identification.
6.3.3. Statistical Analysis

The data were arcsine transformed to stabilize variance before analysis was done. The statistical model used was as follows,

\[ Y_{yk} = \mu + T_i + L_y + e_{yk} \]  \hspace{1cm} (6.1)

where \( Y_{yk} \) is the trait under study (fertility, hatchability or embryonic mortality), \( \mu \) is the overall mean, \( T_i \) is the effect of the \( i^{th} \) Treatment line; \( L_y \) is the effect of the \( j^{th} \) replicate within the \( i^{th} \) Treatment, and \( e_{yk} \) is the random error term. Separate analyses were done for Experiments I and II. Differences between Treatments were compared using Duncan multiple range test (SAS, 1985). Coancestry between all individuals within a replicate and inbreeding coefficient of each individual was calculated based on the algorithm of Quaas (1976). Inbreeding depression was investigated by regressing fertility, hatchability, late- and early- embryonic mortality, and pip on the embryo's inbreeding coefficient. Both linear and quadratic regression models were fitted. In Experiment I, except for pips there was no significant difference between the different treatment lines, so they were all combined for the regression analysis. The frequencies of pips were too small to yield any meaningful results under separate analysis for the different treatments, so they were also pooled. In Experiment II, separate analyses were done for the different mating systems.
6.4. RESULTS

Means of the analyzed traits for Experiments I and II are given in Tables 6.3 and 6.4, respectively. Average inbreeding, as well as its ranges and standard deviation are presented. Fertility decreased from 97.1% (Table 6.2) to about 87% after 3 generations of selection in both Experiments I and II. In Experiment I, hatchability was lower (P≤.05) in the L lines (62%) than in the S lines (68%). In Experiment II, the MX lines showed a lower (P≤.05) hatchability (61%) compared to the RM, MN and C lines. There was no significant difference (P>.05) in hatchability between the RM and MN lines. The hatchability of C lines was comparable to that prior to selection (Table 6.2).

The quadratic part in all the regression analyses were not significant (P = .10 ~ .30), so they were dropped from the regression model. Tables 6.5 and 6.6 showed the regression coefficients of fertility, hatchability and embryonic mortality with 10% increase in inbreeding in Experiments I and II, respectively. There was a significant reduction (P≤.05) in fertility of about 11% per 10% increase in inbreeding in both Experiments I and II.

In Experiment I, there was a significant reduction (P≤.05) in hatchability of about 11% per 10% increase in inbreeding. Regression coefficients for hatchability in Experiment II varied among the different mating strategies. Hatchability reduced (P≤.05) by about 12% in the MN and RM lines, and about 15% in the MX lines. The reduction in hatchability of about 5% in the C lines was not significant. There was an increasing tendency found in early embryonic death at the expense of late embryonic death in Experiment I and the selected lines in Experiment II (RM, MN and MX). Regression coefficients for pips varied. Pips reduced by 7% per 10% increase in inbreeding in Experiment I. In Experiment II, there was a significant decrease of about 7% per
10% increase in inbreeding in the MX lines.

**TABLE 6.2. Fertility, hatchability and embryonic mortality (early death, late death and pips) in Japanese quail population prior to selection.**

<p>| | |</p>
<table>
<thead>
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<tbody>
<tr>
<td>Number of eggs set</td>
<td>2740</td>
</tr>
<tr>
<td>Fertility (%)</td>
<td>97.1</td>
</tr>
<tr>
<td>Hatchability (%)</td>
<td>76.5</td>
</tr>
<tr>
<td>Number of unhatched eggs (fertile)</td>
<td>624</td>
</tr>
<tr>
<td>Early death (%)</td>
<td>70.1</td>
</tr>
<tr>
<td>Late death (%)</td>
<td>22.4</td>
</tr>
<tr>
<td>Pips (%)</td>
<td>7.3</td>
</tr>
</tbody>
</table>
TABLE 6.3. Fertility, hatchability and embryonic mortality (early death, late death and pips) in Large and Small Japanese quail populations selected for body weight for 3 generations.

<table>
<thead>
<tr>
<th></th>
<th>LS</th>
<th>LC</th>
<th>SS</th>
<th>SC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of fertile eggs</td>
<td>252</td>
<td>255</td>
<td>158</td>
<td>152</td>
</tr>
<tr>
<td>Fertility (%)</td>
<td>86.11±8.9</td>
<td>88.80±2.9</td>
<td>87.38±5.07</td>
<td>88.61±4.8</td>
</tr>
<tr>
<td>Hatchability (%)</td>
<td>62.93±34.2a</td>
<td>61.39±30.7a</td>
<td>67.06±20.4b</td>
<td>68.10±34.4b</td>
</tr>
<tr>
<td>Early death (%)</td>
<td>82.48±31.6</td>
<td>81.84±27.1</td>
<td>73.46±29.7</td>
<td>79.33±32.3</td>
</tr>
<tr>
<td>Late death (%)</td>
<td>6.66±17.6</td>
<td>11.13±19.1</td>
<td>14.41±22.5</td>
<td>18.66±32.3</td>
</tr>
<tr>
<td>Pips (%)</td>
<td>10.84±23.7</td>
<td>6.66±23.2</td>
<td>9.09±24.3</td>
<td>2.00±6.32</td>
</tr>
</tbody>
</table>

Inbreeding coefficient

<table>
<thead>
<tr>
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<th>(.00-.25)</th>
<th>(.06-.25)</th>
<th>(.06-.25)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>.13±.10</td>
<td>.09±.08</td>
<td>.14±.05</td>
<td>.15±.07</td>
</tr>
</tbody>
</table>

* the range of inbreeding coefficient

Means within rows with different superscript were significantly different, (P≤.05)
TABLE 6.4. Fertility, hatchability and embryonic mortality (early death, late death and pips) in Japanese quail populations under 3 mating strategies selected for body weight for 3 generations.

<table>
<thead>
<tr>
<th></th>
<th>RM</th>
<th>MN</th>
<th>MX</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of fertile eggs</td>
<td>186</td>
<td>165</td>
<td>201</td>
<td>216</td>
</tr>
<tr>
<td>Fertility (%)</td>
<td>88.53±6.2</td>
<td>87.91±2.5</td>
<td>89.07±8.6</td>
<td>88.95±2.8</td>
</tr>
<tr>
<td>Hatchability (%)</td>
<td>62.54±29.8a</td>
<td>69.03±24.9a</td>
<td>61.12±29.6b</td>
<td>75.37±24.8c</td>
</tr>
<tr>
<td>Early death (%)</td>
<td>79.27±28.8</td>
<td>74.22±31.9</td>
<td>78.88±31.3</td>
<td>72.77±35.1</td>
</tr>
<tr>
<td>Late death (%)</td>
<td>16.04±21.7</td>
<td>16.44±23.5</td>
<td>15.57±34.6</td>
<td>16.11±27.2</td>
</tr>
<tr>
<td>Pips (%)</td>
<td>6.25±25.0</td>
<td>9.33±26.0</td>
<td>5.41±11.9</td>
<td>11.11±19.6</td>
</tr>
<tr>
<td>Inbreeding coefficient</td>
<td>.11±.11</td>
<td>.05±.06</td>
<td>.13±.10</td>
<td>.05±.07</td>
</tr>
<tr>
<td></td>
<td>(.00-.25)</td>
<td>(.06-.25)</td>
<td>(.00-.25)</td>
<td>(.00-.25)</td>
</tr>
</tbody>
</table>

* the range of inbreeding coefficient

Means within rows with different superscripts were significantly different (P ≤ .05)
TABLE 6.5. Regression coefficients of traits on 10% increase in embryo's inbreeding in Experiment I

<table>
<thead>
<tr>
<th>Trait</th>
<th>b±se</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertility</td>
<td>-10.7±.04*</td>
</tr>
<tr>
<td>Hatchability</td>
<td>-10.8±.02*</td>
</tr>
<tr>
<td>Early death</td>
<td>+5.0±.06</td>
</tr>
<tr>
<td>Late death</td>
<td>-4.0±.07</td>
</tr>
<tr>
<td>Pips</td>
<td>-7.0±.21*</td>
</tr>
</tbody>
</table>

* slope significantly different from 0 at P≤.05

TABLE 6.6. Regression coefficients of traits on 10% increase in embryo's inbreeding in Experiment II

<table>
<thead>
<tr>
<th>Trait</th>
<th>RM</th>
<th>MN</th>
<th>MX</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertility</td>
<td>-10.91±.04*</td>
<td>-10.21±.07*</td>
<td>-10.44±.21*</td>
<td>-9.22±.06*</td>
</tr>
<tr>
<td>Hatchability</td>
<td>-12.26±.03*</td>
<td>-12.44±.05*</td>
<td>-15.23±.12*</td>
<td>-5.31±.03</td>
</tr>
<tr>
<td>Early death</td>
<td>+5.41±.05</td>
<td>+3.52±.08</td>
<td>+8.80±.05</td>
<td>+1.00±.01</td>
</tr>
<tr>
<td>Late death</td>
<td>-4.00±.05</td>
<td>-3.60±.13</td>
<td>-5.00±.06</td>
<td>-0.00±.05</td>
</tr>
<tr>
<td>Pips</td>
<td>-1.20±.22</td>
<td>-3.41±.04</td>
<td>-7.44±.07*</td>
<td>-3.13±.09</td>
</tr>
</tbody>
</table>

* slope significantly different from 0 at P≤.05
6.5. DISCUSSION

6.5.1. Effect of inbreeding on fertility and hatchability

The results of this study indicate that inbreeding caused a significant reduction in fertility and hatchability in Japanese quail, and was consistent with results from previous studies (Sittman et al., 1966; Kulenkamp et al., 1973). In this study, fertility decreased by 10% with a 10% increase in inbreeding in both Experiments I and II. This value is higher than 2.16% reported by Sato et al. (1984a), but comparable with 11% obtained by Sittman et al. (1966). Fertility is the union of gametes and both parents are equally involved. The decline in fertility can be attributed in part to the male reproductive ability such as low frequency of mating (Cheng et al., 1985), decreased testes weight, small semen volume, low sperm concentration and high abnormal sperm frequency as inbreeding progresses (Sato et al., 1984b). Cheng et al., (1985) reported a low mating frequency in inbred dams and indicated that male and female mating behaviour seem to contribute equally to fertility. Physiological studies on the properties of the egg cell in terms of receptability to sperm in inbred dams are not available. Such information is important in understanding both physiological and behavioral mechanisms underlying fertility.

Hatchability was depressed by about 11% in Experiment I, 12% in MN and RM lines, and about 15% in MX lines in Experiment II with 10% increase in inbreeding. These percentages were higher than 7% reported by Sittman et al. (1966) and 6.2% by Sato et al., (1984a), but lower than 26% reported by Kulenkamp et al., (1973). Matings in the MX lines were predominately among full-sibs.
6.5.2. Effect of inbreeding on embryonic mortality

Hatchability is a compound trait which includes the survival of the embryo as well as extra-embryonic membrane contribution of the dam (Abplanalp and Kosin, 1953). Sittman et al., (1966) demonstrated that inbreeding of the embryo is more important than maternal effects in embryonic mortality. Results from previous studies (Sittman et al., 1966; Kulenkamp et al., 1973; Sato et al., 1984a) attributed the reduction in hatchability to an increase in embryonic mortality. This study shows that the proportion of early embryonic deaths increased whilst late deaths and pips decreased, thus suggesting that with rising levels of inbreeding, embryonic death before Day 8 of incubation may be the primary cause of reduced hatchability. There was a significant reduction (P ≤ .05) in pips in Experiment I and MX lines in Experiment II. Some of the embryonic mortality classified as late deaths may have hatched eventually given an extra day or two. Aggrey and Cheng (1994) reported an increase in egg size in Experiment II. Large eggs usually hatch late compared to medium eggs as a result of their size (Shanawany, 1987) and possibly, the microenvironmental changes in hatching baskets caused by chicks which had already hatched.

6.5.3. Inbreeding and phenodeviants

The selection experiment caused a reduction in effective population size thereby increasing the level of inbreeding. Japanese quail is known to be susceptible to inbreeding depression (Sittman et al., 1966; Abplanalp, 1990) and therefore it would be expected that lethal or semilethal mutations would be revealed when a population of quail is subjected to inbreeding.
About 0.05% of the chicks hatched had either crossed legs, crossed beaks or crooked necks, and most of these abnormalities were found in the MX lines. These abnormalities among others have been reported in other quail populations (Lucotte, 1973). Inbreeding therefore caused the appearance of the deleterious recessive genes responsible for such abnormalities. Almost all the chicks hatched with abnormalities died in the first week. The few individuals which survived had severe impaired growth.

6.5.4. Synthesis and Conclusion

The level of inbreeding is inversely related to the effective population size, but the inbreeding depression appears to be similar in random mating populations regardless of the population size. However, under non-random mating, the consequences of inbreeding appeared to be more severe in the MX lines than in the MN and RM lines at the same level of inbreeding.

The decline of fertility and hatchability due to inbreeding indicates that there is directional dominance of the loci concerned (Falconer, 1953), but does not discriminate between simple dominance and overdominance. There was also a strong tendency of a non-linear decline in the traits considered, thereby implicating the involvement of epistatic interactions.

In summary, results from this experiment regarding the effects of inbreeding on fertility and hatchability are consistent with previous studies on inbreeding in Japanese quail. Furthermore, this study showed that increased embryonic death before Day 8 of incubation may be among the primary causes of reduced hatchability in inbred quail populations. In addition, it was observed that the severity of inbreeding depression is similar in random mating populations.
at the same level of inbreeding regardless of population size. However, under non-random matings the effects of inbreeding were more severe in matings of closely related individuals than in matings of least related individuals at the same level of inbreeding.
CHAPTER 7

7. GENERAL DISCUSSION AND CONCLUSIONS

7.1. GENERAL DISCUSSION

The development of theory for the prediction of selection response, inbreeding, genetic drift and loss of additive genetic variance in short-term selection experiments, provide the basis for the efficient design of breeding programs. In the short term, the goal of mass selection has been to maximize response to selection (Hill, 1985, 1986; Lopéz-Fanjul, 1989), but only at the expense of reducing effective population size of the selected line. However, the maximum advance at the selection limit is expected from selecting the better half of the population every generation (Robertson, 1961), so short-term selection is sacrificed to ultimate gain. Models for an optimum proportion that maximize the genetic advance achieved in a fixed number of generations have been developed (Smith, 1969; Robertson, 1970; James, 1972). The underlying assumptions for short- and medium-term selection are that the effective population size is not effected by selection, selection response depends on genetic variance in the base population and there is no correlation between directional selection for quantitative traits and fitness. Results from the present study show that in small populations under artificial selection the aforementioned assumptions are not true. There is a need therefore to formulate a new selection scheme for small populations under artificial selection for quantitative traits. The present study demonstrates that in small populations however, rate of response is limited largely by reduced heritability, inbreeding and genetic drift, and negative association between the trait selected for and fitness.
Artificial selection in small populations results in the chance loss of some desirable alleles, and consequently decrease the limit to selection. Also in small populations, gene frequencies are not stable and are subject to random fluctuation (Wright, 1955). The most important effect of genetic drift on a selection experiment is the variation in response (Nicholas, 1980). Since genetic drift is a function of effective population size, to achieve a significant result in a selection experiment, one should ensure that the effective population size is adequate. To determine the effective population size required for a selection experiment, a simple measure which provides a useful guide is the coefficient of variation of response, CV(\(R_0\)). In Chapter 2, the effective population size required to reduce genetic drift to a predefined level was determined for short-term experiments. In this study, it was concluded that measurement error variance is an important component of the variance of response, and the effective population size required was mainly dependent on the predefined level of CV(\(R_0\)). The more stringent requirement imposed on CV(\(R_0\)) will help alleviate the impact of genetic drift and inbreeding in selection experiments. There were however, some shortcomings in the model used for the prediction of population size. The models did not account for the effects of directional selection (i.e. linkage disequilibrium, loss of additive genetic variance, and inbreeding depression) and also the effect of selection differential on the intra-class correlation of family members. Inability of the model to account for intrinsic effects of selection led to overprediction of the selection variance and consequently the required effective population size for a predefined CV(\(R_0\)).

Attempts have been made to provide a better formula for predicting drift of populations under selection (Wray and Thompson, 1990a,b), but their expressions were of limited application to small populations and was also limited to only 2 generations. Bias in predicting drift and
inbreeding in a population under selection remains high. There is still a need for an accurate prediction method for inbreeding and genetic gain under any choice of population design, genetic evaluation and selection methods. Such a method would enable the rapid assessment of alternative decisions regarding the design of a breeding scheme.

Accurate estimation of genetic parameters is a prerequisite for the success of any breeding program. Traditional analysis of variance (ANOVA) and animal model (AM) methodologies have been described in Chapter 3. Mixed model methodologies under AM have become the method of choice in the predicting of additive genetic effects not only because they provide the best linear unbiased predictors (BLUP) of additive genetic effects, but because they simultaneously estimate genetic and environmental effects taking into account the relationship among animals (Sorensen and Kennedy, 1983). Animal models also account for the effect of selection and nonrandom mating when the complete relationship matrix is used (Kennedy et al., 1988). Among the assumptions of the AM are that the correct model, including variance is known at least to proportionality, the random effects have multivariate normal distribution implying a large number of loci (Henderson, 1988). Although the base population used in Chapter 3 had previously undergone selection, relationships among individuals used to establish the population were not known and thus not accounted for completely. Genetic parameters estimated in Chapter 3 with both AM and ANOVA methodologies showed that AM is preferred over ANOVA for estimating genetic parameters for unbalanced data.

In Chapters 4 and 5, selection response, variability of response and inbreeding were evaluated under alternative breeding strategies (i.e. population size and mating scheme) in the short term. The large population exceeded the small population in rate of response after the first
generation of selection. Differences in rates of response were also observed under alternative mating strategies after the first generation of selection. Theory on the effects of population size in artificial selection did not emphasize rates but limits to selection, which may be attained fairly rapidly in small populations (Robertson, 1960). In this study, because of the duration of the experiments, rates are more obvious than limits. It is therefore necessary to look at the dynamic process of selection, from the beginning instead of the end. Earlier studies on the effect of population size on response (Frankham et al., 1968; Hanrahan et al, 1973) reported differences in selection response but did not provide detailed explanation other than the differences in population size. In this study, it was observed that the efficiency of a single generation selection experiment is not affected by population size. Beyond one generation, reduced apparent additive genetic variance, and inbreeding which also reduces additive genetic variability and caused depression in Week 2 body weight were the main causes of the differences in the rates of response in population of different sizes. The impact of these factors are more severe in small populations than in large ones. Thus, estimation of base population parameters from short-term selection experiment is biased. The degree of bias may be negligible in large populations, but not in small populations.

The rate of selection response under three mating strategies was studied in search of a strategy to increase response to selection with limited inbreeding. This study showed that avoidance of mating of relatives under mass selection contributed to a strategy that aims at a limited rise of inbreeding especially when effective population size is small. Mating least related individuals among the selected parents led to an increase in the effective population size. Application of such a strategy may be useful as far as consanguinity in the population is below
what would be expected from random mating. The net effect of such an approach on selection response when consanguinity goes ahead of what would be expected under random mating, needs to be examined.

Variability of response is among the criteria used to assess alternative breeding schemes. Variance of response is a function of inbreeding and additive genetic variance. It was generally expected that variance of response in the maximum coancestry mating lines (MX) will be smaller because of less genetic variability among selected parents leading to reduced additive genetic variance. However, if the rate of increase in inbreeding goes ahead of the rate of decline in additive genetic variance as was observed in the MX lines, variance of response will be higher than expected. In evaluating breeding schemes, the level of inbreeding as well as inbreeding depression are equally important. Rising levels of inbreeding decreases the additive genetic variance and increase inbreeding depression which reduces the response to selection. The choice of a mating strategy should therefore be a function of the time horizon, expected inbreeding levels, rate of response, variability of response and inbreeding depression.

Information about the biology of the species under study is very important. Reduction in reproductive performance as a result of inbreeding varies among species (Applanalp, 1990). For example, fertility in the chucker partridge (Woodard et al., 1982) suffers severely from inbreeding depression compared to white leghorn (Applanalp, 1974) at 25% of inbreeding. In general, Japanese quail suffer from reduced reproduction performance compared to many poultry and livestock species at the same level of inbreeding. In the present study, hatchability decreased greatly due to increased early embryonic mortality. The particular breeding strategy chosen should be suitable for the species in question. Practising intense selection to maximize selection
response as a short term goal may be feasible for chicken but may not be successful in Japanese quail.

Any breeding scheme designed for small populations should lead to a continuous genetic improvement over the period of time of interest. Available genetic variance should therefore be used efficiently. The goal of a breeding program for small populations in the short term should shift from maximization of response to optimization of genetic gain and effective population size. Among the parameters to be optimized are rate of response, variability of response, inbreeding depression in selected trait and fitness, and financial and logistic limitations. Such an approach may be more useful in maintaining genetic stability in small populations.

When it comes to designing an effective breeding scheme for small populations under selection for quantitative traits, there is no simple solution. Various strategies that maximize the effective population size have been proposed (Wright, 1939, 1955; Crow, 1952; Kimura and Crow, 1963b; Gill and Harland, 1989). Among the proposals are: (i) use maximum number of males, (ii) rotational breeding scheme, and (iii) crossing inbred lines. Strategies which aim solely at maximizing the effective population size are often used in conservation programs (Gill and Harland, 1989), with no directional selection for quantitative traits.

Three mating systems, namely maximum avoidance (M), circular mating (C) and circular pair mating (CP) have also been evaluated by Kimura and Crow (1963b) in unselected populations. They showed that the ultimate rate of decrease in heterozygosity is less in circular mating than in circular pair mating and maximum avoidance. Despite the efficiency of circular mating in slowing down the progress towards homozygosis in the long run, it is not a convenient mating system in practice because each individual has to be mated twice.
Other proposals which also aim at maximizing response to selection in small populations include practising within-family selection (Dempfle, 1975). Through a simulation study, Dempfle (1975) showed that practising within-family selection implied a relatively lower rate of decay of the genetic variance than individual selection and may therefore result in higher limit. The underlying assumption was that the trait is controlled by a large number of loci. However, if the trait under selection is determined by a small number of loci, then within-family selection leads to a quicker exhaustion of the additive genetic variance (Lopéz-Fanjul, 1989).

Another approach suggested by Crow (1952) and Dickerson (1977) is to maximize selection response regardless of inbreeding in two or more sublines followed by intercrossing to take advantage of genetic diversity among sublines. Crossing sublines would reduce inbreeding and increase the frequency of heterozygotes. However, selection within-line is expected to be less effective with higher rate of inbreeding, except for more elimination of rare recessive lethals and semi-lethals which have little influence on performance of crosses (Crow, 1952). Sublining and intercrossing periodically may not result in maximum response in the whole population (Smith and Quinton, 1993), but may limit the rate of increase in inbreeding. Such a strategy requires sufficient animals for initiating sublines.

Another alternative design for the selection against genes causing inbreeding depression is based on cyclic inbreeding. Under such a strategy, one or more generations of close inbreeding such as full-sib mating is followed by a cross of unrelated inbreds, followed by another close inbreeding (Abplanalp, 1974). Cyclic inbreeding systems have been investigated for chickens by Abplanalp (1974) and for Japanese quail by MacNeil et al. (1984). In both experiments, cyclic inbreeding was successful in reducing inbreeding. However, selection response was lower than
that of mass selection.

In designing an optimum breeding scheme for small populations under artificial selection, combinations of different strategies may be useful. A plan based on restriction on family size coupled with circular pair or maximum avoidance mating is proposed now. Practising within-family selection with either maximum avoidance or circular pair mating should be more efficient in reducing inbreeding in small populations under selection as compared to within-family selection under random mating (Dempfle, 1975) or mass selection with maximum avoidance (Chapter 5). With within-family selection coupled with circular pair mating, the top male and female per full-sib family should be selected. At each generation, the top males from the full-sib families should be rotated among the full-sib families. By selecting the best male and female in each full-sib family, the variance in the number of offspring equals zero, and the equal number of males and females gives the maximum possible effective population size. This approach may be more efficient in reducing inbreeding in small populations but selection response would be lower than in mass selection.

Genetic variation should be the central theme of plans for the long-term maintenance of populations. However, short-term demographic factors such as size of a population may take precedence in management practices because genetic variation is not important if the population becomes extinct. Once the short-term persistence of the population is ensured, management practices can be adjusted to enhance the maintenance of genetic variability and the potential for long-term evolution (Lande and Barrowclough, 1987). In the short-term employing mating strategy such as the minimum coancestry mating has proven to be useful in controlling the level of inbreeding. It would therefore be necessary either to measure the effective population size of
a population, or monitor the level of genetic variation directly in order to assess the population.

Also, better exploitation of the available genetic variability and tapping new sources of genetic variation should be considered. Inbreeding caused depression in Week 2 body weight implying the presence of dominance. Future genetic models should include the effect of selection on selection differential, non-additive gene action, the effects of major genes, and linkages. Genetic variation due to non-nuclear (e.g. mitochondria) DNA deserves consideration as it has been shown to explain a tangible amount of variation in milk production (Bell et al., 1985). However, the difficulties of estimating the importance of any novel types of genetic variation as illustrated for mitochondria inheritance (Rothschild and Ollivier, 1987), should be kept in mind.

7.2. CONCLUSIONS

1. In predicting the effective population size required for short-term selection, the measurement error variance is an important component of the variance of response and should not be ignored. Ignoring the measurement error variance leads to underprediction of the required effective population size at a predefined drift level.

2. In estimating genetic parameters, best linear unbiased prediction procedures under an animal model is more efficient than conventional analysis of variance methods when the data are unbalanced. Heritability estimates for Week 2 and Week 4 body weights were .45 and .47, respectively, suggesting that selection would be effective in improving Weeks 2 and 4 body weights. Genetic correlation estimate of .76 between Week 2 and Week 4 body weights indicates the possibility of improving Week 4 body weight by selecting for Week 2 body weight.
3. In small populations under mass selection, reduced efficiency of selection, reduced heritability, increased variability of response and inbreeding depression were responsible for lower rate of selection response.

4. In short-term selection, practising minimum coancestry mating with mass selection caused an increase in the effective population size thereby reducing the rate of inbreeding.

5. Inbreeding caused reduction in reproductive performance. Rising levels of inbreeding reduced fertility and hatchability and increased early embryonic mortality in Japanese quail.

6. Optimization of effective population size and selection response is suggested as a new approach for small populations under artificial selection. Practising within-family selection with either circular pair mating or maximum avoidance of mating may be useful in limiting inbreeding in the long run. However, this strategy may result in a reduced selection response.
REFERENCES


APPENDIX 1 Measurement error variance

Consider a population undergoing artificial selection with discrete generations. Let $M$ males and $F$ females ($F = \alpha M$) be scored every generation ($M + F = T = $ a constant), and from these, $m$ males and $f$ females ($f = \beta m$) be selected. The proportions selected in each sex are $p_m = m/M$ and $p_f = f/F$. In the population so defined, the effective population size, $N_e$, is given by

\[ N_e = \frac{4mf}{m+f} = \frac{4\beta m}{1+\beta} = \frac{4f}{1+\beta} \quad (1) \]

From Equation (1)

\[ m = \frac{N_e(1 + \beta)}{4\beta} \quad (2) \]

and

\[ f = \frac{N_e(1 + \beta)}{4} \quad (3) \]

Let $p$ be the proportions of individuals selected ($m + f$) selected from the number of individuals scored, $T$.

\[ p = \frac{m+f}{T} = \frac{m+\beta m}{(1+\alpha)M} = \frac{p_m + \beta p_m}{1 + \alpha} = \frac{p_m(1+\beta)}{1 + \alpha} \quad (4) \]

Expressing $T$ in terms of $N_e$ and $p$

\[ Tp = \frac{p_m(1+\beta)}{1 + \alpha} \times (1+\alpha)M = (1 + \beta)m \quad (5) \]
Substituting \( m \) from Equation (2), Equation (5) can be rearranged as

\[
Tp = \frac{N_e(1 + \beta)^2}{4\beta}
\]

Therefore, \( T \) can be expressed as

\[
\frac{1}{T} = \frac{4\beta p}{N_e(1 + \beta)^2}
\]  \( \text{(6)} \)

The measurement error variance was given by Hill (1980) as,

\[
\sigma_e^2 = \sigma_p^2 \left[ \frac{c^2}{f} + \frac{(1 - c^2 - h^2/2)}{T} \right]
\]  \( \text{(7)} \)

Substituting Equations (3) and (6), Equation (7) now becomes

\[
\sigma_e^2 = \frac{4\sigma_p^2}{N_e(1 + \beta)} \left[ c + \frac{\beta p}{1 + \beta} (1 - c^2 - h^2/2) \right]
\]

Substituting \( p \) from Equation (4), the measurement error variance becomes

\[
\sigma_e^2 = \frac{4\sigma_p^2}{N_e(1 + \beta)} \left[ c^2 + \frac{\beta p_m}{1 + \alpha} (1 - c^2 - h^2/2) \right]
\]  \( \text{(8)} \)
## APPENDIX 2 ANOVA estimates of genetic parameters

**TABLE A2.1** Means, standard deviation, coefficients of variation and heritability ($h^2$) for body weight and weight gain at different ages.

<table>
<thead>
<tr>
<th>Trait</th>
<th>$h_s^2 \pm SE$</th>
<th>$h_d^2 \pm SE$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Body weight</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 d</td>
<td>.57 ± .41</td>
<td>2.57 ± .44</td>
</tr>
<tr>
<td>7 d</td>
<td>.08 ± .35</td>
<td>1.96 ± .28</td>
</tr>
<tr>
<td>14 d</td>
<td>.28 ± .23</td>
<td>1.36 ± .26</td>
</tr>
<tr>
<td>21 d</td>
<td>.15 ± .18</td>
<td>1.31 ± .25</td>
</tr>
<tr>
<td>28 d</td>
<td>.47 ± .21</td>
<td>1.03 ± .20</td>
</tr>
<tr>
<td><strong>Weight gain</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 to 7 d</td>
<td>.14 ± .25</td>
<td>1.57 ± .29</td>
</tr>
<tr>
<td>8 to 14 d</td>
<td>.41 ± .18</td>
<td>.69 ± .16</td>
</tr>
<tr>
<td>15 to 21 d</td>
<td>.40 ± .13</td>
<td>.41 ± .12</td>
</tr>
<tr>
<td>22 to 28 d</td>
<td>.62 ± .19</td>
<td>.24 ± .08</td>
</tr>
</tbody>
</table>

$^1h_s^2$ based on sire component of variance

$^2h_d^2$ based on dam component of variance
TABLE A2.2 Genetie (above diagonal) and phenotypic (below diagonal) correlations among body weights at various ages

<table>
<thead>
<tr>
<th>Age (day)</th>
<th>Age (day)</th>
<th>0</th>
<th>7</th>
<th>14</th>
<th>21</th>
<th>28</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>S</td>
<td>.19</td>
<td>.15</td>
<td>.08</td>
<td>.05</td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>D</td>
<td>.75</td>
<td>.71</td>
<td>.68</td>
<td>.65</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>S</td>
<td>.43</td>
<td>.08</td>
<td>.20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>D</td>
<td>.94</td>
<td>.90</td>
<td>.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>S</td>
<td>.16</td>
<td>.32</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>D</td>
<td>.97</td>
<td>1.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>S</td>
<td>.39</td>
<td>.73</td>
<td></td>
<td></td>
<td></td>
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<td>21</td>
<td>D</td>
<td>.34</td>
<td>.64</td>
<td>.72</td>
<td>.96</td>
<td></td>
</tr>
<tr>
<td>28</td>
<td></td>
<td>.29</td>
<td>.55</td>
<td>.68</td>
<td>.76</td>
<td></td>
</tr>
</tbody>
</table>

\( ^1 r_s \) based on sire component of covariance  
\( ^2 r_s \) based on dam component of covariance
TABLE A2.3  Genetic (above diagonal) and phenotypic (below diagonal) correlations among weight gains to 28 days of age.

<table>
<thead>
<tr>
<th>Age interval (day)</th>
<th>0 - 7</th>
<th>8 - 14</th>
<th>15 - 21</th>
<th>22 - 28</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 7 $^1$S</td>
<td>.27</td>
<td>-.63</td>
<td>-.32</td>
<td></td>
</tr>
<tr>
<td>0 - 7 $^2$D</td>
<td>.75</td>
<td>.68</td>
<td>.08</td>
<td></td>
</tr>
<tr>
<td>8 - 14 $^3$S</td>
<td></td>
<td>.94</td>
<td>.48</td>
<td></td>
</tr>
<tr>
<td>8 - 14 $^3$D</td>
<td></td>
<td>.70</td>
<td>.46</td>
<td>.39</td>
</tr>
<tr>
<td>15 - 21 $^3$S</td>
<td></td>
<td></td>
<td>.08</td>
<td></td>
</tr>
<tr>
<td>15 - 21 $^3$D</td>
<td></td>
<td>.15</td>
<td>-.03</td>
<td>.13</td>
</tr>
<tr>
<td>22 - 28</td>
<td>.11</td>
<td>.28</td>
<td>.00</td>
<td></td>
</tr>
</tbody>
</table>

$^1$r$_s$ based on sire component of covariance
$^2$r$_s$ based on dam component of covariance
APPENDIX 3 Week 2 body weight (g) means and standard deviations (SD) of lines and replicates in Experiment I

<table>
<thead>
<tr>
<th>GEN.</th>
<th>LINE</th>
<th>REP</th>
<th>MEAN</th>
<th>SD</th>
<th>LINE</th>
<th>REP</th>
<th>MEAN</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>LS</td>
<td>1</td>
<td>80.50</td>
<td>7.96</td>
<td>SS</td>
<td>1</td>
<td>79.24</td>
<td>5.47</td>
</tr>
<tr>
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APPENDIX 4 Week 2 body weight (g) means and standard deviations (SD) of lines and replicates in Experiment II

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