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QUANTITATIVE GENETICS OF POSTPONED SENESCENCE  
IN DROSOPHILA MELANOGASTER

by

Edward Wellington Hutchinson

A thesis submitted to the  
Faculty of Graduate Studies of  
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of the requirements for the degree of  
Doctor of Philosophy

Department of Biology

1990



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## ABSTRACT

The quantitative genetics of postponed senescence in Drosophila melanogaster were investigated using postponed-senescence stocks created by selection. There was little evidence of non-Mendelian inheritance, inbreeding depression, net directional dominance, or sex-linkage.

The apparently simple additive inheritance of postponed senescence allowed the use of conventional quantitative genetic estimators for gene number. Assays of 24-hour fecundity, ovary weight, starvation resistance (female and male), and longevity (female and male) did not indicate a small number of loci involved in postponed aging.

Heritability estimates for early starvation resistance, a character closely related to longevity, revealed abundant genetic variability in selected and control lines, indicating that neither were near fixation. Selection experiments designed to push each of the two sets of lines towards fixation were performed, although a second series of heritability estimates, conducted after cessation of selection response, revealed that fixation had not occurred.

A genetic analysis was performed on the newly selected lines. Again there was little evidence of non-Mendelian inheritance, inbreeding depression, net directional dominance, or sex-linkage. The results for a second set of gene number experiments on these stocks also did not indicate the action of a single locus postponing senescence.

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PART I

INTRODUCTION

CHAPTER 1  
General Introduction

### 1.1 Definition

Senescence may be defined as the persistent, and ultimately catastrophic, decline in viability and fertility which afflicts most reproductively mature organisms when they are protected from death due to external factors. A great deal of information has been gathered concerning the biology of senescence, or at least phenomena associated with it (Lamb 1977; Comfort 1979). However, while the scientific problem of the physiological cause(s) of senescence has been recognized since Aristotle, solutions to this problem have proven elusive (Lamb 1977; Comfort 1979).

### 1.2 General Evolutionary Theory of Senescence

Evolutionary analyses of senescence began to appear in the 1880's (Weismann 1889; Kirkwood and Cremer 1982). There was an initial flirtation with the idea of senescence as an adaptation for the benefit of populations, and so brought about by group selection (Weismann 1889; Wilson 1974; Wade 1978; Kirkwood and Cremer 1982). Evolutionary biologists have since almost always argued for the view that senescence is a result of the indifference of natural selection to deleterious genetic effects expressed some time after the onset of reproduction: the declining force of natural selection with the age of the adult soma.

Whereas this was realized intuitively by August Weismann and R.A. Fisher in the period 1910-1930, modern research on the evolution of senescence in terms of natural selection acting on gene frequencies begins with Haldane (1941) and Medawar (1946, 1952). Both drew attention to the central point of all evolutionary analyses of senescence: In multicellular organisms, deleterious effects on the survival of the adult soma will have a strictly decreasing impact on fitness as the age at which these effects are expressed increases, all other things being equal.

Once an individual ceases to reproduce, its direct importance to subsequent generations is effectively zero; any post-reproductive genetic changes will be irrelevant to the process of evolution. Specifically, if a gene is given phenotypic expression only after reproduction has ceased, then it has no effect on fitness. Further, if a gene exists which is slightly beneficial in early ages but highly deleterious at later ages, the gene is unlikely to be eliminated since "selection favors early over late reproduction when a conflict in interest arises" (Williams 1957). Thus, due to the decline in the force of natural selection with age of the adult soma, the health of the adult soma declines as well.

This general theory was further elaborated and clarified by Hamilton (1966), Edney and Gill (1968), Emlen (1970), Charlesworth and Williamson (1975), and Charlesworth (1980). The decline in the force of natural

selection has been made mathematically explicit, and is shown in Figure 1.1, from Charlesworth (1980), using U.S. human data.

The general evolutionary theory can be tested in two distinct ways -- the first experimental, the second comparative. Edney and Gill (1968) outlined an experimental procedure designed to test the general theory of senescence. It is based on the corollary of the general theory that reproductive schedules should determine patterns of senescence. If the appropriate terms are changed in the laboratory, by imposing different reproductive schedules, senescence should evolve accordingly. There are two such tests possible: 1) selection for earlier reproduction, which should give accelerated senescence; and 2) selection for later reproduction, which should give postponed senescence. An illustration of the second test, selection for later reproduction, is shown in Figure 1.2.

The dependence of senescence on a population's reproductive schedule has been demonstrated repeatedly. In experiments where late reproductive opportunities were denied and early reproduction is favored, it has been found that longevity was reduced (Mertz 1975; Sokal 1970), although there are problems of consistency over replicates and thus statistical significance. Evidence of postponed senescence in *Drosophila* populations with delayed reproduction has been published by Wattiaux (1968a,b),

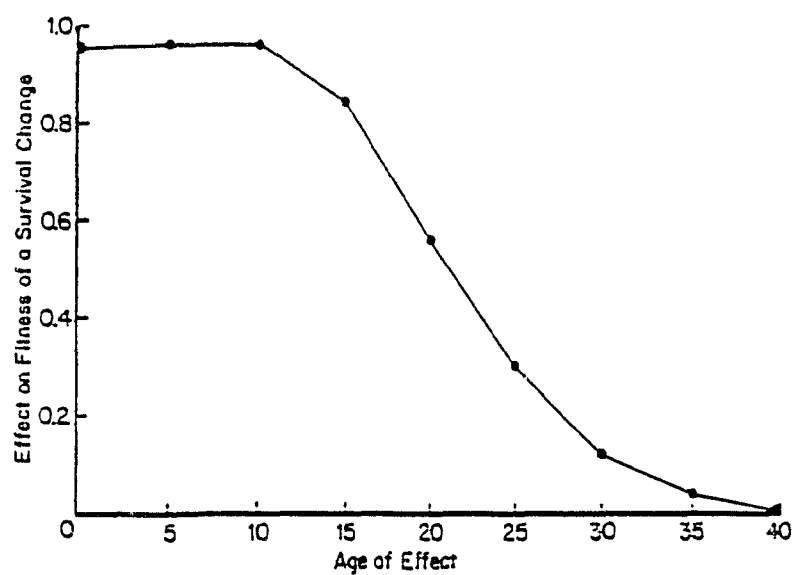


Figure 1.1. The decline in the intensity of selection on alleles having proportionately equal effects on mortality rates at different ages. After Charlesworth (1980, p. 215).

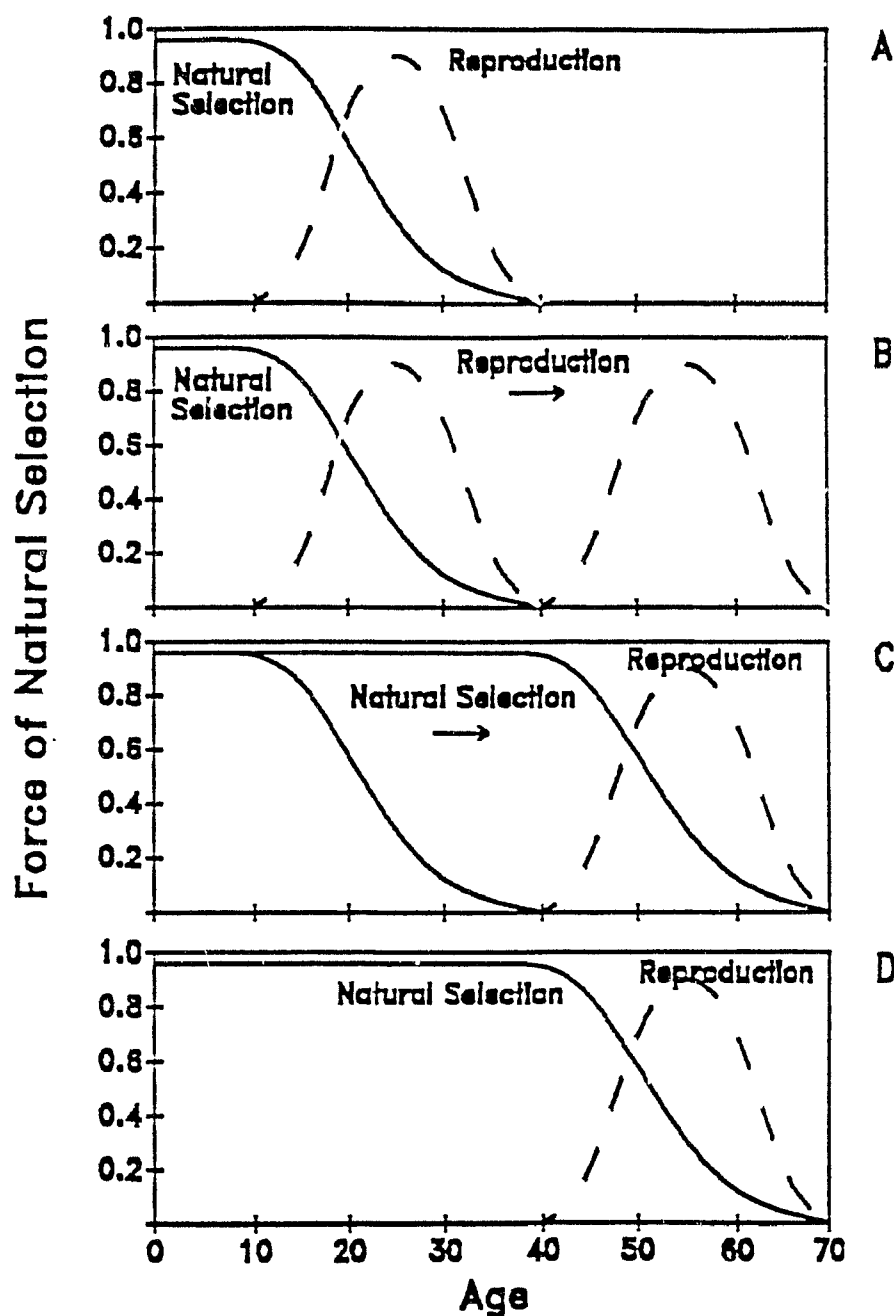


Figure 1.2. Illustration of the evolution of postponed senescence through the action of selection for later reproduction. In A the force of natural selection falls off as the age-specific reproductive rate increases. Shifting the time of reproduction to a later age, B, results in an extension of the time period when the force of natural selection is high, C. This results in D, where the force of natural selection does not fall off until a later age, thereby causing selection of longer-lived individuals.

Taylor and Condra (1980), and Rose and Charlesworth (1980, 1981b), although all of this work suffered from a lack of replication, and not all of these authors discussed their results from the standpoint of natural selection molding senescence. More recently Rose (1984a) and Luckinbill et al. (1984) have repeated these experiments with greater replication, creating populations with postponed senescence when reproduction was delayed. Therefore the central corollary of the evolutionary theory of senescence has been corroborated in a number of independent laboratory studies.

There are those who have sought to cast doubts on these results, emphasizing difficulties in the interpretation of the data from experiments of this kind (Lints 1978; Lints and Hoste 1974, 1977). However, Clare and Luckinbill (1985) and Luckinbill and Clare (1985) presented a penetrating analysis of the disparity between the *Drosophila* experiments of Wattiaux (1968a,b) and others and those of Lints and colleagues. As well as corroborating the general theory, they showed that there is a gene-environment interaction which results in reduced expression of genetic effects when fruit flies are reared in uncrowded conditions, an interaction which can then prevent a response of senescence to selection when low rearing densities are artificially maintained in the laboratory. Thus the experiments of Lints et al. (1979) probably would have corroborated the general evolutionary



theory if they had been performed at higher rearing densities or had been continued for a longer period, since the data of Clare and Luckinbill (1985) show that even at low rearing densities, there are genetic differences which could eventually produce a response to selection for postponed senescence.

The second way of testing the evolutionary theory of senescence is comparative. It is based on the correspondence between evolutionary age-structure and the evolution of senescence implicit in the theory. When there is no soma, there should be no senescence. For the most part the data are corroborative, although the quality is poor (see Williams 1957; Rose in prep.).

Bell (1984a) has performed the first direct, critical, comparative test, checking the central prediction that senescence should evolve only in the presence of soma. Bell chose six asexual freshwater invertebrates to assay for age-dependent mortality patterns in the laboratory, two of those reproducing paratomically, four reproducing ovigerously. As predicted by evolutionary theory, the paratomical species did not exhibit statistically significant declines in age-specific mortality rates, whereas all of the ovigerous species had such declines.

Overall, then, the general evolutionary theory of senescence first explicitly propounded by Medawar (1946, 1952) seems as well developed mathematically and as well corroborated empirically as could be reasonably

expected. There have been no refutations of the evolutionary theory of senescence which are free of artifactual problems.

### 1.3 Particular Mechanisms of Senescence

Two cogent population genetic mechanisms for the evolution of senescence have been proposed, both based on the decline of the force of natural selection with adult age. 1) Mutation-accumulation: maintenance of high-frequency deleterious alleles by mutation pressure, when they have such late effects that natural selection has little impact on their frequency compared with mutation (Medawar 1952; Edney and Gill 1968). 2) Antagonistic pleiotropy: natural selection favoring genes with early beneficial effects which have later deleterious effects, because the latter have little impact on fitness (Medawar 1952; Williams 1957; Rose 1985). The general evolutionary theory of senescence is compatible with either the mutation-accumulation or antagonistic pleiotropy mechanism and can be tested independently of them. In particular, evidence in favor of the general theory may have no bearing on the validity of these two subsidiary mechanisms. On the other hand, the subsidiary mechanisms cannot hold if the general theory does not, as they both presume its validity. Either or both mechanisms may apply to any particular population, depending on the gene action.

They are not mutually incompatible (Rose 1985).

The mutation-accumulation theory is based on the consequences of the decline with age in the force of natural selection for the evolutionary fate of genes with effects confined to late age classes. This theory assumes the existence of alleles with solely deleterious effects which are confined to late ages. They would thus be largely free of natural selection acting to reduce their frequency. Accordingly there should be an increase with adult age in the genetic variability of age-specific life history characters. This was first tested by Rose and Charlesworth (1980, 1981a) for 24-hour fecundity in Drosophila melanogaster. Even after an upward correction favoring the hypothesis, to compensate for the possibility of proportionate gene action, there was no evidence for an increase with age in the genetic variance for daily fecundity, thus making unlikely the action of the mutation-accumulation mechanism in their population. In opposition to these findings, Kosuda (1985) used chromosomally homozygous and heterozygous lines of D. melanogaster to study age dependence in the genetic variation affecting male mating success. He found that the genetic variation at later ages was greater than that affecting mating success at earlier ages, in keeping with the mutation-accumulation mechanism for the evolution of senescence.

More recently, there have been two sets of relaxed

selection experiments showing evidence of the action of mutation-accumulation. Firstly, Rose et al. (1987) and Service et al. (1988) found evidence in the absence of a reversal in response in some characters which had responded to selection for postponed aging, when selection for early reproduction was re-imposed. Secondly, Mueller (1987) found that relaxing selection on late fecundity caused it to fall without an associated change in early reproduction. Both of these studies are explicable in terms of population genetic processes in which deleterious mutations accumulate at later ages.

The antagonistic pleiotropy theory leads naturally to the reproductive effort theory (Williams 1966a,b) and to optimal life history theory (Stearns 1976; Charlesworth 1980). Thus, there are a number of experiments supporting the hypothesis that there are genes which enhance early life history characters at the expense of later life history characters. It should be noted that phenotypic correlations within outbred populations are not relevant. They could be due to physiological interdependence which is strictly environmental. Suitable corroborative evidence has come from three types of experiments: 1) negative correlations between the life history characters in cases of clones (Snell and King 1977) and genetically distinct, somewhat inbred, populations grown under standardized conditions (Gowen and Johnson 1946); 2) negative additive genetic correlations, or their equivalents, between early

and late life history characters within outbred populations (Law 1975; Rose and Charlesworth 1981a); and 3) negative correlations in selection response between early and late life history characters (Wattiaux 1968a; Law et al. 1977; Rose and Charlesworth 1980, 1981b; Doyle and Hunte 1981; Rose 1984; Luckinbill et al. 1984). These will be discussed in turn.

Snell and King (1977) examined lifespan and fecundity patterns in rotifers and found negative correlations between these two characters. Gowen and Johnson (1946) found a negative genetic correlation between egg-laying rate and longevity among laboratory strains of wild-type D. melanogaster.

Law (1979) found that high early reproduction was correlated with reduced later survival and reproduction in lineages of Poa annua, the annual meadow grass. Rose and Charlesworth (1981a) found a negative additive genetic correlation between early fecundity and longevity in a sib analysis of D. melanogaster.

Wattiaux (1968a) found reduced early male mating success in a D. subobscura population which had evolved greater longevity. Comparisons of populations of Poa annua show that plants from transient habitats, where survivorship to later ages is reduced, exhibit accelerated senescence compared with plants from permanent pastures. Those from the stable environment, in turn, showed reduced early reproductive output (Law et al. 1977). Doyle and

Hunte (1981) found reduced longevity in Gammarus laurencianus which had been selected in the laboratory for increased early reproduction. Rose and Charlesworth (1980, 1981b), Rose (1984), and Luckinbill et al. (1984) all found reduced early female fecundity in D. melanogaster populations which had been selected in the laboratory for increased late reproduction. All these results support antagonistic pleiotropy as a mechanism for the evolution of senescence.

Evidence against antagonistic pleiotropy was claimed by Bell (1983, 1984a, 1984b) and Geisel (Geisel 1979; Geisel and Zettler 1980; Geisel et al. 1982). Bell studied patterns of life history variation among individuals within clones of Daphnia pulex (Bell 1983), assayed the life histories of clones of Platytias patulus (Bell 1984a), and compared the life histories of five freshwater invertebrates (Bell 1984b). No evidence of antagonistic pleiotropy was found between reproduction and longevity. However, these three experiments suffered from errors in experimental design which invalidate their conclusions. The most serious error was that of gene-environment interactions caused by rearing the progeny in a novel environment. Specifically, Bell (1983, 1984a, 1984b) sampled individuals from nature and assayed them or their progeny in the laboratory. The populations would therefore not be at selective equilibrium, leading to bias in the estimation of the genetic parameters. It is well

established that many organisms, especially insects, exhibit genotype-environment interactions that make the attributes of a genotype in one environment a poor guide to its attributes in another (Service and Lenski 1982; Service 1984). Service and Rose (1985) demonstrated experimentally using D. melanogaster that genetic correlations between survival and reproductive characters are subject to upward perturbations by rearing of progeny in novel environments. The genetics of a population should therefore be analyzed in the setting in which it has evolved, if evolutionarily meaningful results are to be obtained (Rose and Service 1985).

Another type of error in experimental design has been demonstrated by Geisel (1979), Geisel and Zettler (1980), Geisel et al. (1982), and Murphy et al. (1983). Geisel and colleagues studied the life history genetics of D. melanogaster using heavily inbred lines, arguing against the antagonistic pleiotropy theory due to the positive genetic correlations they observed in early and late life history characters in these lines. However, it has been shown by Rose (1984b) that artificially inbreeding *Drosophila* populations can produce predominantly positive genetic correlations among life history characters, even when the ancestral outbred population does not exhibit such predominantly positive correlations. Thus Geisel's arguments are not supported by his experiments, because inbreeding produces artifactual positive genetic

correlations (Rose 1984b). There seems to be little cause to doubt that antagonistic pleiotropy has often been important in the evolution of senescence.

The significance of this research, and other evolutionary research on aging (see Rose 1983; Rose and Service 1985; Rose and Hutchinson 1987 for reviews), is that the evolutionary theory of senescence is reasonably well corroborated, as are the two population genetic mechanisms, antagonistic pleiotropy and mutation-accumulation.

#### 1.4 Physiological Genetics of Postponed Senescence

The first attempt at unravelling the specific physiological and genetic mechanisms which underlie the evolution of aging was by Rose et al. (1984). They showed that the only gross morphological difference between postponed senescence lines and their controls was a substantial reduction in early ovary weight associated with postponed senescence, in keeping with the reduced early fecundity in these flies. These flies did not differ from the controls with respect to egg weight, larval growth pattern, adult weight, digestive tract weight, thorax weight or male reproductive system weight.

Service et al. (1985) performed numerous assays of stress resistance in adult flies of the two types. Postponed senescence is associated with increased



resistance to starvation, desiccation, and low levels of ambient ethanol. Other forms of stress, such as heat shock response or resistance to high levels of ambient ethanol, were not better resisted by flies from postponed senescence populations. Starvation and desiccation resistance differences were sustained over a wide range of adult ages.

Service (1987) found that the starvation character differences described above can be explained in terms of differing lipid levels between postponed senescence populations and the controls. Females from postponed senescence populations had greater proportional lipid content than did females from control populations over the range of ages examined.

Luckinbill et al. (1988a) confirmed the finding of Rose et al. (1984) that there was no significant variation in adult body size between postponed senescence populations and control populations. They also examined another character, duration of tethered flight, finding that the long-lived populations flew from three to five times longer than did the controls. Graves et al. (1988) and Graves and Rose (in press) have repeated the flight duration studies with the same results as Luckinbill et al. (1988a): The long-lived stocks flying longer than the short-lived stocks.

Table 1.1 provides a summary of the characteristics of the short-lived (control) and long-lived stocks. For those characters which have to do with reproduction, early

Table 1.1. Some characteristics of short-lived and long-lived stocks. The "+" indicates that the population type has a greater value for the character, the "-" that it has a lesser value, and the "0" that there is no statistical differentiation between the population types for that character.

Character	Short-lived "B"	Long-Lived "O"
Generation Time	2 weeks	10 weeks
Early Fecundity <sup>1,2,3,4,5,6,7</sup>	+	-
Early Ovary Weight <sup>6,8</sup>	+	-
Female Total Body Weight <sup>8,9</sup>	0	0
Male Total Body Weight <sup>8,9</sup>	0	0
Female Longevity <sup>1,2,3,4,5,6,9</sup>	-	+
Male Longevity <sup>9,6,10</sup>	-	+
Female Starvation Resistance <sup>6,7,11,12</sup>	-	+
Male Starvation Resistance <sup>6,11,12</sup>	-	+
Female Desiccation Resistance <sup>7,11,12</sup>	-	+
Male Desiccation Resistance <sup>11,12</sup>	-	+
Female Ethanol Resistance <sup>7,11,12</sup>	-	+
Male Ethanol Resistance <sup>11,12</sup>	-	+
Female Lipid Content <sup>12</sup>	-	+
Male Lipid Content <sup>12</sup>	-	+
Female Flight Duration <sup>9,13,14</sup>	-	+
Male Flight Duration <sup>9,13,14</sup>	-	+

1. Rose (1984a)

2. Rose (1984b)

3. Luckinbill et al. (1984)

4. Luckinbill and Clare (1985)

5. Clare and Luckinbill (1985)

6. Hutchinson and Rose (in press)

7. Service et al. (1988)

8. Rose et al. (1984)

9. Luckinbill et al. (1988a)

10. Service (in press)

11. Service et al. (1985)

12. Service (1987)

13. Graves et al. (1988)

14. Graves et al. (in press)

fecundity and early ovary weight, the short-lived stocks have higher values. For total body weight there is no difference between the stocks. For the rest of the characters (longevities, stress resistances, flight durations, and lipid contents), the long-lived stocks show higher values than do the short-lived stocks. [Since these findings were consistent over strains exhibiting increased lifespan, and outbred populations were used in selection, these characters are almost certainly involved in the biological changes which underlie postponed aging.] There seems to have been a shift from investment in reproduction to investment in survival capabilities.

Collectively, the findings of Rose et al. (1984), Service et al. (1985, 1988), Service and Rose (1985), Service (1987), and Luckinbill et al. (1988a) suggest the existence of a common physiological basis of longevity. Improved lipid and/or glycogen metabolism might form the basis of extended life span, as reflected in the various stress characters assayed.

### 1.5 Scope of This Study

This thesis combines both the physiological and the biometrical avenues of research in an attempt to unravel the quantitative genetic basis of postponed aging in D. melanogaster. This work has three main purposes. Firstly,

to establish whether or not maternal effect, inbreeding, and directional dominance have affected the evolution of postponed senescence in the selected populations of Rose (1984a). Secondly, to investigate differences between replicated postponed senescence populations to determine if they respond similarly to the same selection regime. Thirdly, to determine the number of loci that are involved in the postponed senescence response.

The basic techniques used involve crosses of populations, both within and between types of stocks. I report experiments in which: (i) diallel analysis and other types of population crosses were performed on the short-lived and long-lived stocks; (ii) effective factor estimates were performed on these stocks; (iii) the genetic variability present in postponed aging stocks was assayed by means of a sib analysis; (iv) artificial selection was applied to both control and postponed-aging stocks to make them diverge farther; (v) sib analysis was used to assess the degree to which selection reduced genetic variability; (vi) diallel analysis and other types of population crosses were performed on the derived stocks; and (vii) effective factor estimates were performed on these derived stocks. Taken together, these results indicate additive inheritance and an absence of differentiation between lines within a given type. The number of loci involved in postponed aging in these stocks is not significantly different from infinity.

CHAPTER 2  
General Methods and Materials

## 2.1 Source of the Drosophila melanogaster Populations

The experimental populations used in these experiments were obtained from an outbred laboratory population in turn derived from the wild South Amherst, Massachusetts, Drosophila melanogaster population studied by Ives (1970), as outlined in Rose and Charlesworth (1981a). This population was extensively studied during 1977-1979, when it was found to have a great deal of additive genetic variability for many life-history characters (Rose and Charlesworth 1981a,b). In particular, there were several lines of evidence indicating negative additive genetic correlations between early and late life-history characters, such as early fecundity and longevity.

In February, 1980, after more than 130 generations of laboratory culture at 25°C with unlimited food and 14 day discrete generations, 10 experimental populations were derived from a single generation of the base population (Rose 1984a). Five of those were maintained in the same fashion as the base populations. They are referred to as the "B" populations, with subscripts 1 -> 5 to indicate replicate number. The remaining five populations were kept under the same culture conditions as the B's, but the day on which eggs were collected for the next generation was progressively postponed. Eventually the females used were 10 weeks of age from the egg. For more details, consult Rose (1984a) and Service et al. (1985). These five

populations in which only surviving older females were able to reproduce are called "O" populations with subscripts 1 -> 5 as before. Approximately 140 two week generations had elapsed in the "B" populations and approximately 23 ten week generations had elapsed in the "O" populations when the work described in this thesis was begun.

## 2.2 Culture Methods

The B stocks, maintained in discrete generations of 14-day length, have been subjected to strong selection for the early-life fitness-components. The O stocks, maintained in 70-day-long discrete generations, have been subjected to strong selection for late-life fitness-components. Larval, pupal, and early-adult development of each O generation takes place in 25- x 95-mm. shell vials. At 2-4 days of adult age (11 days after oviposition), O flies are transferred to population cages. Food, in 100- x 15-mm. plastic petri dishes, is replaced in the O population cages three times weekly. B flies spend their entire 14-day lives in shell vials. All stocks are maintained on banana-agar medium that contains corn and malt syrup and baker's yeast. At the start of these experiments, there had been approximately 105 B generations and 26 O generations. Population sizes are in the thousands at the start of each generation.

Stocks and experimental flies are maintained at 25°C

under a 24L:0D regime. Food is always abundant in the rearing tubes used for experimental flies. All handling is performed at room temperature using CO<sub>2</sub> anaesthesia.

### 2.3 Assay Methods

At the start of all experiments large samples of eggs were obtained from the stocks and transferred, at a density of 30 or 90 eggs per vial, to 25- x 95-mm. shell vials. This controlled density sampling was repeated for a second generation before any assays were performed. This was done to remove parental and grandparental effects. These effects have been shown to affect the phenotypic expression of life history traits.

Throughout, when comparisons between the control and postponed senescence populations were assayed, B and O populations were handled as pairs in a consistent order. The pairing followed their replicate number. B1 was paired with O1, B2 with O2, B3 with O3, B4 with O4, and B5 with O5. This reduced the possibility of uncontrolled biases and also resulted in five independent assays. The pairing was also followed with the three F and the three S stocks, whose formation is the subject of Chapter 7.

There were always large numbers, between 30 and 60, of both females and males used to create the populations assayed in the experiments of this thesis.

Six life history characters were measured throughout



this study: ovary weight, 24-hour fecundity, female starvation time, male starvation time, female longevity, and male longevity. These were not all measured for any one experiment, with anywhere from one to five being assayed at one time. The age at assay was always between 3 to 4 days after eclosion unless otherwise noted. The protocol for each assay is as follows:

#### Ovary Weight

Female flies were frozen in an ultralow freezer. They were later thawed and dissected under a microscope. The ovaries were individually dried in a desiccating oven for at least 24 hours at 75 C. All measurements were made with a Cahn electronic microbalance to the nearest 0.0001 mg.

#### 24-Hour Fecundity

One female and one male were placed in a plastic 22- x 70- mm. shell vials with black "charcoal" food. (The food being black facilitates counting the white eggs.) They were left in this vial for approximately 24 hours and then transferred to a new black food vial. After exactly 24 hours the flies were removed and the number of eggs laid was assayed under a dissecting microscope with the aid of a precision counter. The term "conditional fecundity" (Rose and Charlesworth, 1981a) refers to fecundity data in which zero fecundity is treated as a missing data point.

### Starvation Assay (Female and Male)

Foam-plastic test tube stoppers (35 mm. long) were used to confine adult flies to the lower 15 mm. of empty 25- x 95-mm. shell vials. Approximately 0.7 g. of absorbent rayon and 3 ml. of distilled water were added above the plugs. The open ends were covered with Parafilm M laboratory film. The number and sex of the flies varied between the experiments. (More details will be given in the methods and materials of each specific experiment.) The vials were checked at regular intervals, every 4, 6 or 8 hours depending on the experiment, and the time was recorded when the flies were dead, as determined by lack of movement upon provocation.

### Longevity Assay (Female and Male)

Between 3 to 5 pairs of flies were placed in a brown banana food vial. The number dead was checked each day. Every 3 or 4 days the flies were transferred to fresh food vials. At this time the flies were mixed between vials so as to keep constant densities and sex ratios. The age at death was recorded for each fly.

## 2.4 General Statistical Methods

For biometrical analysis it is desirable to choose a scale of measurement where the variance is not a significant function of the mean. There are various methods to use to

choose the appropriate transformation, the two used here are Taylor's Power Law method (Downing 1979) and Wright's method (Wright 1968).

Taylor's method consists of linear regression of the log of the variance of the populations on their log means. The slope of the regression is equal to  $b$  in the resulting transformation  $x' = x^{1-b/2}$ .

Wright's method consists of a linear regression of the standard deviations of the populations on their mean values, resulting in a formula of the form  $F(x) = C_1 + C_2X$ . The resulting transformation is given by  $x' = \log(x + C_1/C_2)$ .

Both of these methods were used on all the data presented in this thesis. As well, all data were transformed by  $x' = \log(x+1)$  and  $x' = \sqrt{x}$ . None of the transformations changed the results of any hypothesis test, so only the data analysis with untransformed data is reported. Throughout the tables, a single asterisk (\*) is used to indicate a result with  $p < 0.05$ , while a double asterisk (\*\*) is used to indicate a result with  $p < 0.01$ .

All data analysis was done using the software SYSTAT: The System for Statistics. The ANOVA and Regression models use least squares methods. These procedures can estimate and test any univariate or multivariate general linear model, balanced or unbalanced. Specific details will be given in discussing the separate experiments.

## PART II

### ANALYSIS OF OUTBRED (B and O) POPULATIONS

## CHAPTER 3

### Diallel Analysis of B and O Populations

### 3.1 Introduction

Schmidt (1919) introduced the term diallel to denote all possible crosses among a collection of male and female animals. More generally, a diallel cross refers to a set of all possible crosses among a collection of genetic entities, such as individuals or lines (Hinkelmann 1977). Crossing a set of  $n$  lines in this way will result in  $n^2$  combinations. These can be divided into three groups: (i) the  $n$  parental lines themselves; (ii) one set of  $n(n-1)/2$   $F_1$ 's ; and (iii) the set of  $n(n-1)/2$  reciprocal  $F_1$ 's. Diallel crossing techniques vary depending upon which of these groups are included in the analysis.

The diallel cross has been used as a genetic tool for evaluating the performance of lines and breeds in crossbred combinations and to gain a better understanding of the nature of gene action involved in determining quantitative traits (Paroda and Joshi 1970; Fejer 1977; Gupta et al. 1983; Lynch and Sulzbach 1984; Sulzbach and Lynch 1984).

Three separate questions are addressed in the present diallel analysis. Firstly, to what extent are the lines within a given stock-type differentiated from each other? Secondly, to what extent do maternal effects outweigh paternal effects, within stock-types? Thirdly, is there any evidence for heterosis, or, conversely, inbreeding depression, in crosses between lines within stock-types?

### 3.2 Experimental Procedure

A series of diallel analyses (cf. Mather and Jinks 1982) were performed within the O (long-lived) stocks and, separately, within the B (control) stocks. The coding for these experiments involves three character positions: In the first position, D indicates that it is a diallel experiment; in the second position, B or O indicates whether the populations used were B or O stocks; and the character in the third position is a numeral indicating which experiment it was, in chronological order. Thus the first experiment performed was DB1. Tables 3.1 and 3.2 give the experiment codes, the characters assayed, the populations assayed, and a number of individuals assayed. In experiment DO2, starvation was assayed in individuals of 17-20 days of age from pupal eclosion. In all other experiments the characters were assayed in individuals of 3-4 days of age from pupal eclosion.

### 3.3 Results and Discussion

The summary statistics for each character in each experiment are given in Appendix A, Tables A1 through A9. The order of these tables follows the order of the experiments and the characters within the experiments as presented in Tables 3.1 and 3.2. The corresponding detailed

Table 3.1 : B Diallel Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>DB1</u>				
	Ovary Weight	5x5 = 25	29.6	740
	Female Starvation	5x5 = 25	54.7	1,368
<u>DB2</u>				
	Ovary Weight	3x3 = 9	26.1	235
Total		59		2,343



Table 3.2 : O Diallel Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>DO1</u>	Ovary Weight	5x5 = 25	28.0	700
	Female Starvation	5x5 = 25	55.4	1,384
<u>DO2</u>	Female Starvation	5x5 = 25	52.8	1,321
<u>DO3</u>	Ovary Weight	3x3 = 9	26.0	234
<u>DO4</u>	Female Starvation	5x5 = 25	25.6	639
	Male Starvation	5x5 = 25	25.4	636
Total		84		4,914

analysis for each character in each experiment is given in Appendix B, Tables B1 through B9. These Appendix B tables present the analysis in three sections; line effects, maternal effects, and heterosis/inbreeding effects. I will discuss these results addressing the three questions stated above.

Firstly, to what extent are the lines within a stock-type differentiated from each other? This was analyzed using a mixed model in which the maternal and paternal lines used in each cross appear as factorial design components. The results are summarized in Table 3.3 for the maternal line effect, the paternal line effect, and the combined maternal and paternal line effect. In some cases, there were significant differences between lines, but these were not usually reproducible for the characters concerned. The only reproducible significant differences were for ovary weight in the O populations. A weakness of this design, however, is that it confounds the effects of a line with of the parents' sex from that line. This can lead to the erroneous inference of a line effect when none is present. Therefore, the absence of any reproducible line effect in this design, except for ovary weight in the O populations, suggests that there is only slight differentiation between lines within stock-types.

Secondly, to what extent do maternal effects outweigh paternal effects, within stock-types? This question is

Table 3.3 : B and O Diallel Line Differentiation

<u>Character</u>	ANOVA					
Experiment	Line of Mother F	SIG.	Line of Father F	SIG.	Combined Effect F	SIG.
<u>Ovary Weight</u>						
DB1	0.28	0.887	1.15	0.370	0.71	0.677
DB2	0.75	0.530	0.57	0.608	0.67	0.648
DO1	4.72	0.010*	1.06	0.409	2.89	0.034*
DO3	34.03	0.003**	0.06	0.944	17.10	0.009**
<u>Female Starvation</u>						
DB1	1.38	0.280	2.63	0.073	2.04	0.107
DO1	1.86	0.167	1.60	0.224	1.74	0.165
DO2	2.44	0.089	5.27	0.007**	3.91	0.010*
DO4	0.98	0.448	1.45	0.263	1.25	0.334
<u>Male Starvation</u>						
DO4	1.03	0.420	2.74	0.065	1.92	0.127

addressed with greater experimental power in the transmission pattern experiments, but there is the possibility that it arises in the diallel designs. This question was examined using the F-statistic produced by the ratio of female parent to male parent variance components in the mixed model ANOVA of the diallels presented above. Methods 1 and 2 differ with respect to inclusion (Method 1) or exclusion (Method 2) of the uncrossed parental lines in the data analysis. The results from the two methods differed only in the analysis of experiment D01. As shown in Table 3.4, significant maternal effects arise only in the cases in which there were significant line effects (from Table 3.3), and those were not reproducible in any case. It would seem dubious to draw any firm conclusions from these maternal-effect results, as opposed to the transmission pattern results (see next chapter).

Thirdly, is there any evidence for heterosis, or, conversely, inbreeding depression, in crosses between lines within either B or O stocks? The data were analyzed using both t-tests and a nested analysis of variance. The contrast being analyzed is that between the  $n$  parental lines (the diagonal in the diallel results of Appendix A) and the  $n(n-1)$  reciprocal crossed lines (the off-diagonals). The results are summarized in Table 3.5. The two types of t-test in this table differ with respect to both the pooling of the sample variances in the calculation of the

Table 3.4 : B and O Diallel Maternal Effects

<u>Character</u> Experiment	ANOVA			
	Method 1		Method 2	
	F	SIG.	F	SIG.
<u>Ovary Weight</u>				
DB1	0.24	0.900	0.98	0.506
DB2	1.32	0.431	2.45	0.290
DO1	4.46	0.088	14.78	0.012*
DO3	576.84	0.002**	40.98	0.024*
<u>Female Starvation</u>				
DB1	0.53	0.723	0.67	0.646
DO1	1.17	0.443	0.96	0.515
DO2	0.46	0.763	0.41	0.795
DO4	0.67	0.645	0.54	0.716
<u>Male Starvation</u>				
DO4	0.38	0.816	0.57	0.698

Table 3.5 : B and O Diallel Heterosis Effects

<u>Character</u> Experiment	T-TEST				ANOVA	
	Separate Var.		Pooled Var.		F	SIG.
	T	SIG.	T	SIG.		
<u>Ovary Weight</u>						
DB1	0.54	0.619	0.78	0.444	0.62	0.438
DB2	0.75	0.480	0.61	0.598	0.33	0.582
DO1	0.98	0.368	1.18	0.249	1.40	0.249
DO3	0.03	0.976	0.03	0.974	0.001	0.974
<u>Female Starvation</u>						
DB1	0.09	0.934	0.12	0.908	0.01	0.908
DO1	0.47	0.658	0.46	0.652	0.21	0.648
DO2	1.27	0.259	1.53	0.139	2.28	0.145
DO4	0.58	0.587	0.61	0.551	0.52	0.478
<u>Male Starvation</u>						
DO4	0.97	0.378	1.02	0.317	1.52	0.230

t-statistic and the number of degrees of freedom. The results consistently indicate an absence of heterosis, whichever way the data are analyzed.

CHAPTER 4

Transmission Patterns of B and O Populations



#### 4.1 Introduction

In the transmission pattern experiments, B and O stocks were crossed between lines, B<sub>1</sub> with O<sub>1</sub>, B<sub>2</sub> with O<sub>2</sub>, etc. The parental populations as well as both the reciprocal cross populations of the F<sub>1</sub> hybrids were then assayed for all six characters (male longevity, female longevity, female early starvation resistance, male early starvation resistance, early fecundity, and early ovary weight). Three features of the transmission data are of importance: (i) preservation of the B-O differences that had been detected in earlier studies (Rose 1984; Rose et al. 1984; Service et al. 1985); (ii) maternal effects, as measured by differences between two reciprocal cross means; and (iii) average dominance, as measured by the deviation of the crosses from the mid-parent value of the parental lines.

#### 4.2 Experimental Procedure

The series of experiments on transmission of postponed aging characters is outlined in Table 4.1. These experiments are coded with "BO" in the first two positions, indicating crosses of B and O populations. The numerals then refer to the specific experiments. In all these experiments, but one (B01), B and O parental populations were assayed together with both their reciprocal crosses. [This gives rise to the "4x" terms.] In experiment B04,

Table 4.1 : B and O Crossing Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>B01</u>	Ovary Weight	3x5 = 15	29.5	443
	Female Starvation	4x5 = 20	31.2	624
	Male Starvation	4x5 = 20	31.2	624
<u>B02</u>	Ovary Weight	4x5 = 20	30.0	600
	Fecundity	4x5 = 20	58.9	1,177
	Conditional Fecund.	4x5 = 20	58.9	1,177
	Female Starvation	4x5 = 20	54.0	1,080
	Female Longevity	4x5 = 20	57.0	1,140
<u>B03</u>	Ovary Weight	4x3 = 12	45.2	542
	Female Starvation	4x3 = 12	40.0	480
	Female Longevity	4x3 = 12	49.9	599
<u>B04</u>	Female Starvation	4x3 = 12	33.7	404
<u>B05</u>	Fecundity	4x3 = 12	76.5	918
	Conditional Fecund.	4x3 = 12	75.3	903
	Female Starvation	4x3 = 12	78.3	940
	Male Starvation	4x3 = 12	78.3	940

Table 4.1 continued : B and O Crossing Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>BO6</u>				
	Fecundity	4x3 = 12	77.4	929
	Conditional Fecund.	4x3 = 12	75.9	911
	Female Starvation	4x3 = 12	78.8	945
	Male Starvation	4x3 = 12	78.8	945
	Female Longevity	3x3 = 9	98.9	890
	Male Longevity	3x3 = 9	98.4	886
<u>BO7</u>				
	Fecundity	4x3 = 12	70.1	841
	Conditional Fecund.	4x3 = 12	69.3	831
	Female Starvation	4x3 = 12	71.8	863
	Male Starvation	4x3 = 12	71.8	861
	Female Longevity	4x3 = 12	58.5	702
	Male Longevity	4x3 = 12	57.8	694
<u>BO8</u>				
	Fecundity	4x1 = 4	59.0	236
	Conditional Fecund.	4x1 = 4	58.0	232
	Female Starvation	4x1 = 4	60.0	240
	Male Starvation	4x1 = 4	60.0	240
	Female Longevity	4x1 = 4	58.2	233
	Male Longevity	4x1 = 4	57.3	229
Total		413		24,299

starvation was assayed at 17-20 days of age. In experiment B07, the flies for assay were reared at a density of 90 per vial. In experiment B08, the parental B and O lines were obtained by a synthetic cross of three B and three O stocks, respectively.

#### 4.3 Results and Discussion

The summary statistics for each character in each experiment are given in Appendix C, Tables C1 through C34. In these tables BB refers to the parental B population, BO to the  $F_1$  population formed through the cross of female B flies with male O flies, OB to the reciprocal  $F_1$  formed through the cross of female O flies with male B flies, and OO to the parental O population. The order of these tables follows the order of the experiments and the characters within the experiments as presented in Table 4.1. The corresponding detailed analysis for each character in each experiment is given in Appendix D, Tables D1 through D34. The Appendix D tables are in three sections corresponding to the three questions of interest: BB - OO differences, maternal effects, and dominance effects.

Table 4.2 provides a summary of the analysis of the BB - OO difference data, which was performed by both independent and paired t-tests and also by using a mixed model analysis of variance. It is apparent that most of the

Table 4.2 : B and O Differences

<u>Character</u> Expt.	<u>Mean <math>\pm</math> S.E.</u>		<u>T-TEST</u>		<u>ANOVA</u>
	B	O	Indep. T	Paired T	F
<u>Ovary Weight</u> (milligrams)					
BO2	0.109 $\pm$ 0.009	0.057 $\pm$ 0.006	4.61**	3.75*	14.09*
BO3	0.177 $\pm$ 0.003	0.112 $\pm$ 0.022	2.94*	3.14	9.65
<u>Fecundity</u> (eggs / 24 hours)					
BO2	102.1 $\pm$ 3.8	92.3 $\pm$ 6.0	1.38	3.86*	14.74*
BO5	80.7 $\pm$ 4.3	85.0 $\pm$ 2.0	0.92	1.91	3.70
BO6	94.2 $\pm$ 1.9	93.3 $\pm$ 2.5	0.26	0.42	0.18
BO7	81.9 $\pm$ 9.7	87.3 $\pm$ 6.3	0.47	0.82	0.68
BO8	95.2 $\pm$ 4.0	98.6 $\pm$ 2.2	--	--	0.57
<u>Conditional Fecundity</u> (eggs / 24 hours)					
BO2	102.1 $\pm$ 3.8	92.3 $\pm$ 6.0	1.38	3.86*	14.74*
BO5	82.2 $\pm$ 3.6	86.2 $\pm$ 2.6	0.90	3.16	10.42
BO6	96.3 $\pm$ 2.9	95.6 $\pm$ 1.4	0.22	0.26	0.06
BO7	83.2 $\pm$ 10.1	88.9 $\pm$ 6.6	0.47	0.80	0.64
BO8	98.9 $\pm$ 3.5	98.6 $\pm$ 2.2	--	--	0.01
<u>Female Starvation</u> (hours)					
BO1	28.7 $\pm$ 0.9	32.7 $\pm$ 0.6	3.74**	2.88*	8.25*
BO2	47.3 $\pm$ 2.7	68.2 $\pm$ 6.3	3.05*	4.10*	16.65*
BO3	44.8 $\pm$ 1.6	55.5 $\pm$ 1.3	5.19**	7.10*	50.40*
BO4	39.6 $\pm$ 2.5	47.2 $\pm$ 2.0	2.38	10.99*	116.65**
BO5	27.9 $\pm$ 1.3	35.8 $\pm$ 1.2	4.42*	7.47*	56.19*

Table 4.2 continued : B and O Differences

Character	Mean $\pm$ S.E.		T-TEST		ANOVA
	B	O	Indep. T	Paired T	F
<u>Female Starvation</u> - continued					
B06	27.3 $\pm$ 1.0	33.8 $\pm$ 2.0	2.89*	6.41*	40.92*
B07	34.3 $\pm$ 1.0	48.1 $\pm$ 1.8	6.54*	6.62*	43.78*
B08	27.2 $\pm$ 0.8	35.4 $\pm$ 0.9	--	--	45.51**
<u>Male Starvation</u> (hours)					
B01	19.9 $\pm$ 0.8	25.6 $\pm$ 0.9	5.04**	10.45**	109.94**
B05	17.8 $\pm$ 0.6	26.7 $\pm$ 0.4	12.96**	53.07**	2799.13**
B06	20.0 $\pm$ 1.8	31.0 $\pm$ 2.6	3.48*	13.86**	191.88**
B07	24.3 $\pm$ 0.8	36.4 $\pm$ 0.5	12.45**	11.62**	135.08**
B08	21.3 $\pm$ 0.8	26.1 $\pm$ 0.6	--	--	25.02**
<u>Female Longevity</u> (days)					
B02	50.1 $\pm$ 2.7	62.5 $\pm$ 2.7	3.26*	9.15**	76.07**
B03	25.2 $\pm$ 2.9	48.3 $\pm$ 2.7	5.86**	5.86*	34.32*
B06	40.4 $\pm$ 2.3	51.4 $\pm$ 2.2	3.48*	2.48	6.15
B07	36.6 $\pm$ 1.1	48.6 $\pm$ 0.9	8.33**	8.41*	71.22*
B08	34.9 $\pm$ 1.5	44.9 $\pm$ 2.0	--	--	16.46**
<u>Male Longevity</u> (days)					
B06	31.9 $\pm$ 0.3	52.0 $\pm$ 1.4	13.83**	11.92**	142.15**
B07	31.8 $\pm$ 1.3	48.0 $\pm$ 0.4	11.87**	9.90**	98.67**
B08	31.1 $\pm$ 1.2	45.0 $\pm$ 1.6	--	--	50.77**

known character differences have been preserved, except for early fecundity. [It should be noted that the cases where statistically significant differences between B and O types were not found were cases where the level of replication was reduced from five-fold to three-fold.] For longevity and starvation resistance, at least, there is consistent duplication of earlier findings.

The maternal effect analysis is presented in Table 4.3. There are only a few cases of statistical significance and these are not consistent for any one character between experiments. Table 4.4 is a summary of the dominance effects analysis. Again, there are only a few cases of statistical significance, which are not consistent between experiments. Given the problem of repeated statistical tests on a body of data, some cases with statistical significance are expected by chance alone. Therefore, it is concluded that the transmission pattern data indicate additive inheritance without maternal effects or dominance effects, averaged over all loci. [This does **not**, however, indicate an absence of dominance in the transmission patterns of the particular loci involved in postponed senescence.]

Table 4.3 : B and O Maternal Effects

Character	Mean $\pm$ S.E.		T-TEST		ANOVA
	BO	OB	Indep. T	Paired T	F
<u>Ovary Weight</u> (milligrams)					
B01	0.7 $\pm$ 0.008	0.124 $\pm$ 0.006	0.28	0.27	0.07
B02	0.098 $\pm$ 0.009	0.090 $\pm$ 0.009	0.47	0.86	0.75
B03	0.143 $\pm$ 0.014	0.16 $\pm$ 0.009	1.04	0.81	0.67
<u>Fecundity</u> (eggs / 24 hours)					
B02	97.9 $\pm$ 4.8	97.0 $\pm$ 3.6	0.15	0.47	0.22
B05	88.0 $\pm$ 3.7	85.3 $\pm$ 5.6	0.41	1.41	2.15
B06	91.1 $\pm$ 3.2	88.2 $\pm$ 3.0	0.67	1.60	2.60
B07	87.7 $\pm$ 4.3	84.5 $\pm$ 3.3	0.54	10.64**	114.70**
B08	98.0 $\pm$ 5.2	102.9 $\pm$ 3.7	--	--	0.28
<u>Conditional Fecundity</u> (eggs / 24 hours)					
B02	97.9 $\pm$ 4.8	97.3 $\pm$ 3.6	0.10	0.33	0.11
B05	89.0 $\pm$ 3.3	86.7 $\pm$ 4.9	0.39	1.18	1.46
B06	91.9 $\pm$ 3.0	90.3 $\pm$ 3.8	0.31	1.43	1.98
B07	87.7 $\pm$ 4.3	85.1 $\pm$ 4.9	0.40	3.77	14.04
B08	99.7 $\pm$ 5.0	102.9 $\pm$ 3.7	--	--	0.13
<u>Female Starvation</u> (hours)					
B01	31.8 $\pm$ 1.1	30.5 $\pm$ 1.2	0.81	0.66	0.44
B02	58.6 $\pm$ 4.8	50.5 $\pm$ 3.8	1.34	3.	7.70
B03	50.8 $\pm$ 1.8	52.2 $\pm$ 2.9	0.41	0.48	0.23
B04	47.0 $\pm$ 3.6	42.8 $\pm$ 5.9	0.60	0.53	0.28



Table 4.3 continued : B and O Maternal Effects

Character	Mean $\pm$ S.E.		T-TEST		ANOVA
	BO	OB	Indep. T	Paired T	F
<u>Female Starvation</u> - continued					
BO5	29.2 $\pm$ 1.4	32.1 $\pm$ 2.6	0.98	1.99	3.89
BO6	27.7 $\pm$ 0.9	28.7 $\pm$ 2.0	0.44	0.76	0.58
BO7	38.3 $\pm$ 0.7	40.7 $\pm$ 0.7	2.34	2.46	6.05
BO8	29.6 $\pm$ 1.0	29.7 $\pm$ 1.3	--	--	0.00
<u>Male Starvation</u> (hours)					
BO1	22.0 $\pm$ 0.6	22.3 $\pm$ 0.8	0.30	0.50	0.25
BO5	20.9 $\pm$ 0.8	25.3 $\pm$ 0.7	4.05	17.51**	300.16**
BO6	25.1 $\pm$ 0.7	27.1 $\pm$ 2.0	0.94	1.30	1.71
BO7	31.0 $\pm$ 0.7	32.0 $\pm$ 0.1	1.52	1.40	1.97
BO8	23.6 $\pm$ 0.6	22.9 $\pm$ 1.0	--	--	0.32
<u>Female Longevity</u> (days)					
BO2	57.7 $\pm$ 2.5	55.9 $\pm$ 2.3	0.53	0.59	0.32
BO3	36.3 $\pm$ 1.7	37.9 $\pm$ 1.5	0.73	0.68	0.47
BO7	41.5 $\pm$ 2.7	41.4 $\pm$ 2.1	0.03	0.04	0.00
BO8	41.4 $\pm$ 2.0	40.6 $\pm$ 2.2	--	--	0.07
<u>Male Longevity</u> (days)					
BO7	35.6 $\pm$ 2.3	39.4 $\pm$ 2.3	1.17	1.66	2.75
BO8	37.1 $\pm$ 1.7	38.4 $\pm$ 1.6	--	--	0.30

Table 4.4 : B and O Average Dominance Effects

Character	Mean $\pm$ S.E.		T-TEST		ANOVA
	Parentals	Crosses	Indep. T	Paired T	F
<u>Ovary Weight</u> (milligrams)					
B02	0.083 $\pm$ 0.004	0.094 $\pm$ 0.008	1.27	1.89	3.58
B03	0.142 $\pm$ 0.010	0.152 $\pm$ 0.004	0.92	1.91	3.66
<u>Fecundity</u> (eggs / 24 hours)					
B02	97.2 $\pm$ 4.9	97.4 $\pm$ 4.1	0.04	0.18	0.03
B05	82.7 $\pm$ 3.2	86.7 $\pm$ 4.6	0.71	1.64	2.62
B06	93.7 $\pm$ 0.9	89.7 $\pm$ 3.1	1.08	0.82	0.67
B07	84.7 $\pm$ 8.0	86.1 $\pm$ 4.3	0.16	0.29	0.08
B08	96.9 $\pm$ 2.3	99.2 $\pm$ 4.0	--	--	0.30
<u>Conditional Fecundity</u> (eggs / 24 hours)					
B02	97.2 $\pm$ 4.9	97.6 $\pm$ 4.2	0.07	0.28	0.08
B05	84.1 $\pm$ 3.1	87.9 $\pm$ 4.1	0.73	1.73	2.91
B06	95.9 $\pm$ 1.8	91.1 $\pm$ 3.4	1.25	1.02	1.03
B07	86.1 $\pm$ 7.8	86.4 $\pm$ 4.6	0.04	0.07	0.01
B08	98.7 $\pm$ 2.0	100.5 $\pm$ 3.8	--	--	0.19
<u>Female Starvation</u> (hours)					
B01	30.4 $\pm$ 0.3	31.1 $\pm$ 0.6	0.94	1.40	2.05
B02	59.0 $\pm$ 4.4	53.9 $\pm$ 4.1	0.84	3.36*	11.21*
B03	50.1 $\pm$ 1.2	51.5 $\pm$ 1.9	0.59	1.92	3.67
B04	44.3 $\pm$ 2.4	45.1 $\pm$ 3.1	0.21	0.89	0.80
B05	31.9 $\pm$ 1.1	30.7 $\pm$ 2.0	0.51	0.84	0.71

Table 4.4 continued : B and O Average Dominance Effects

<u>Character</u>	<u>Mean <math>\pm</math> S.E.</u>		<u>T-TEST</u>		<u>ANOVA</u>
	<u>Parentals</u>	<u>Crosses</u>	<u>Indep. T</u>	<u>Paired T</u>	<u>F</u>
<u>Female Starvation</u> - continued					
B06	30.5 $\pm$ 1.5	28.3 $\pm$ 0.6	1.03	14.33**	202.54**
B07	41.2 $\pm$ 1.1	39.5 $\pm$ 0.5	1.41	2.50	6.23
B08	31.3 $\pm$ 0.7	29.6 $\pm$ 0.8	--	--	2.22
<u>Male Starvation</u> (hours)					
B01	22.3 $\pm$ 0.8	22.1 $\pm$ 0.6	0.22	0.3	0.14
B05	22.2 $\pm$ 0.5	23.1 $\pm$ 0.7	0.99	4.28	18.12
B06	25.5 $\pm$ 2.2	26.3 $\pm$ 1.2	0.31	0.70	0.50
B07	30.3 $\pm$ 0.4	31.5 $\pm$ 0.3	2.28	3.21	10.29
B08	23.7 $\pm$ 0.5	23.4 $\pm$ 0.5	--	--	0.13
<u>Female Longevity</u> (days)					
B02	55.9 $\pm$ 2.8	56.9 $\pm$ 1.9	0.30	0.42	0.19
B03	36.7 $\pm$ 2.0	37.1 $\pm$ 1.0	0.16	0.24	0.06
B06	45.9 $\pm$ 0.3	47.2 $\pm$ 0.9	1.28	1.84	3.39
B07	42.6 $\pm$ 0.8	41.4 $\pm$ 1.9	0.57	0.60	0.36
B08	40.0 $\pm$ 1.3	41.0 $\pm$ 1.5	--	--	0.25
<u>Male Longevity</u> (days)					
B06	42.0 $\pm$ 0.7	39.1 $\pm$ 0.9	2.64	3.03	9.16
B07	40.2 $\pm$ 0.3	37.5 $\pm$ 2.0	1.33	1.53	2.35
B08	37.8 $\pm$ 1.1	37.8 $\pm$ 1.2	--	--	0.00

CHAPTER 5

Gene Number Analysis of B and O Populations

## 5.1 Introduction

Experiments were performed to estimate the number of "effective factors" (Lande 1981) involved in postponed aging. Effective factors are a measure of the number of loci of "equivalent effect" that are responsible for the differentiation of a quantitative character between two populations.

## 5.2 Experimental Procedure

The actual number of factors contributing to the phenotypic difference between samples from parental populations raised in a common environment is (Lande 1981)

$$n = \frac{(m_1 - m_2)^2}{8V_S} [ 1 + (V_V / V)^2 ] \quad 5.1$$

where  $m_i$  gives the mean of one of the parental populations,  $V_S$  gives the segregation variance, where

$$V_S = \text{Var}(F_2) - \text{Var}(F_1), \quad 5.2$$

and where the last term in parenthesis is the squared coefficient of the magnitudes of the genetic factors. This last term is generally unknown, but must be positive, as noted by Mather and Jinks (1982). Therefore, estimates of

the minimum number of genetic factors, also known as the effective number of factors, were calculated from the formula (Lande 1981)

$$n_e = (m_1 - m_2)^2 / 8V_S \quad 5.3$$

This method of factor estimation is based on the relationship between parental and hybrid crosses with respect to their means and variances (Figure 5.1). It is to be noted that the method hinges on the basic Mendelian phenomenon of  $F_2$  segregation giving rise to increased variance relative to that of the  $F_1$ . For example, with fixation of distinct alleles at a locus in two ancestral populations, the  $F_1$  will consist solely of heterozygotes, whereas the  $F_2$  will have both types of homozygotes, as well as the heterozygote, in the Hardy-Weinberg proportions of 1:2:1. With an infinite number of loci,  $F_1$  and  $F_2$  variances will be equal to each other.

As well as the  $n_e$  estimates, we calculated the inverse estimates:

$$1/n_e = 8V_S / (m_1 - m_2)^2. \quad 5.4$$

The reason for this is that there is a mathematical singularity in  $n_e$  when  $V_S = 0$ . When  $V_S$  is just above zero,  $n_e$  diverges to positive infinity. When  $V_S$  is just below zero,  $n_e$  diverges to negative infinity. Figure 5.2

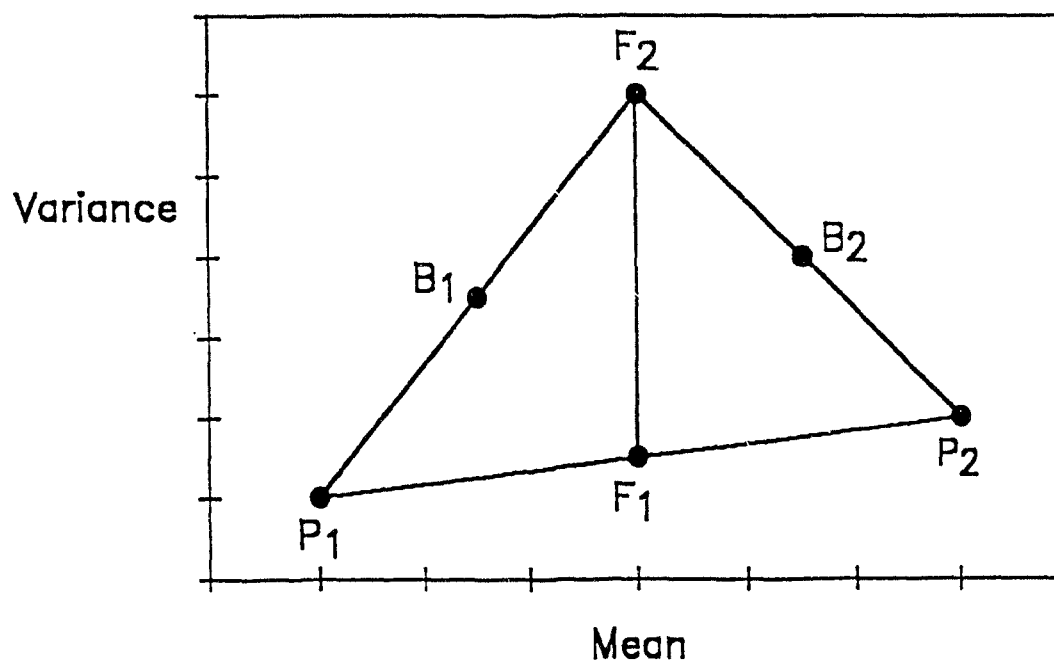


Figure 5.1. Relationship between parental lines ( $P_1$  and  $P_2$ ), hybrid crosses ( $F_1$  and  $F_2$ ), and backcrosses ( $B_1$  and  $B_2$ ) with respect to the means and variances of a quantitative trait. After Lande (1982, p. 545)

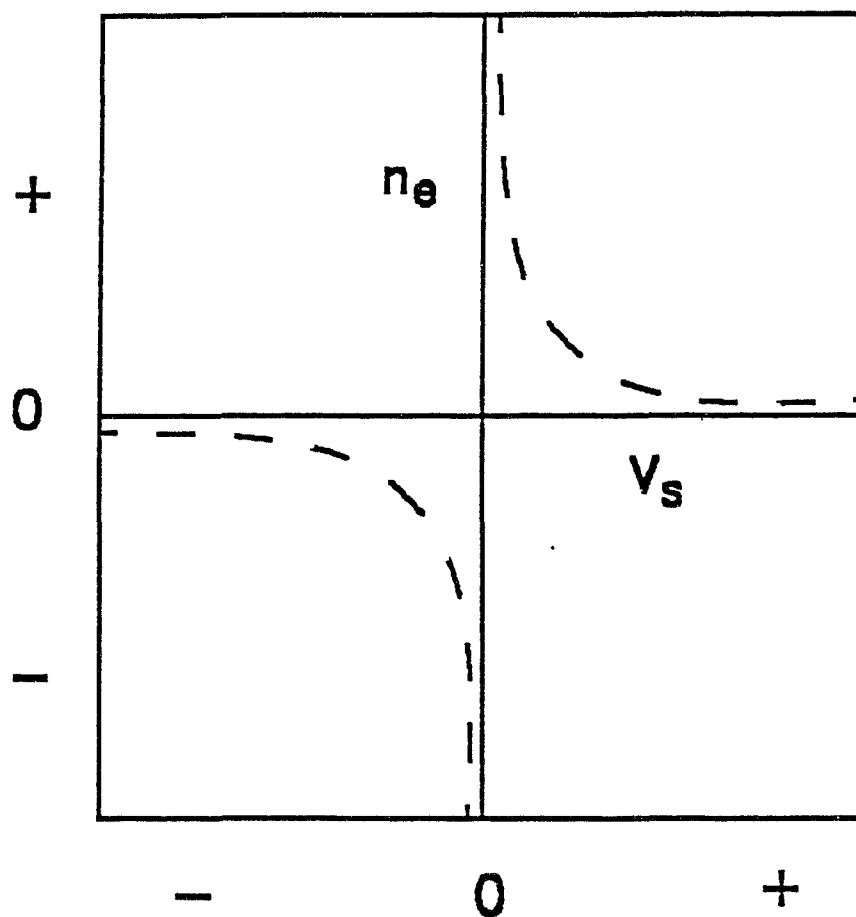


Figure 5.2. Effective Factor Estimation. Illustration of the general form of the function relating the number of effective factors,  $n_e$ , to the segregation variance,  $V_s$ .



illustrates this situation. This creates a problem of interpreting negative values of  $n_e$  when the data are replicated. When  $1/n_e$  is used as a test statistic, none of these problems arise, providing only that there is in fact differentiation between the parental lines under consideration. [And this proviso is almost always satisfied in this type of experiment.] Figure 5.3 illustrates the function of  $1/n_e$  against  $V_S$ . In addition, when  $1/n_e = 0$ , we must have  $n_e$  approaching infinity. This is an appropriate null hypothesis, because  $n_e$  is biased toward small values (Lande 1981). Effectively,  $n_e$  constitutes a lower bound on the actual number of loci involved in population differentiation. Testing  $1/n_e$  for significant deviation above zero tests whether or not there is any statistical reason to conclude that there are fewer than an arbitrarily large number of loci involved in population differentiation.

Table 5.1 outlines the experiments that were performed to estimate the number of effective factors involved in postponed senescence of the B and O populations. The "GB0" coding indicates that these are gene number experiments for the B and O populations, and the numeral indicates the particular experiment. GB01 and GB02 had a larval density of 30/vial, while GB03 had a larval density of 90/vial. These experiments had the same type of design as the transmission pattern experiments, except that  $F_2$ 's were

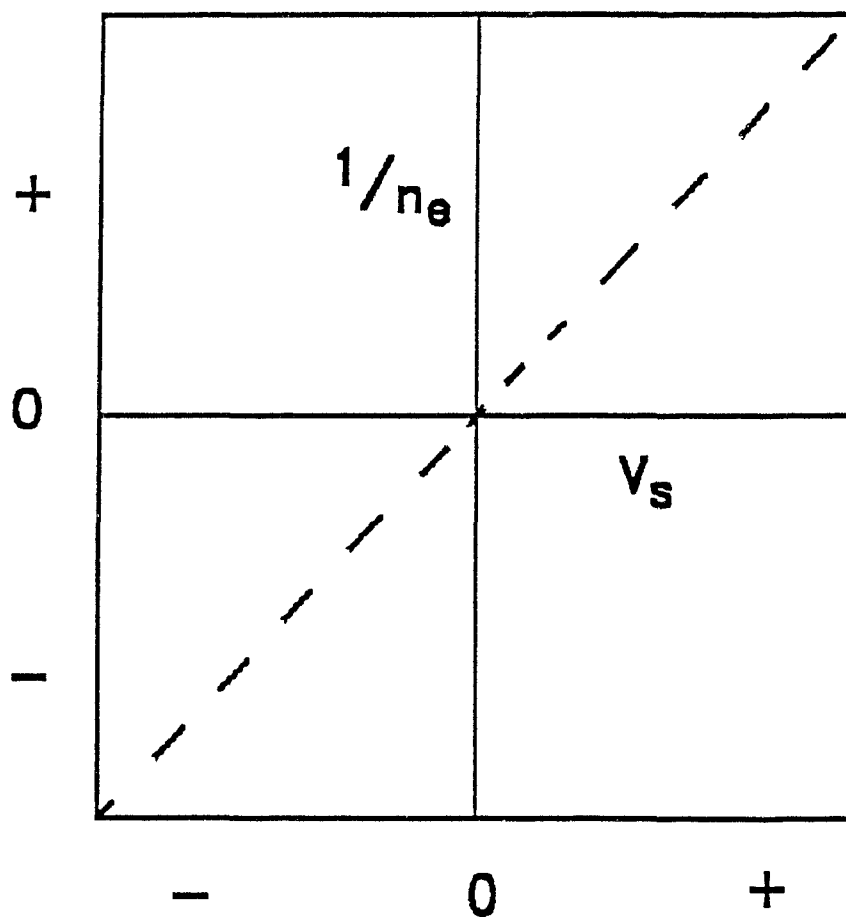


Figure 5.3. Inverse Effective Factor Estimation. Illustration of the general form of the function relating the inverse of the number of effective factors,  $1/n_e$ , to the segregation variance,  $V_s$ .

Table 5.1 : B and O Gene Number Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<hr/>				
<u>GB01</u>				
	Ovary Weight	4x5 = 20	43.2	864
	Female Starvation	3x5 = 15	41.6	624
		5x2x5 = 60	41.2	2,061
	Male Starvation	3x5 = 15	41.6	624
		5x2x5 = 60	41.2	2,061
<u>GB02</u>				
	Fecundity	4x3 = 12	112.8	1,353
	Conditional Fecund.	4x3 = 12	110.5	1,326
	Female Starvation	4x3 = 12	114.3	1,371
	Male Starvation	4x3 = 12	114.3	1,371
	Female Longevity	4x3 = 12	113.3	1,360
	Male Longevity	4x3 = 12	113.7	1,364
<u>GB03</u>				
	Fecundity	4x3 = 12	116.5	1,398
	Conditional Fecund.	4x3 = 12	115.1	1,381
	Female Starvation	4x3 = 12	118.3	1,420
	Male Starvation	4x3 = 12	118.3	1,420
	Female Longevity	4x3 = 12	98.3	1,179
	Male Longevity	4x3 = 12	98.2	1,178
<hr/>				
Total		314		22,355

obtained from the  $F_1$ 's of B and O stocks. In experiment GBO1, generations  $F_3$  to  $F_6$  were obtained, as well. Two effective factor estimates were calculated for these characters -- one using the  $F_2$  data together with the  $F_1$  and parental data, and one using the average of the effective factor estimates calculated using these later generations' variance estimates in place of the  $F_2$  variance estimate.

[These calculations also used control lines, to standardize environmental sources of fluctuation in variance estimates.]

These later generations were used in the estimation procedure because the technique assumes free recombination of all contributing loci in the production of the  $F_2$  generation. For an organism with many chromosomes this may be a reasonable assumption. In *Drosophila* it is not, because there are few chromosomes and there is suppression of recombination in males. In fact, it is often found that the calculated  $n_e$  values increase when the means and variances of  $F_3$ ,  $F_4$ , etc. are used in place of those for  $F_2$  (Jinks and Towey 1976; Towey and Jinks 1977). This reflects the action of recombination in freeing loci from cosegregation when they are on the same chromosome, in turn reducing the variance of the hybrid population. Thus,  $F_3$  and subsequent generations were used as a check against a low estimate of  $n_e$  due to a relative lack of recombination per generation. The two types of estimates are distinguished in the tabulation of the results.

### 5.3 Results and Discussion

The summary statistics for each character in each experiment are given in Appendix E, Tables E1 through E15. The order of the tables follows the order of the experiments and the characters within each experiment as outlined in Table 5.1.

Figure 5.4 is a set of frequency histograms of fecundity for one of the replicates,  $B_2 \times O_2$ , of experiment GB03. Shown are, from top to bottom, the  $B_2$  parental histogram, the  $O_2$  parental histogram, the  $F_1$  hybrid histogram, and the  $F_2$  hybrid histogram. It is clear that there is not a trimodal distribution in the histogram of the  $F_2$  hybrid; evidence against the existence of only one gene being responsible for the differentiation of the parental populations. Figures 5.5 through 5.8 are similar sets of histograms for female starvation time, male starvation time, female longevity, and male longevity, respectively. All of these are from the same replicate,  $B_2 \times O_2$ , of experiment GB03 and are intended to be representative of the patterns found in all of the crosses. [To have presented all sixty-two of the sets of histograms in these experiments would have been a bit excessive.] In none of the  $F_2$  histograms is there a trimodal distribution, again evidence against the existence of only one gene differentiating the parental populations. Further, the distributions of the

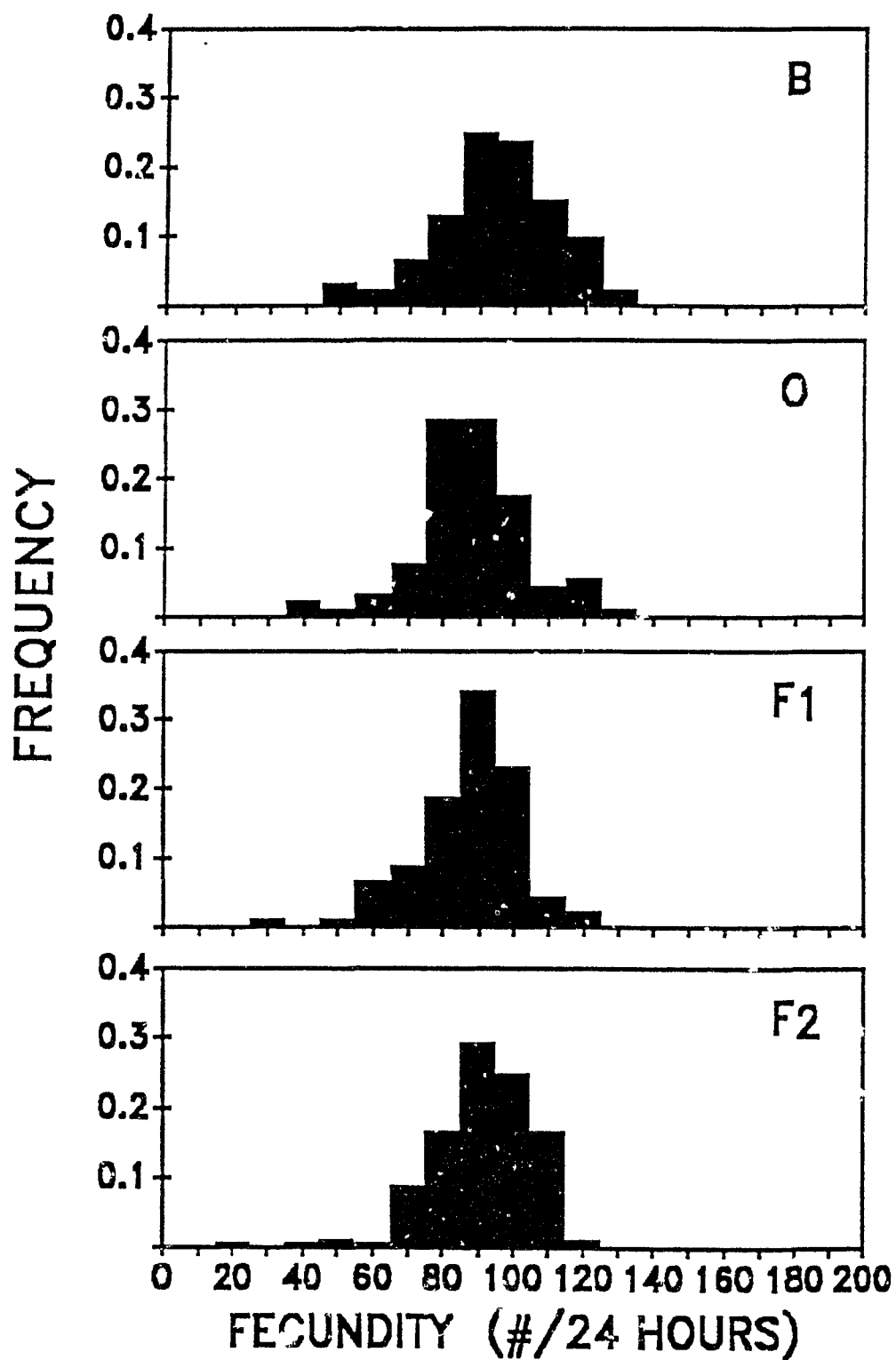


Figure 3.4. Frequency histograms of fecundity in replicate B<sub>2</sub> x O<sub>2</sub> of experiment GBO3.

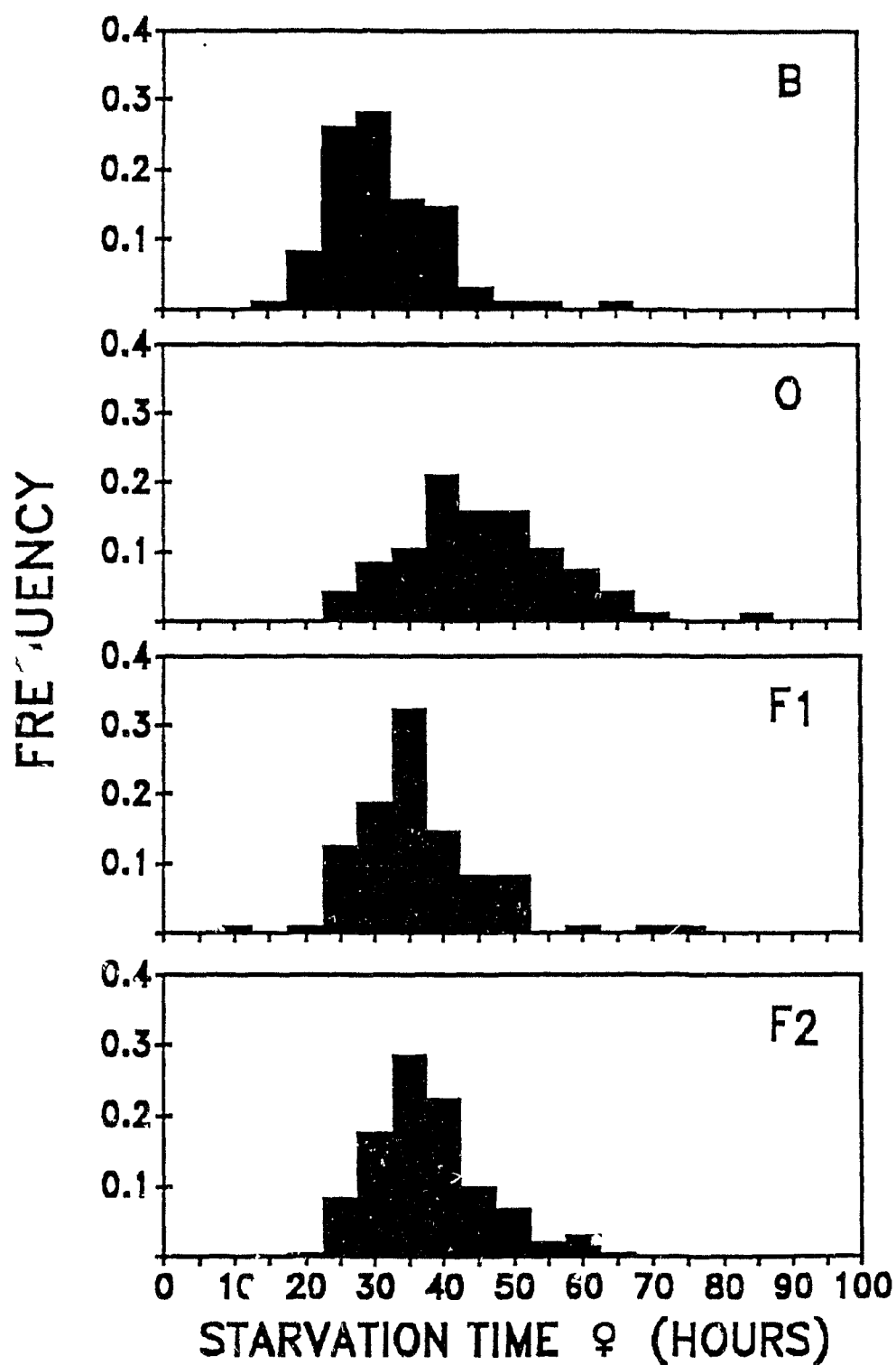


Figure 5.3. Frequency histograms of female starvation time in replicate B<sub>2</sub> x O<sub>2</sub> of experiment GBO3.

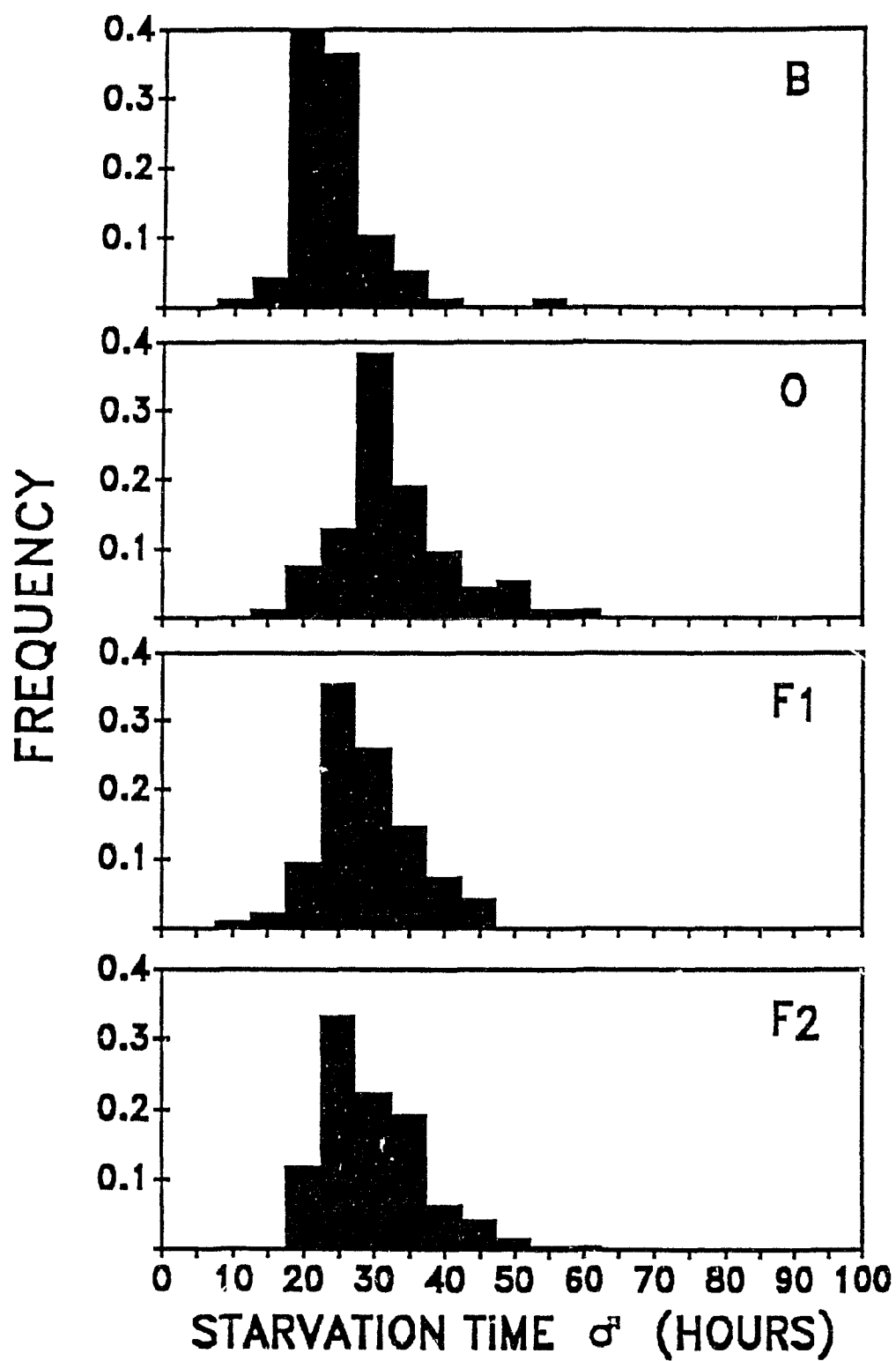


Figure 5.6. Frequency histograms of male starvation time in replicate  $B_2 \times O_2$  of experiment GBO3.



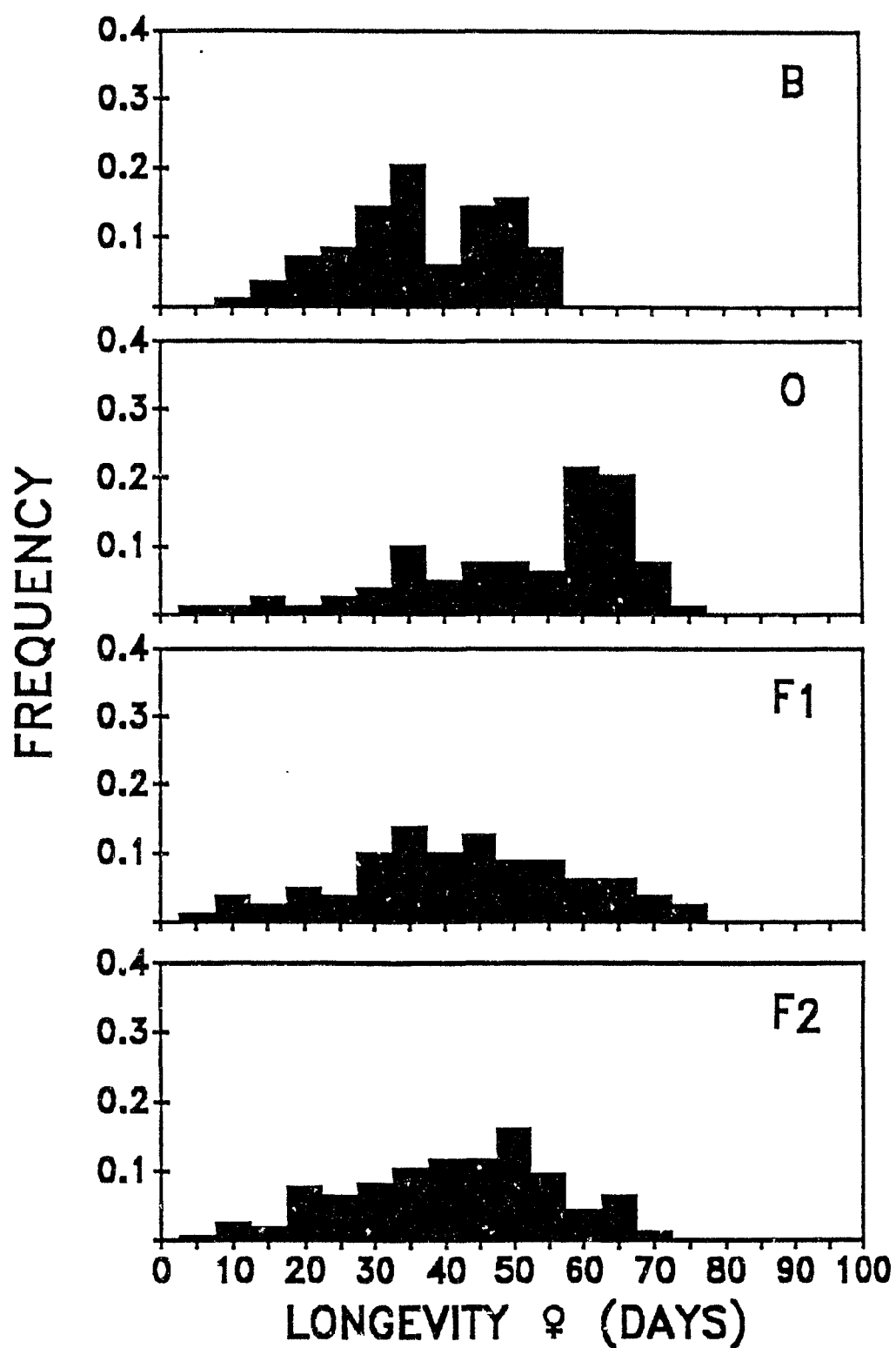


Figure 5.7. Frequency histograms of female longevity in replicate  $B_2 \times O_2$  of experiment GBO3.

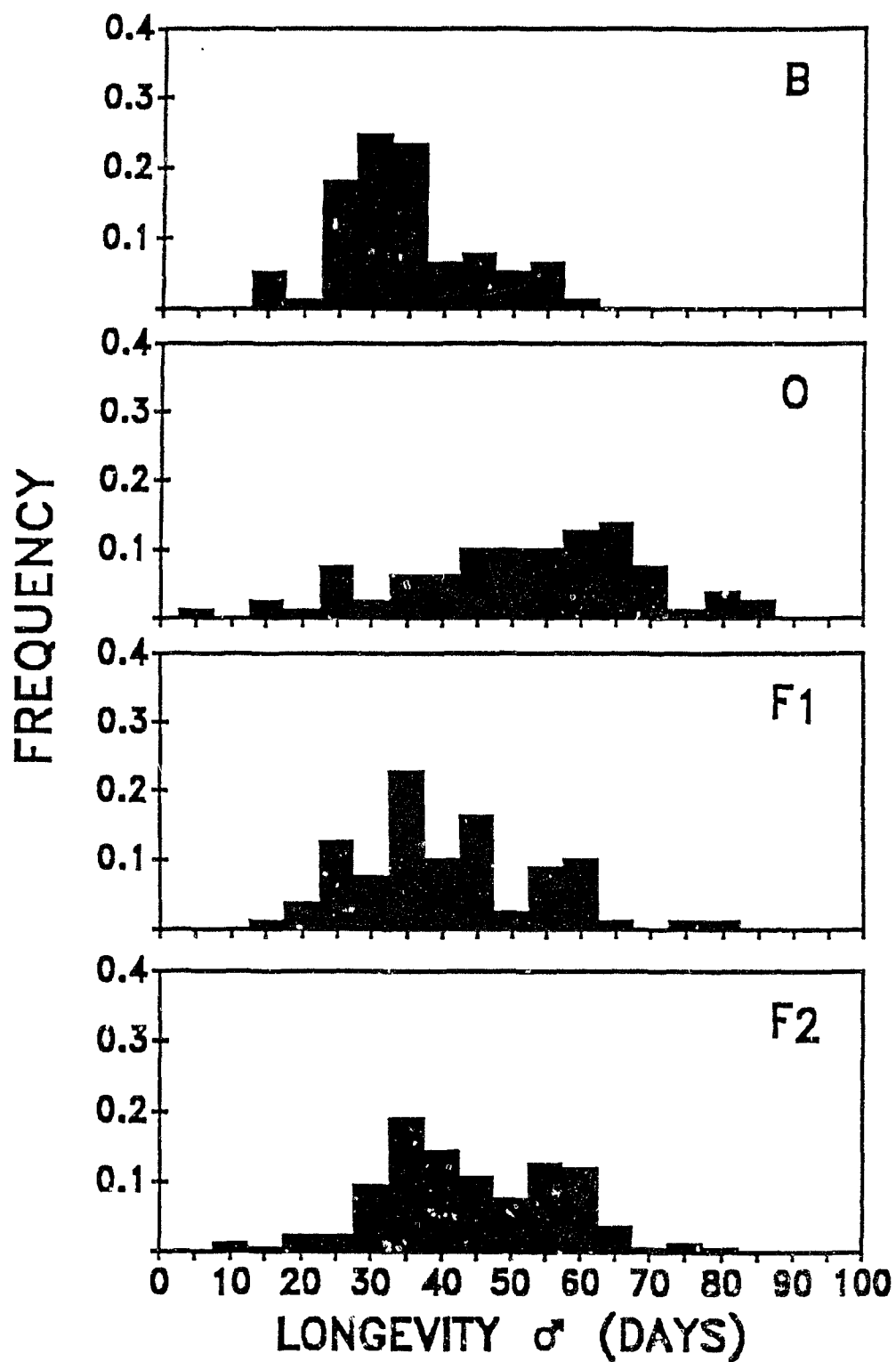


Figure 5.8. Frequency histograms of male longevity in replicate B<sub>2</sub> x O<sub>2</sub> of experiment GB03.

$F_2$ 's does not appear to be very different from the distributions of their paired  $F_1$ 's; evidence for a large number of genes being involved in the differentiation of the parental populations. It should be noted, however, that the distributions of the parental populations are not discrete, which could cause an overlapping of a possible trimodal distribution in the  $F_2$  and also cause the  $F_2$  and the  $F_1$  distributions to resemble each other. This is one of the reasons for the selection experiments of Part III; to create populations which are well separated, allowing a better analysis of the  $F_1$  and the  $F_2$  distributions.

The estimates of the number of effective factors are given in Table 5.2. Table 5.3 gives the results with the inverted effective factor estimates. The effective factor results themselves suggest that there are a small number of loci involved. The mean  $n_e$  values over replicates tend to be below 1, and the standard errors for these estimates are reasonably small. It is only when the inverse  $n_e$  values are considered statistically that these results can be seen to be misleading. The  $1/n_e$  estimates are not significantly different from zero. This different behavior probably arises from the role of the negative estimates in the two cases. Negative  $n_e$  data decrease the average  $n_e$  value, biasing the results toward underestimates, even though the negative segregation variances that generate the negative data in fact indicate a large number of segregating factors.

Table 5.2 : B and O Effective Factor Estimates

<u>Character</u> Experiment	1	2	Line 3	4	5	Mean $\pm$ SEM
<u>Ovary Weight</u>						
GB01	-0.18	0.25	0.14	0.94	-0.04	0.22 $\pm$ 0.19
<u>Fecundity</u>						
GB02	0.00	-0.01	0.07			0.02 $\pm$ 0.02
GB03	0.03	-0.32	0.89			0.20 $\pm$ 0.36
<u>Conditional Fecundity</u>						
GB02	0.01	0.12	0.53			0.22 $\pm$ 0.16
GB03	0.13	-0.32	2.29			0.70 $\pm$ 0.81
<u>Female Starvation</u>						
GB01:						
F2	0.04	0.05	-0.00	0.09	0.15	0.07 $\pm$ 0.03
F2-F6	0.05	0.64	0.67	-0.13	10.07	2.26 $\pm$ 1.96
GB02	0.19	0.32	0.08			0.19 $\pm$ 0.07
GB03	0.90	-1.08	0.23			0.02 $\pm$ 0.58
<u>Male Starvation</u>						
GB01:						
F2	0.97	0.36	0.23	-0.43	0.69	0.36 $\pm$ 0.24
F2-F6	0.40	0.49	-0.15	0.17	0.12	0.20 $\pm$ 0.11
GB02	2.94	-1.31	0.54			0.72 $\pm$ 1.23
GB03	0.59	0.99	-10.79			-3.07 $\pm$ 3.86
<u>Female Longevity</u>						
GB02	-0.06	0.75	0.59			0.43 $\pm$ 0.25
GB03	0.39	-0.50	-0.45			-0.19 $\pm$ 0.29
<u>Male Longevity</u>						
GB02	-5.18	4.33	2.67			0.61 $\pm$ 2.93
GB03	3.75	-8.13	2.58			-0.60 $\pm$ 3.78

Table 5.3 : B and O Inverse Effective Factor Estimates

Character	Line					Mean $\pm$ SEM
Experiment	1	2	3	4	5	
<u>Ovary Weight</u>						
GB01	-5.56	4.00	7.14	1.06	-25.02	-3.67 $\pm$ 5.73
<u>Fecundity</u>						
GB02	10 <sup>6</sup>	-98.93	14.86			10 <sup>5</sup> $\pm$ 10 <sup>5</sup>
GB03	33.39	-3.15	1.13			10.46 $\pm$ 11.5
<u>Conditional Fecundity</u>						
GB02	68.31	8.61	1.88			26.27 $\pm$ 21.1
GB03	7.62	-3.15	0.44			1.64 $\pm$ 3.16
<u>Female Starvation</u>						
GB01:						
F2	28.65	19.94	-5182	11.24	6.58	-1023 $\pm$ 1039
F2-F6	18.70	1.56	1.50	-7.58	0.10	2.86 $\pm$ 4.31
GB02	5.35	3.15	12.72			7.07 $\pm$ 2.89*
GB03	1.11	-0.93	4.32			1.50 $\pm$ 1.78
<u>Male Starvation</u>						
GB01:						
F2	1.03	2.78	4.35	-2.33	1.45	1.46 $\pm$ 1.11
F2-F6	2.50	2.04	-6.67	5.88	8.33	2.42 $\pm$ 2.55
GB02	0.34	-0.77	1.86			0.48 $\pm$ 0.76
GB03	1.71	1.01	-0.09			0.88 $\pm$ 0.52
<u>Female Longevity</u>						
GB02	-16.88	1.34	1.70			-4.61 $\pm$ 6.13
GB03	2.55	-2.00	-2.21			-0.55 $\pm$ 1.55
<u>Male Longevity</u>						
GB02	-0.19	0.23	0.38			0.14 $\pm$ 0.17
GB03	0.27	-0.12	0.39			0.18 $\pm$ 0.15

The reason that these negative  $n_e$  estimates should be interpreted as evidence for a large number of effective factors is straightforward. Negative  $n_e$  estimates arise when the variance of the  $F_2$  is less than the variance of the  $F_1$ . In theory, of course, this should not happen. The variance of the  $F_2$  should be equal to or greater than the variance of the  $F_1$ . What we are seeing when the  $F_2$  variance is less than the  $F_1$  variance is simply statistical fluctuation around the situation where the  $F_2$  variance is equal to the  $F_1$  variance, indicating a large number of effective factors. In the inverse effective factor data, negative estimates pull the mean toward zero, indicating more effective factors, which is the appropriate effect. Taken together, the histograms and the results of Table 5.3 indicate the involvement of many loci in the postponed aging of the O stocks, relative to the B stocks.

## CHAPTER 6

### Discussion of Analysis of Outbred Populations

## 6.1 Discussion

There is little or no evidence in the present results that suggests anything other than polygenic additive inheritance in the laboratory evolution of postponed aging in the D. melanogaster stocks studied. Maternal or line effects, when present, are inconsistent over lines and characters. It cannot be said that any of the postponed senescence stocks is superior to any other. On average, hybrids of postponed senescence and control stocks appear to be intermediate; there is no consistent heterosis, inbreeding depression, or directional dominance. While average effective factor estimates seem to be small, in fact there is no statistical evidence that the results indicate a small number of loci involved in postponed aging. In general, then, the characters examined here seem to be classic "quantitative characters" (cf. Falconer 1981).

These results may be compared with those found before by Luckinbill and co-workers. Like Clare and Luckinbill (1985), who studied fewer characters, fewer lines, and far fewer individuals, essentially additive inheritance was found in the population crosses. [This is in fact a prerequisite for effective factor number estimation (Lande 1981).] Like Luckinbill et al. (1987), there are small estimates of effective factor number. Indeed, many of the estimates tend to be smaller than those of Luckinbill et al. (1987), and the amount of replication in the present study



is considerably greater. However, I disagree with the interpretation that Luckinbill et al. (1987) offer of their findings. They discarded negative estimates of  $n_e$ , failing to treat them as evidence for a large number of effective factors. The method of averaging inverse effective factor estimates gives hypothesis tests which are not as biased toward the conclusion that only a few loci are involved in the differentiation of the populations crossed. The actual results, then, are not particularly different from those of Luckinbill et al. (1987); only the analysis is. This analysis then leads to a differing conclusion. Considering the data alone, there seems to be a remarkable degree of congruence between the results of the present study and those of Luckinbill and co-workers. Since the stocks involved are independent, and those in the present study are considerably more replicated, the conclusions of Clare and Luckinbill (1985) seem to be strongly supported.

However, the gene number estimates are at least somewhat placed in doubt by the possibility that the populations that have been analyzed are still highly polymorphic for the alleles involved in postponed senescence. In particular, if the alleles that postpone aging are not consistently differentiated over loci, such that some alleles postponing aging are at higher frequencies in the control populations than in the populations with postponed aging, as some of the results of Luckinbill et al. (1988b) suggest, then the effective factor estimates will

not be valid (Lande 1981). More generally, crosses of highly polymorphic populations will not give clean tests of average dominance of differentiated alleles. In addition, parental lines that aren't extremely differentiated will not be as distinguishable from their  $F_1$ 's, nor will segregation in the  $F_2$ 's be as detectable. For these reasons, selected lines were created that would be more differentiated with respect to at least some of the characters involved in postponed aging, in the hope of then performing a more refined genetic analysis. The creation of these stocks is the subject of Part III of this thesis and their subsequent analysis is described in Part IV.

PART III

ARTIFICIAL SELECTION OF F AND S POPULATIONS

CHAPTER 7

Creation of F and S Selected Populations

## 7.1 Introduction

The artificial selection experiments described in this chapter were an attempt to fix those alleles with strong effects on senescence. There were three stages to these experiments. Firstly, the heritabilities ( $h^2$ ) of female starvation resistance and male starvation resistance were assayed in the outbred populations  $B_{1 \rightarrow 3}$  and  $O_{1 \rightarrow 3}$ . Secondly, these six populations were subjected to a rigorous selection regime designed to drive to fixation those alleles having a strong effect on senescence, in so doing creating the selected populations  $F_{1 \rightarrow 3}$  and  $S_{1 \rightarrow 3}$ . Thirdly, the heritabilities ( $h^2$ ) of female starvation resistance, male starvation resistance, and 24-hour fecundity were assayed in the selected populations. If the alleles had been fixed, the heritabilities would have declined.

The narrow-sense heritability of a trait,  $h^2$ , is defined as the ratio of additive genetic variance,  $V_A$ , to phenotypic variance,  $V_P$  :

$$h^2 = V_A / V_P. \quad 7.1$$

This ratio determines the extent to which phenotypes are determined by the genes transmitted from the parents (Falconer 1981). Its theoretical value must lie between 0 and +1 since the numerator is part of the denominator.  $h^2$  is widely used to predict genetic gains following selection

(Turner and Young 1969). As pointed out by Falconer (1981), heritability is a property not only of a character, but also of the population and of the environmental circumstances to which the individuals are subjected. Whenever a value is stated for the heritability of a given character, it refers to a particular population under particular circumstances. Particular populations where fixation has taken place are expected to show lower heritabilities than non-fixed populations. The characters with the lowest heritabilities are those most closely connected with reproductive fitness (Falconer 1981).

Heritability is estimated as the degree of resemblance between relatives. The choice of what sort of relatives to use depends on the circumstances. The heritability can be calculated using parent-offspring regressions, sib analysis, or through selection responses. Here, a half-sib analysis was used before and after the selection regime and realized heritability estimates were calculated from the selection experiments.

The basic effect of selection is to change the array of gene frequencies, as described in Falconer (1981, Chapter 2). When dealing with a metric character, however, the changes in the gene frequencies are hidden from view. The effects of selection are restricted mainly to changes in the population mean. Artificial selection produces a change of the gene frequencies by selecting individuals which differ in the expression of the character under selection. The

measure of the selection applied is called the selection differential,  $S$ : the difference between the mean phenotypic value of the selected parents and the mean of the whole parental population before selection. The change produced in the population mean is the response to selection,  $R$ : the difference between the mean phenotypic value of the offspring of the selected parents and the mean of the parental generation before selection. The relationship between the response and the selection differential is given by:

$$R = h^2 S. \qquad 7.2$$

The ratio of response to selection differential is thus equal to the heritability (Falconer 1981).

Three B populations,  $B_{1-3}$ , and three O populations,  $O_{1-3}$ , were subject to selection for two different characters, early fecundity and starvation resistance, respectively. The rationale for this is that B stocks have enhanced early fecundity relative to O stocks (Rose 1984a), while O stocks have enhanced starvation resistance relative to B stocks (Service et al. 1985). More extreme differentiation is thereby obtainable by selecting further in those directions. In addition, since there is a negative additive genetic correlation between these characters of large magnitude,  $-0.913$  (Service and Rose 1985), selecting up on fecundity should depress starvation resistance and conversely. The O populations were therefore selected

upward for starvation resistance and the B populations were selected upward on 24-hour fecundity. Selecting upwards on both characters avoids the possibility of inadvertent selection for generally deleterious alleles, as could happen with downward selection. Thus, the high fecundity/low starvation resistance alleles can be selected for by artificial selection for increased fecundity. The high starvation resistance/low fecundity alleles can be selected for by artificial selection for increase starvation resistance.

## 7.2 Experimental Procedure

### Half-Sib Heritability Experiments

#### a) Before selection

Experimental flies were derived from the  $B_{1-3}$  and  $O_{1-3}$  populations. In the B populations, flies were collected between 3 and 4 days after eclosion. Two hundred and sixty sets of 3 males and 3 females were established for each population. Each set was put in a yeasted charcoal vial for approximately 24 hours, at which time 30 eggs from each vial were transferred to 260 new vials containing banana-agar media.

When the adult flies began emerging 8-9 days later, 50 males (sires) and 600 females (dams) were collected as virgins. Fifty groups of 12 dams and 1 sire were randomly



mated for each population. These were left for 3 days to ensure male mating success. Subsequently, males were discarded and individual females were placed in separate vials containing charcoal media, family groupings conserved. After 48 hours of laying, 30 eggs from each female were transferred to rearing tubes containing banana media. (Vials in which females had laid less than 26 eggs were discarded in order to reduce the potential for confounding results due to different larval densities, as were entire families if less than 6 females had succeeded in laying the required number of eggs.) Adult flies emerging within vials were full-sibs (these were also discarded if less than 10 flies emerged). Adult flies from different vials within the family groupings were half-sibs (they have the same sire but different dams). One full sibling of each sex from each vial within all families was assayed for starvation resistance, with 6-hour check intervals.

Identical procedures were followed with the O populations except that the initial egg collection was sampled from four petri dishes containing yeasted charcoal media which had been placed in the population cages for 24 hours. The replicate B populations were offset in experimental handling times by 2 days from each other; the O populations were treated identically but assays began 1 week later than for the B lines.

b) After selection

Experimental procedures for estimating heritability after selection were identical with those of the original estimates. Replicate selected  $B_{1 \rightarrow 3}$  and  $O_{1 \rightarrow 3}$  lines, renamed  $F_{1 \rightarrow 3}$  and  $S_{1 \rightarrow 3}$ , respectively (where F stands for fecundity selection and S stands for starvation resistance selection) were derived after 21 generations of selection in the F's and 22 generations of selection in the O's.

Differences in procedure were as follows. Firstly, the  $F_1$  population flies died off more quickly than had been expected when subjected to starvation, hence checks for the  $F_2$  and  $F_3$  populations were conducted every 3 hours as opposed to every 6. Secondly, egg viability in many cases was severely reduced, hence the total number of families per replicate was lower. Thirdly, 24-hour fecundity was assayed as well as starvation resistance.

### Selection Experiments

Experimental flies were derived from the  $O_{1 \rightarrow 3}$  and  $B_{1 \rightarrow 3}$  stock populations, as described in the Heritability experiments. Each replicate was created with 250 vials, with a two-generation run-in at a controlled density of 30 eggs per vial. For both the O's and the B's, selection proceeded with control lines matched to each of the selection lines for the first 11 generations in  $B_1$  and  $B_3$ , the first 14 generations in  $F_2$ , and the first 13 generations in  $O_{1 \rightarrow 3}$ . Over that same period, 250 flies (or pairs of

flies in the case of starvation resistance) were assayed for the selected character from each selected line in each generation, while 120 were assayed from each control line. The character which was **not** selected was also observed in 120 flies from both selected and control lines. Both selected and control lines were maintained using 50 separately reared couples as parents of the next generation, the control-line parents being chosen at random. The selected-line parents were chosen from those individuals in the top 50 of their generation. While starvation resistance was not selected in B-derived lines, and fecundity was not selected in O-derived lines, both characters were monitored in both sets of selection lines. The control lines were discarded after 13 generations, but selection was continued for another 12 generations, at reduced intensity (90 selected out of 160). These later generations of selection cannot, because of the lack of controls, be used for quantitative genetic hypothesis testing. Selection was continued in order to produce more extremely differentiated stocks. The total number of observations made in the course of all the selection experiments exceeded 70,000.

The lines eventually produced by selection for fecundity are designated "F" lines. The lines eventually produced by selection for starvation resistance are designated "S" lines (Figure 7.1).

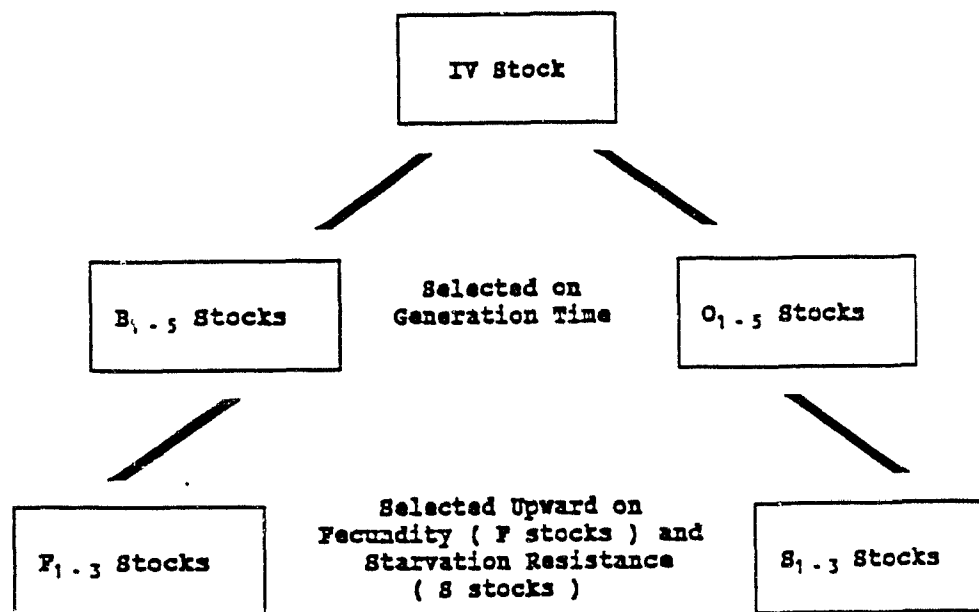


Figure 7.1. Creation of Short-Lived (B), Long-Lived (O), and their derived selected populations (F and S, respectively).

### 7.3 Statistical Analysis

#### Half-Sib Heritability

The estimation of the heritability from half-sibs is made with an Analysis of Variance. The phenotypic variance is divided into components attributed to differences between the progeny of different males (the between-sire component) and to differences between the progeny of females mated to the same male (the within-sire component). There are  $s$  sires each mated to  $k$  dams. The values of the mean squares are denoted by  $MS_S$  and  $MS_e$ .

The mean square within sires,  $MS_e$ , is the estimate of the within-sire variance component,  $\sigma_e^2$ . The mean square between sires,  $MS_S$ , however, is not the variance component, its composition being equal to  $\sigma_e^2 + k \sigma_s^2$ . Therefore, the between-sire variance component is estimated as (Falconer 1981):

$$\sigma_s^2 = (1/k) (MS_S - MS_e). \quad 7.2$$

If there are unequal numbers of dams within the sire groups, as in the present experiments, the exact solution for  $k$ , the average number of dams is:

$$k = (1/(s-1)) (N - (\sum n_i^2 / N)), \quad 7.3$$

where  $s$  equals the number of sires,  $n_i$  equals the number of dams of the  $i$ th sire, and  $N$  equals the total number of dams ( $N = \sum n_i$ ) (Turner and Young 1969). The estimation of the heritability is:

$$h^2 = \frac{4\{(MS_S - MS_e)/k\}}{MS_e + (MS_S - MS_e)/k} \quad 7.4$$

The standard error of  $h^2$  can be calculated as 4 times the standard error of the intraclass correlation. The intraclass correlation,  $t$ , is calculated as:

$$t = \frac{(MS_S - MS_e)/k}{MS_e + (MS_S - MS_e)/k} \quad 7.5$$

and standard error of the intraclass correlation is:

$$S_t = \frac{\{1 + (k-1)t\} (1-t)}{\{1/2 (k)(k-1)(s-1)\}^2}, \quad 7.6$$

where  $k$  and  $s$  are the average number of dams per sire and the total number of sires, respectively (Turner and Young 1969).

#### Realized Heritability

Realized heritability was calculated as the regression of cumulative response on cumulative selection differential. Estimates for cumulative response were calculated using the

differences between the selected groups and the control groups and then summed over successive generations. The cumulative selection differential is the selection differential in each generation summed over successive generations.

#### 7.4 Results

##### Heritability Estimates

###### a) Before selection

The initial heritability estimates for Female Starvation and Male Starvation in  $B_{1 \rightarrow 3}$  and  $O_{1 \rightarrow 3}$  are presented in Table 7.1. The mean heritabilities  $\pm$  standard error in the B populations are  $0.747 \pm 0.325$  for Female Starvation and  $0.177 \pm 0.118$  for Male Starvation. In the O populations the mean heritabilities are  $0.842 \pm 0.273$  and  $0.592 \pm 0.279$  for Female and Male Starvation, respectively.

###### b) After selection

Heritability estimates for Female Starvation and Male Starvation in  $F_{1 \rightarrow 3}$  and  $S_{1 \rightarrow 3}$  are presented in Table 7.2. The mean heritabilities  $\pm$  standard error in the F populations are  $0.485 \pm 0.020$  for Female Starvation and  $0.307 \pm 0.058$  for Male Starvation. In the S populations the mean heritabilities are  $0.516 \pm 0.205$  and  $0.463 \pm 0.057$  for Female and Male Starvation, respectively.

Table 7.1 : Heritabilities of Selected Characters in  
B and C Populations Before Selection

Population Type	Character	Line (Mean $\pm$ SEM)		
		1	2	3
B	Female Starvation	0.47 $\pm$ 0.18	1.40 $\pm$ 0.25	0.38 $\pm$ 0.16
B	Male Starvation	0.00 $\pm$ 0.11	0.40 $\pm$ 0.16	0.14 $\pm$ 0.13
O	Female Starvation	0.68 $\pm$ 0.19	1.37 $\pm$ 0.31	0.47 $\pm$ 0.17
O	Male Starvation	0.38 $\pm$ 0.15	1.15 $\pm$ 0.30	0.25 $\pm$ 0.14



Table 7.2 : Heritabilities of Selected Characters in  
F and S Populations After 25 Generations of  
Directional Selection

Population Type	Character	Line (Mean $\pm$ SEM)		
		1	2	3
F	Female Starvation	0.50 $\pm$ 0.18	0.45 $\pm$ 0.18	0.51 $\pm$ 0.19
F	Male Starvation	0.34 $\pm$ 0.16	0.39 $\pm$ 0.17	0.20 $\pm$ 0.14
F	Fecundity	0.24 $\pm$ 0.14	0.35 $\pm$ 0.17	0.27 $\pm$ 0.16
S	Female Starvation	0.78 $\pm$ 0.20	0.11 $\pm$ 0.14	0.65 $\pm$ 0.21
S	Male Starvation	0.57 $\pm$ 0.18	0.37 $\pm$ 0.18	0.45 $\pm$ 0.18
S	Fecundity	1.27 $\pm$ 0.24	0.92 $\pm$ 0.25	0.07 $\pm$ 0.14

Table F.1 (Appendix F) presents the analysis of the effects of the selection process on the heritability estimates. There was no significant reduction in the heritabilities of Female Starvation or Male Starvation , in the B to F selection regime. Nor was there a reduction in the heritabilities of Female Starvation or Male Starvation in the O to S selection regime.

Heritability estimates for 24-hour fecundity in the  $F_{1 \rightarrow 3}$  and  $S_{1 \rightarrow 3}$  lines are also presented in Table 7.2. The mean heritabilities  $\pm$  standard error are  $0.287 \pm 0.033$  and  $0.755 \pm 0.356$  in the F and S lines, respectively.

#### B -> F Selection Experiments

a) With controls: generations 1-11 (14 in  $B_2$ )

Figure 7.2 shows the direct response to selection for increased 24-hour fecundity in the three B replicates. In these graphs and those which follow, the selected group is represented by solid triangles connected by a solid line, the control group by empty triangles connected by a dashed line. The 95% confidence intervals are shown around the mean 24-hour fecundity for generations 1 through 12 in  $B_1$  and  $B_3$  and generations 1 through 14 in  $B_2$ . The selected and control lines start to diverge in the second generation. A mixed model ANOVA of the last 6 generations with controls shows significant differences between selected and control

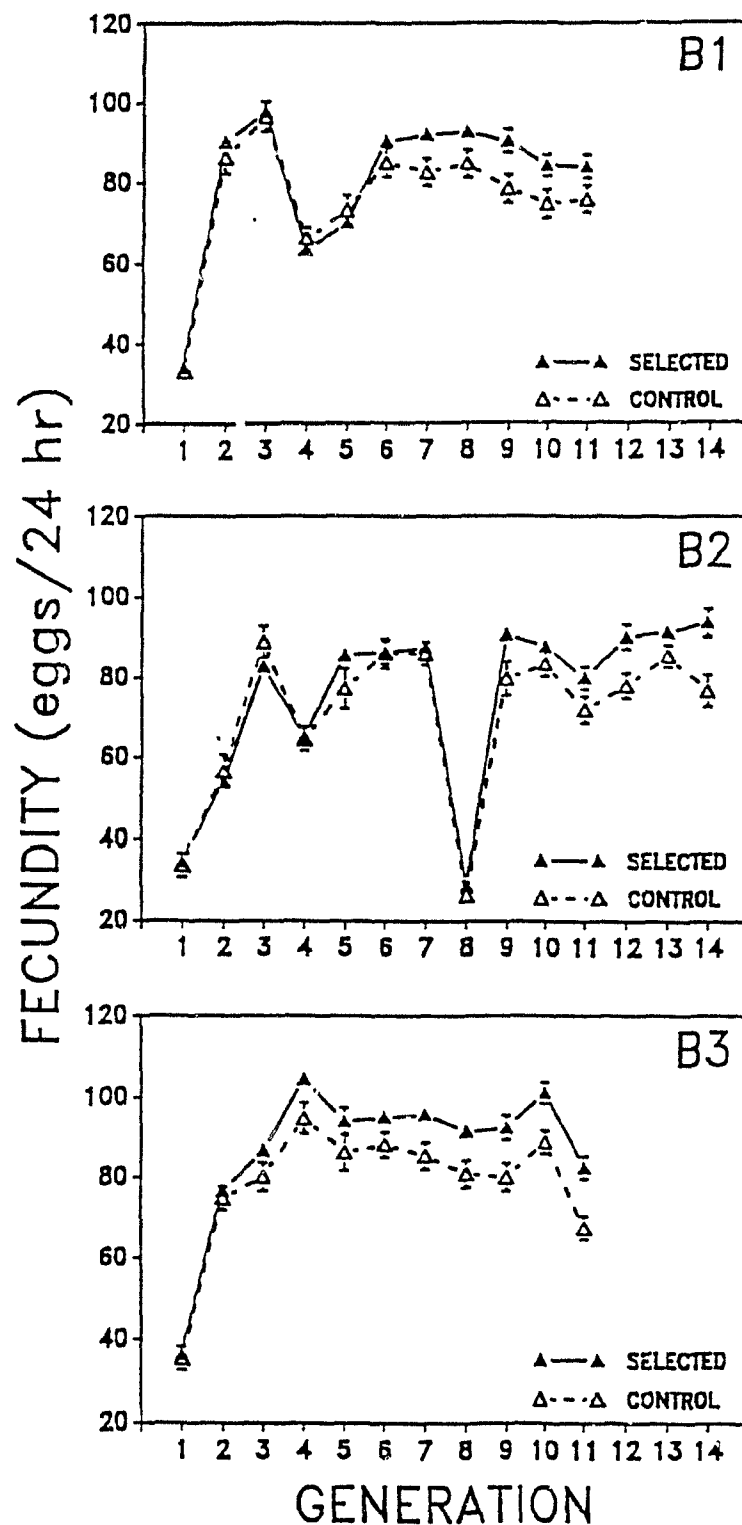


Figure 7.2. Direct response of the three B populations to selection for increased early fecundity.

groups ( $F = 199.87^{**}$  for Fecundity,  $F = 275.64^{**}$  for Conditional Fecundity (Table F.2)).

Figure 7.3 plots the cumulative response on the cumulative selection differential, the regression being shown as the dashed line. The slope of the regression is the realized heritability (Table 7.3). The mean  $\pm$  SEM of the realized heritability of early fecundity in the three lines is  $0.058 \pm 0.001$ .

The indirect response of female starvation time to selection on 24 hour fecundity is shown in Figure 7.4. Although not as striking as the direct responses, these indirect responses are significant in a mixed model ANOVA ( $F = 15.83^{**}$ , Table F.3).

#### b) Without controls: generations 1->25

After 11 generations in replicates  $B_1$  and  $B_3$  and 14 generations in  $B_2$  the paired controls were no longer used. The direct responses to selection for increased fecundity for all 25 generations are shown in Figure 7.5. As is clear in the figure, the mean fecundity in each generation is seen to increase throughout the experiment.

### O -> S Selection Experiments

#### a) With controls: generations 1->13

Figure 7.6 shows the direct response to selection for

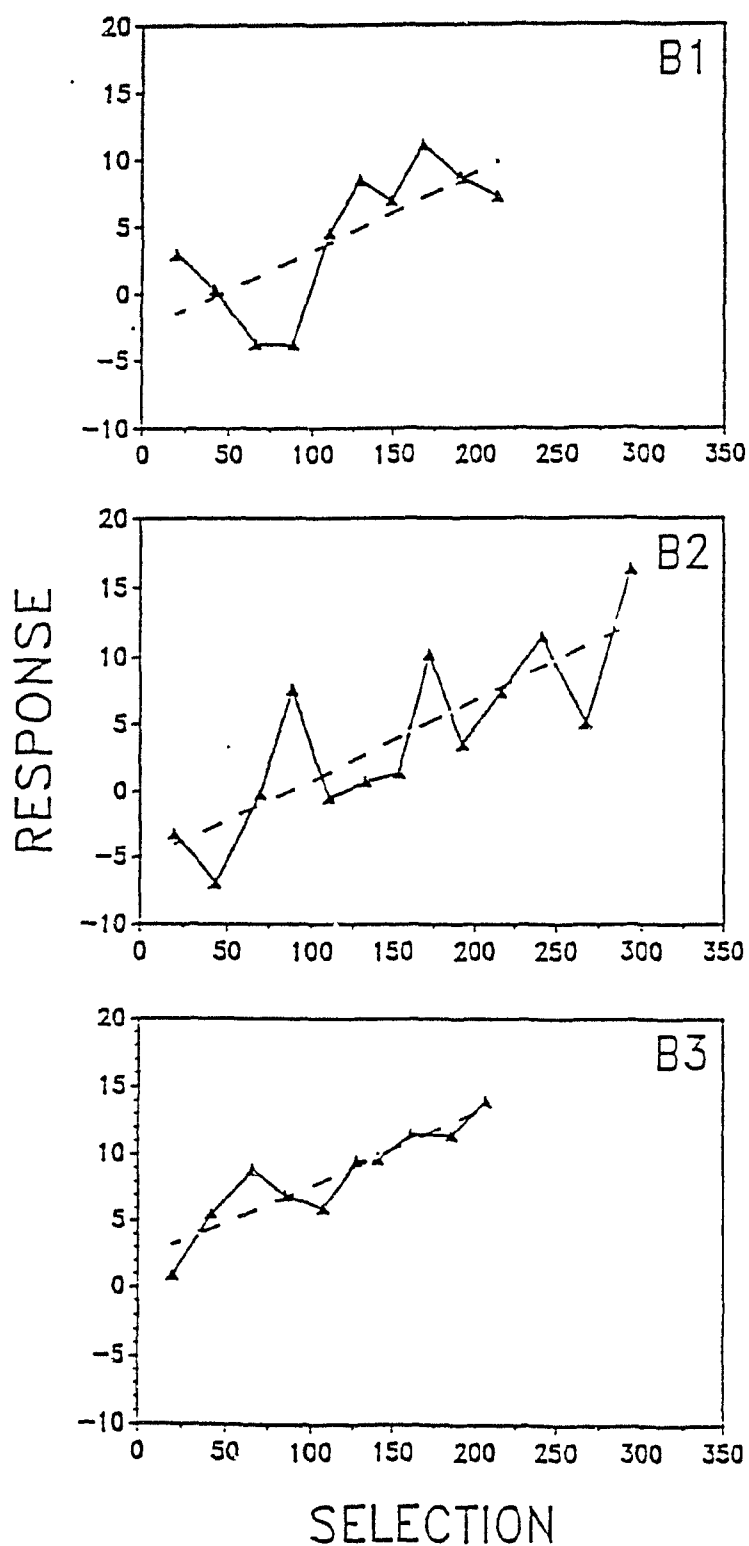


Figure 7.3. Regression of selection response on the cumulative selection differential for selection on early fecundity in the three B populations.

Table 7.3 : Realized Heritabilities for Selection on  
Early Fecundity in the Three B Populations

Replicate	Slope $\pm$ SEM
1	0.058 $\pm$ 0.020
2	0.060 $\pm$ 0.013
3	0.055 $\pm$ 0.009
Mean	0.058 $\pm$ 0.001

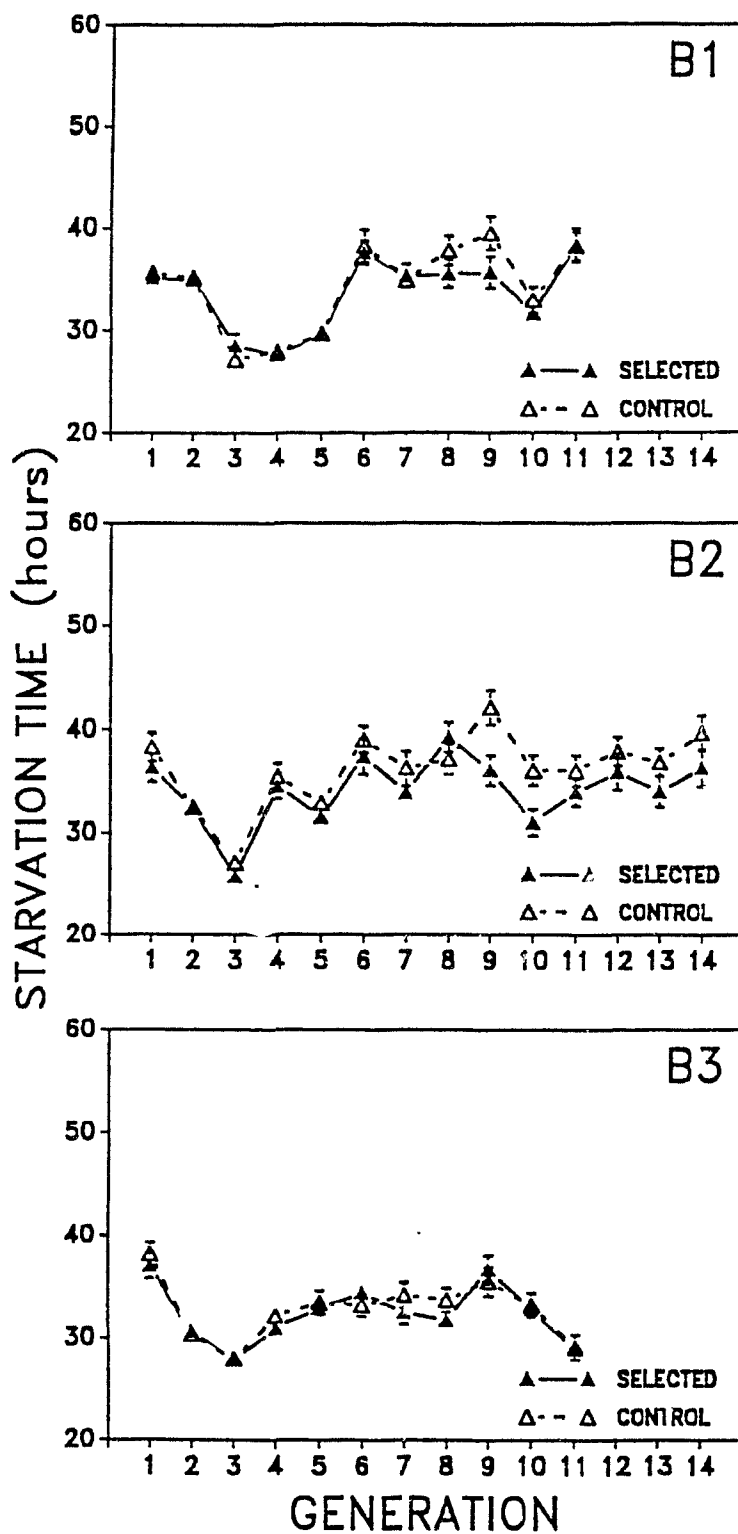


Figure 7.4. Indirect response of mid-parent starvation resistance to selection for increased early fecundity in the three B populations.

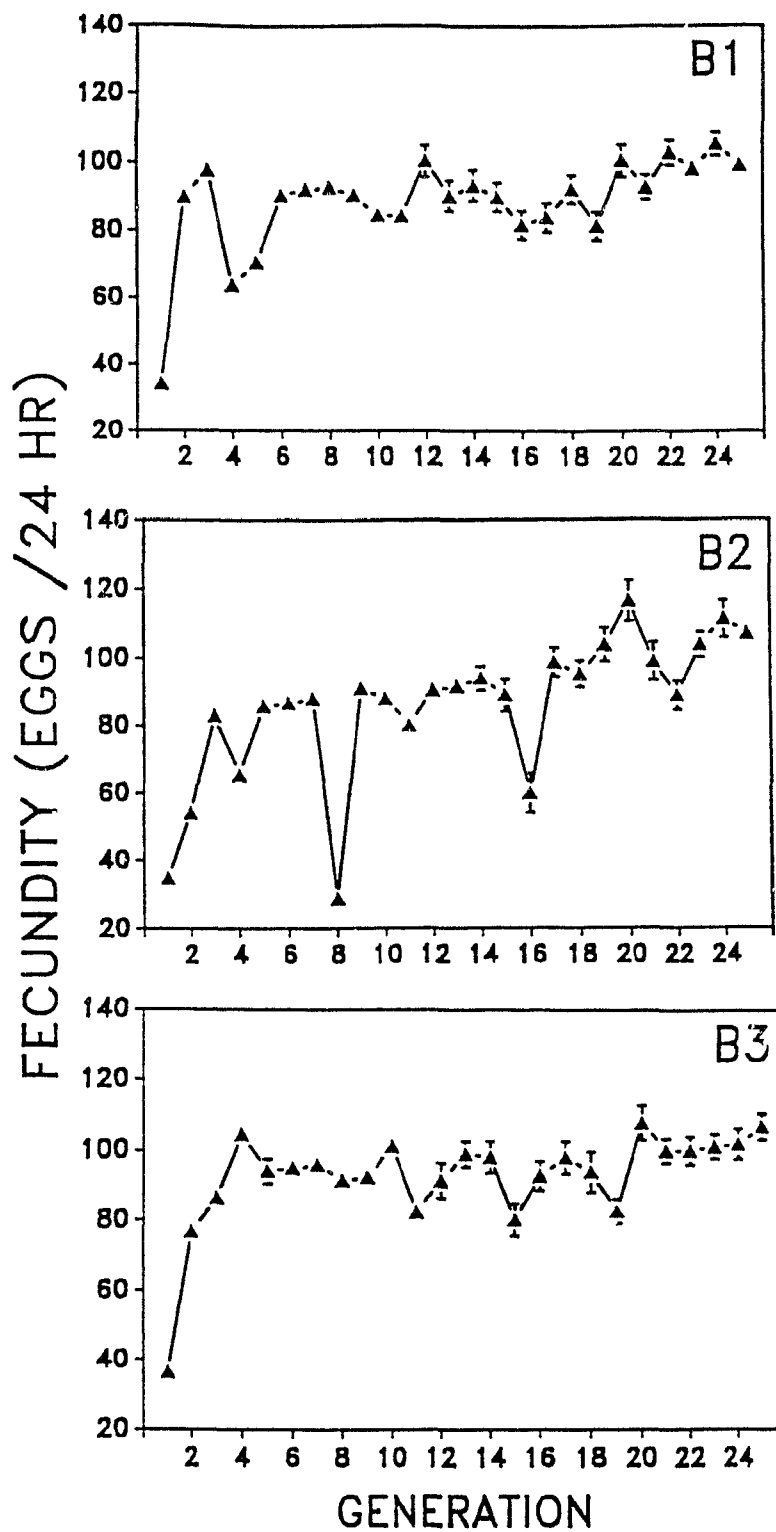


Figure 7.5. Direct response of the three B populations to selection over 25 generations for increased early fecundity.



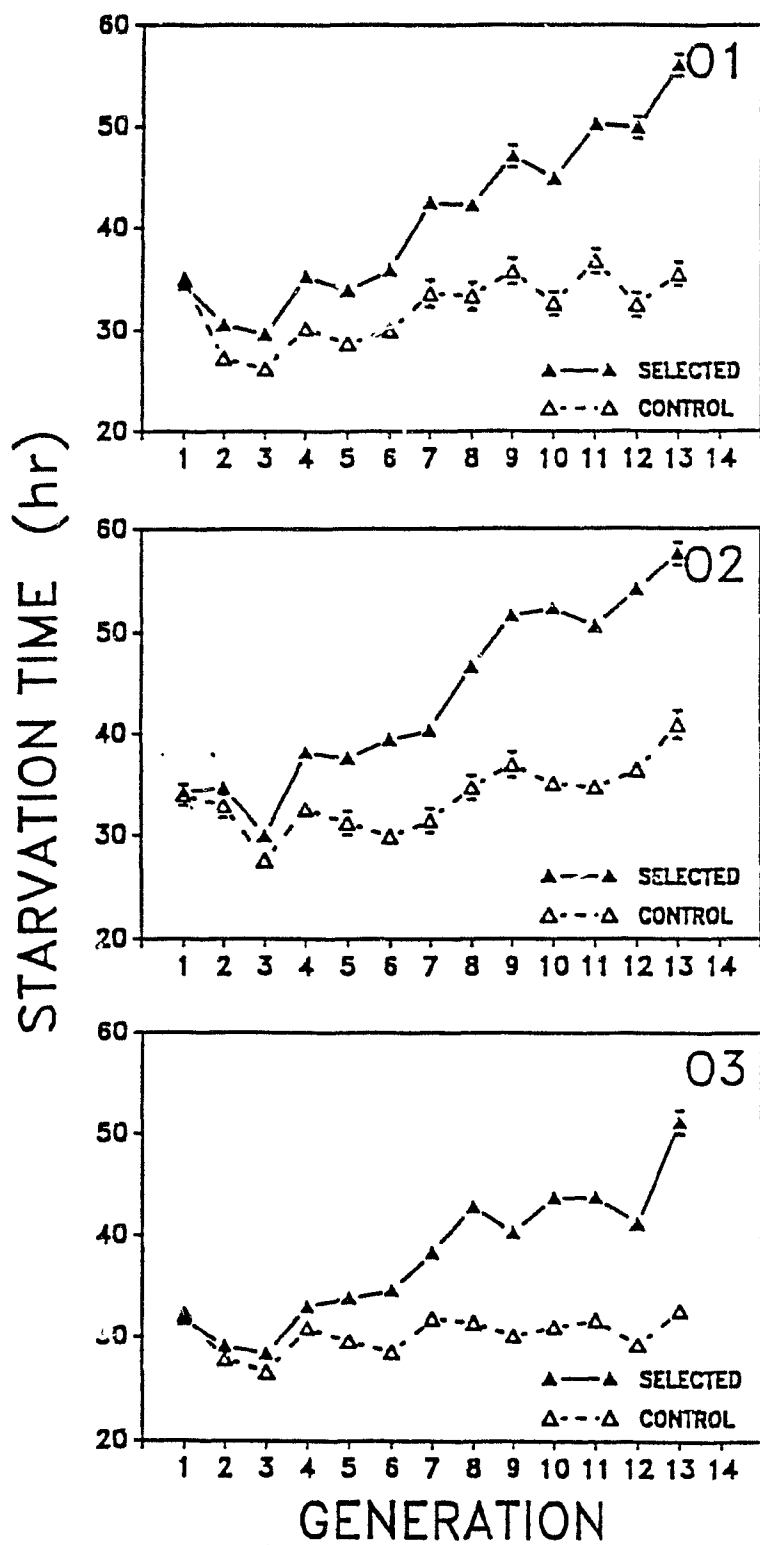


Figure 7.6. Direct response of the three O populations to selection for increased starvation time.

increased starvation time in the three O replicates. As before, solid triangles and empty triangles signify the selected and control groups. The 95% confidence intervals are shown around the mean mid-parent starvation time for generations 1 through 13. Some points appear not to have the 95% confidence intervals. This is caused by the interval being smaller than could be graphed. As with the B lines, the selected and control lines diverge in the second generation. After 13 generations there was an increase of 68% in the mid parent starvation time in the selected lines. An ANOVA of the last 6 generations (8 through 13) shows significant differences between the selected and control groups, ( $F = 584.93^{**}$  for Female Starvation,  $F = 679.88^{**}$  for Male Starvation,  $F = 841.41$  for Mid-Parent Starvation (Table F.4)).

Figure 7.7 plots the cumulative response on the cumulative selection differential for starvation in the three O lines. The realized heritabilities, the slopes of the regression, are presented in Table 7.4. The mean and standard error of the heritability in the three lines is  $0.172 \pm 0.012$ .

The indirect response of 24-hour fecundity to selection on mid-parent starvation time is shown in Figure 7.8. These indirect responses are significant ( $F = 36.84^{**}$  for Fecundity,  $F = 39.12^{**}$  for Conditional Fecundity (Table F7)) with the selected groups having lower fecundities than their

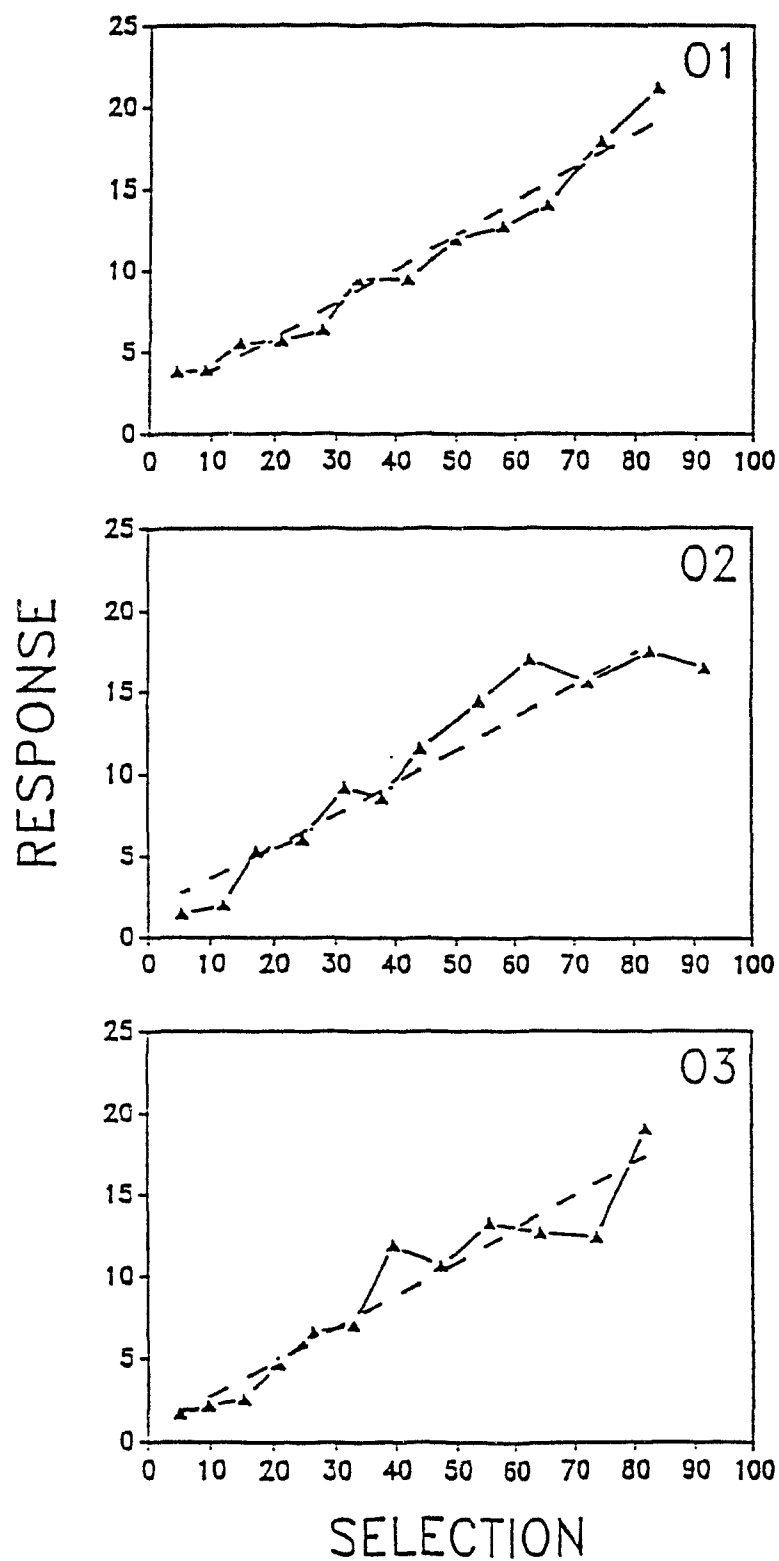


Figure 7.7. Regression of selection response on the cumulative selection differential for selection on starvation time in the three  $\odot$  populations.

Table 7.4 : Realized Heritabilities for Selection on  
Starvation Time in the Three O Populations

Replicate	Slope $\pm$ SEM		
	Female	Male	Mid-Parent
1	0.293 $\pm$ 0.016	0.144 $\pm$ 0.013	0.209 $\pm$ 0.013
2	0.211 $\pm$ 0.019	0.188 $\pm$ 0.026	0.196 $\pm$ 0.020
3	0.251 $\pm$ 0.020	0.174 $\pm$ 0.024	0.204 $\pm$ 0.020
Mean	0.252 $\pm$ 0.024	0.169 $\pm$ 0.013	0.203 $\pm$ 0.004

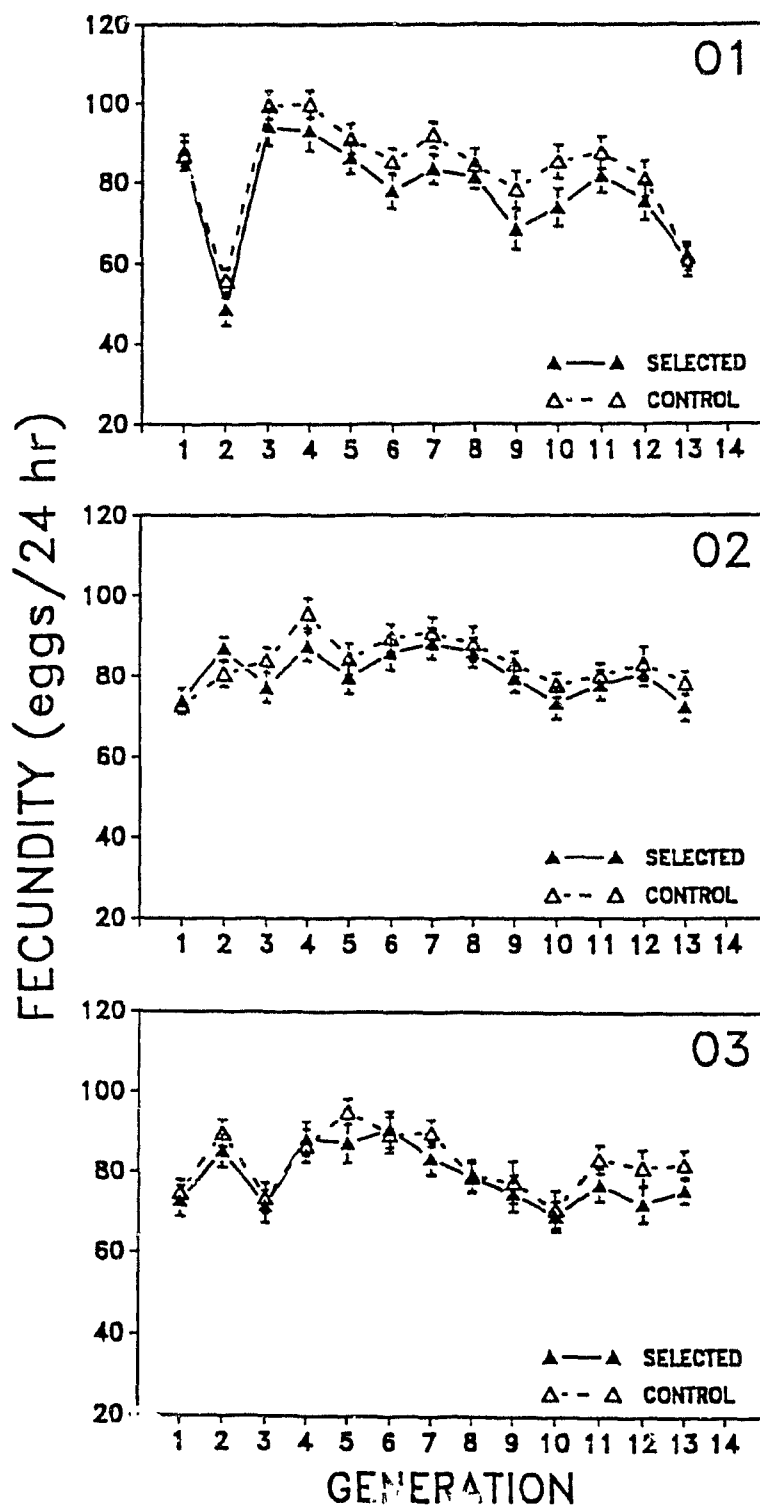


Figure 7.8. Indirect response of early fecundity to selection for mid-parent starvation time in the three O populations.

paired controls.

b) Without controls: generations 1->25

After 13 generations of selection the paired control groups were no longer used. The direct responses to selection for increased starvation time are shown in Figure 7.9. Again, 95% confidence intervals are plotted about the mean but in some cases they are too small to show.

### 7.5 Discussion

These selection experiments were an attempt to fix the extreme alleles of high fecundity/low starvation resistance in the B populations and low fecundity/high starvation resistance in the O populations. Heritability experiments before selection showed that there was abundant genetic variance for starvation resistance in both the B and the O populations. The strong selection applied resulted in a 58% increase in starvation time in the O lines and a 15% increase in fecundity in the B lines. However, even with this level of response, over 25 generations, the additive genetic variance did not seem to decrease, as shown by the heritability estimates after selection. The lines, therefore, do not seem to have been pushed towards fixation. However, these lines are considerably farther apart after selection, offering some hope of clearer results from population crosses.

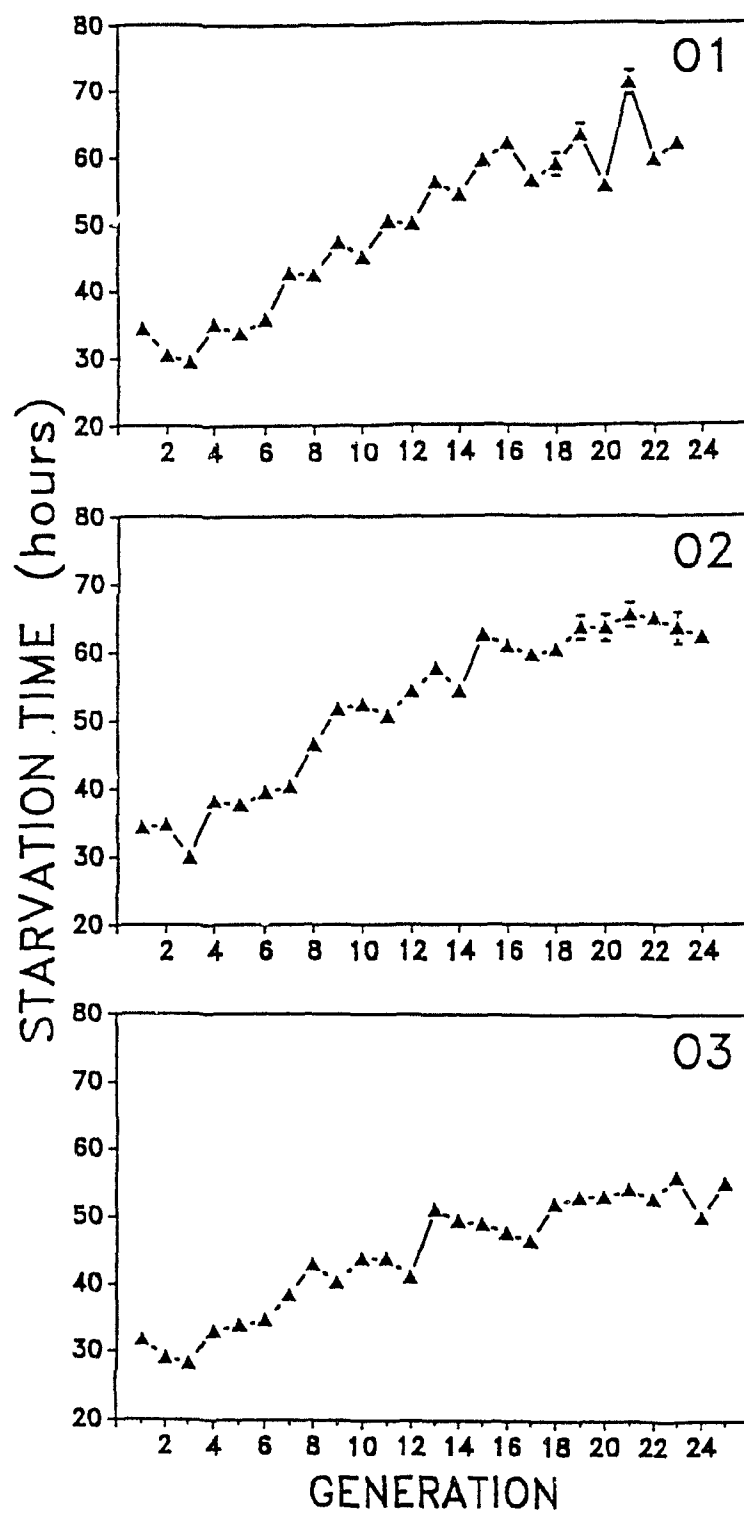


Figure 7.9. Direct response of the three O populations to selection over 25 generations for increased starvation time.

There was a large discrepancy between the heritability estimates arrived at using the half-sib method and using the realized heritability method. In general this is probably due to the difficulty in getting reliable estimates with the half-sib analysis. There are many cases in the literature where theoretically impossible heritabilities are estimated, that is, heritabilities which are negative or which are greater than one.

Realized heritability estimates do not necessarily provide estimates of the heritability either. As noted by Falconer (1981), systematic changes due to environmental trends, inbreeding depression, or random drift will confound the response to selection. However, these were probably not important in the selection experiments due to the use of comparisons with control lines, which would account for environmental trends and inbreeding depression, and also due to the three-fold replication of the selection, which would allow detection of random drift.

The lack of fixation in the presence of such a strong response to selection could be due to many factors:

- 1) The appearance of mutations favored under artificial selection.

- 2) The decrease in linkage disequilibrium resulting from renewal recombination between alleles (unlikely since it was shown in Chapter 4 that linkage disequilibrium was not detectable).



3) The effects of confounding environmental factors (unlikely since the experiments were well controlled with respect to environmental variables).

4) The opposing action of natural and artificial selection.

5) The presence of many genes involved in the determination of the characters.

The simplest explanation is of course the fifth, the presence of many genes. Selection limits are less readily obtained the greater the number of loci involved (Falconer 1981). Further, in combination with the fourth factor, if several genes are implicated in the control of survivorship and fertility, differential responses of these loci to the actions of artificial and natural selection may be generated, resulting in the maintenance of genetic variability.

PART IV

ANALYSIS OF SELECTED (F and S) POPULATIONS

## CHAPTER 8

### Diallel Analysis of F and S Populations

## 8.1 Introduction

The same principles of diallel analysis as those described in Chapter 3 were practiced. As before, there are three separate questions which are addressed in the present diallel analysis. Firstly, to what extent are the lines within a given stock-type differentiated from each other? Secondly, to what extent do maternal effects outweigh paternal effects, within stock-types? Thirdly, is there any evidence for heterosis, or, conversely, inbreeding depression, in crosses between lines within stock-types?

## 8.2 Experimental Procedure

Again, the experiments were coded: D in the first position indicating a diallel design; F or S in the second position indicating the nature of the populations analyzed; and the third position numeral indicating the particular experiment. Table 8.1 and Table 8.2 give the experiment codes, the characters assayed, the number of populations assayed, and the number of individuals assayed. In the DF1 and DS1 experiments, reciprocal crosses were not followed. The DF2 and DS2 experiments were performed in order to remedy this deficiency. The DF3 experiment was performed because of a lack of numbers in some of the cells of experiment DF2.

Table 8.1 : F Diallel Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>DF1</u>				
	Fecundity	3+3 = 6	60.0	360
	Conditional Fecund.	3+3 = 6	59.5	357
<u>DF2</u>				
	Fecundity	3x3 = 9	30.9	278
	Conditional Fecund.	3x3 = 9	29.7	267
	Female Starvation	3x3 = 9	34.0	306
	Male Starvation	3x3 = 9	34.0	306
<u>DF3</u>				
	Fecundity	3x3 = 9	51.9	467
	Conditional Fecund.	3x3 = 9	50.7	456
	Female Starvation	3x3 = 9	52.4	472
	Male Starvation	3x3 = 9	52.3	471
Total		84		3,740

Table 8.2 : S Diallel Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>DS1</u>				
	Fecundity	3+3 = 6	59.7	358
	Conditional Fecund.	3+3 = 6	54.7	348
<u>DS2</u>				
	Fecundity	3x3 = 9	46.1	415
	Conditional Fecund.	3x3 = 9	43.9	395
	Female Starvation	3x3 = 9	47.8	430
	Male Starvation	3x3 = 9	47.6	428
Total		48		2,374

### 8.3 Results and Discussion

The summary statistics for each character in each experiment are given in Appendix G, Tables G1 through G16. The order of these tables follows the order of the experiments and the characters within the experiments as presented in Tables 8.1 and 8.2. The corresponding detailed analysis for each character in each experiment is given in Appendix H, Tables H1 through H16. As before, the results will be addressed with respect to the three questions stated above.

The results of the analysis of F and S lines for line effects are presented in Table 8.3. There is little evidence for consistent between-line heterogeneity. Table 8.4 contains the analysis of maternal versus paternal contribution. In none of the experiments was there a significant result. As to the heterosis question, Table 8.5 shows that in only one experiment (DF2) and for only one character (female starvation) was there any evidence of inbreeding depression. The other 15 assays do not show a significant result. [The missing columns in Tables 8.4 and 8.5 arise from the lack of reciprocal crosses in DF1 and DF2, as discussed in the Experimental Procedure section.] As in the diallel analysis of B and O stocks, in Chapter 3, these F and S diallels exhibit simple additive inheritance.

Table 8.3 : F and S Diallel Line Differentiation

<u>Character</u> Experiment	Line of Mother		ANOVA Line of Father		Combined Effect	
	F	SIG.	F	SIG.	F	SIG.
<u>Fecundity</u>						
DF2	0.34	0.730	0.90	0.477	0.58	0.694
DF3	1.60	0.390	1.75	0.284	2.00	0.259
DS2	1.32	0.364	0.71	0.545	1.04	0.484
<u>Conditional Fecundity</u>						
DF2	1.15	0.403	2.00	0.445	1.24	0.420
DF3	1.63	0.303	1.93	0.258	2.11	0.244
DS2	0.97	0.454	1.25	0.380	0.94	0.523
<u>Female Starvation</u>						
DF2	2.58	0.191	0.20	0.830	1.47	0.360
DF3	0.41	0.691	0.03	0.966	0.21	0.922
DS2	0.92	0.468	0.43	0.675	0.82	0.573
<u>Male Starvation</u>						
DF2	0.26	0.784	0.14	0.870	0.15	0.953
DF3	7.37	0.046*	4.77	0.087	5.83	0.058
DS2	1.35	0.356	0.17	0.847	0.82	0.573



Table 8.4 : F and S Parallel Maternal Effects

<u>Character</u> Experiment	ANOVA			
	Method 1		Method 2	
	F	SIG.	F	SIG.
<u>Fecundity</u>				
DF1	7.15	0.123	---	---
DF2	0.38	0.724	0.11	0.898
DF3	0.91	0.523	1.55	0.393
DS1	0.79	0.557	---	---
DS2	1.86	0.350	0.06	0.942
<u>Conditional Fecundity</u>				
DF1	2.95	0.253	---	---
DF2	1.15	0.465	0.33	0.751
DF3	0.85	0.542	1.38	0.420
DS1	1.18	0.460	---	---
DS2	0.78	0.563	0.03	0.976
<u>Female Starvation</u>				
DF2	13.21	0.070	1.04	0.489
DF3	11.79	0.078	5.56	0.153
DS2	2.13	0.320	0.86	0.538
<u>Male Starvation</u>				
DF2	1.80	0.357	0.42	0.703
DF3	1.50	0.393	1.30	0.435
DS2	7.78	0.114	2.08	0.325

Table 8.5 : F and S Diallel Heterosis Effects

<u>Character</u> Experiment	T-TEST				ANOVA	
	Separate Var.		Pooled Var.		F	SIG.
	T	SIG.	T	SIG.		
<u>Fecundity</u>						
DF1	---	---	0.62	0.567	0.39	0.567
DF2	0.30	0.775	0.27	0.795	0.06	0.809
DF3	0.31	0.784	0.37	0.721	0.14	0.723
DS1	---	---	2.51	0.066	6.27	0.066
DS2	1.65	0.198	1.68	0.138	3.08	0.123
<u>Conditional Fecundity</u>						
DF1	---	---	0.17	0.873	0.03	0.872
DF2	0.04	0.975	0.04	0.970	0.001	0.978
DF3	0.39	0.737	0.45	0.666	0.21	0.663
DS1	---	---	2.51	0.066	6.36	0.065
DS2	1.71	0.138	1.31	0.233	2.24	0.178
<u>Female Starvation</u>						
DF2	0.72	0.524	0.73	0.487	0.51	0.500
DF3	3.32	0.016*	2.62	0.034*	9.58	0.017*
DS2	0.59	0.589	0.58	0.581	0.36	0.566
<u>Male Starvation</u>						
DF2	1.70	0.165	1.63	0.148	2.94	0.130
DF3	0.90	0.401	0.71	0.502	0.68	0.436
DS2	0.13	0.909	0.13	0.899	0.12	0.896

## CHAPTER 9

### Transmission Patterns of F and S Populations

## 9.1 Introduction

These F and S transmission pattern experiments follow the same protocol as the B and O transmission experiments. The F and S stocks were crossed between lines,  $F_1$  with  $S_1$ ,  $F_2$  with  $S_2$ , etc. The parental populations as well as both the reciprocal cross populations of the  $F_1$  hybrids were then assayed for six characters (fecundity, conditional fecundity, female starvation resistance, male starvation resistance, female longevity, and male longevity). As before, three features of the transmission data are of importance: (i) documentation of the parental line (F & S) differences; (ii) maternal effects, as measured by differences between two reciprocal cross means; and (iii) average dominance, as measured by the deviation of the crosses from the mid-parent value.

## 9.2 Experimental Procedure

The series of experiments on transmission patterns in the F and S stocks is outlined in Table 9.1. These experiments are coded with "FS" in the first two positions, indicating crosses of F and S populations. The numerals then refer to the sequence of experiments. In experiments FS1 and FS4, larvae were reared at a density of 90/vial. In experiments FS2, FS3, and FS5, larvae were reared at 30/vial. Experiments FS2 and FS3 were parts of repeated

Table 9.1 : F and S Crossing Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>FS1</u>				
	Fecundity	4x3 = 12	66.8	801
	Conditional Fecund.	4x3 = 12	65.3	783
	Female Starvation	4x3 = 12	71.5	858
	Male Starvation	4x3 = 12	71.9	863
	Female Longevity	3x3 = 9	98.0	882
	Male Longevity	3x3 = 9	97.6	878
<u>FS2</u>				
	Fecundity	4x3 = 12	68.3	820
	Conditional Fecund.	4x3 = 12	66.9	803
	Female Starvation	4x3 = 12	70.4	845
	Male Starvation	4x3 = 12	70.5	846
<u>FS3</u>				
	Fecundity	4x3 = 12	70.2	842
	Conditional Fecund.	4x3 = 12	68.5	822
	Female Starvation	4x3 = 12	70.2	842
	Male Starvation	4x3 = 12	70.1	841
	Female Longevity	3x3 = 9	98.4	886
	Male Longevity	3x3 = 9	98.3	885

Table 9.1 - continued : F and S Crossing Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>FS4</u>				
	Fecundity	4x3 = 12	69.3	832
	Conditional Fecund.	4x3 = 12	68.3	820
	Female Starvation	4x3 = 12	70.9	851
	Male Starvation	4x3 = 12	70.9	851
	Female Longevity	4x3 = 12	58.3	699
	Male Longevity	4x3 = 12	58.0	696
<u>FS5</u>				
	Fecundity	4x1 = 4	59.0	236
	Conditional Fecund.	4x1 = 4	57.8	231
	Female Starvation	4x1 = 4	60.0	240
	Male Starvation	4x1 = 4	60.0	240
	Female Longevity	4x1 = 4	60.0	240
	Male Longevity	4x1 = 4	60.0	240
Total		276		19,373

gene number estimation experiments. In experiment FS5, synthetic crosses was performed involving all F or all S lines, to create multiple-hybrid F and S populations. These two populations were then crossed to test for their transmission patterns.

### 9.3 Results and Discussion

The summary statistics for each character in each experiment are given in Appendix G, Tables G1 through G34, and the corresponding detailed analysis for each character in each experiment is given in Appendix H, Tables H1 through H34.

With the more differentiated F and S lines, there is the prospect of greater clarity in the transmission pattern results. Table 9.2 presents the summary of the analysis of the FF - SS difference data. Most of the tests for significant differentiation of F and S populations yield statistical significance, particularly those for fecundity. Most of the tests for maternal effects, Table 9.3, and average dominance, Table 9.4, give non-significant results. Taken together with the diallel results, the F and S lines also provide strong support for the existence of roughly additive inheritance, without maternal effects or dominance effects, averaged over all loci.

Table 9.2 : F and S Differences

Character	Mean $\pm$ S.E.		T-TEST		ANOVA
	F	S	Indep. T	Paired T	F
<u>Fecundity</u> (eggs / 24 hours)					
FS1	77.0 $\pm$ 2.7	54.5 $\pm$ 1.8	6.95**	17.66**	310.58**
FS2	92.6 $\pm$ 5.7	72.6 $\pm$ 5.3	2.55	18.10**	332.69**
FS3	106.7 $\pm$ 5.1	80.6 $\pm$ 1.5	4.88**	6.75*	50.06*
FS4	88.4 $\pm$ 4.3	72.1 $\pm$ 2.7	3.18*	9.55*	90.66*
FS5	122.3 $\pm$ 3.3	100.0 $\pm$ 2.7	--	--	27.38**
<u>Conditional Fecundity</u> (eggs / 24 hours)					
FS1	78.1 $\pm$ 2.2	57.2 $\pm$ 1.8	7.29**	32.84**	1070.32**
FS2	96.1 $\pm$ 4.1	73.3 $\pm$ 5.0	3.52*	10.54**	116.40**
FS3	109.9 $\pm$ 2.6	83.9 $\pm$ 1.9	7.99**	15.27**	259.25**
FS4	90.2 $\pm$ 4.5	72.9 $\pm$ 3.1	3.19*	12.49**	150.59**
FS5	125.5 $\pm$ 2.4	102.5 $\pm$ 2.1	--	--	51.05**
<u>Female Starvation</u> (hours)					
FS1	35.3 $\pm$ 2.0	67.4 $\pm$ 7.0	4.42*	3.60	13.02
FS2	32.0 $\pm$ 8.7	39.5 $\pm$ 3.9	0.79	0.66	0.42
FS3	25.5 $\pm$ 1.3	47.3 $\pm$ 6.2	3.47*	3.62	11.55
FS4	38.7 $\pm$ 3.9	65.7 $\pm$ 4.4	3.78*	6.50*	45.41*
FS5	31.7 $\pm$ 0.9	51.2 $\pm$ 1.6	--	--	114.39**



Table 9.2 continued : F and S Differences

Character		Mean $\pm$ S.E.		T-TEST		ANOVA
Expt.		F	S	Indep. T	Paired T	F
<u>Male Starvation (hours)</u>						
FS1		24.2 $\pm$ 1.7	51.7 $\pm$ 5.4	4.89**	4.71*	22.15*
FS2		23.9 $\pm$ 7.3	32.8 $\pm$ 4.5	1.03	0.78	0.59
FS3		18.5 $\pm$ 0.8	39.3 $\pm$ 5.4	3.82*	3.90	13.22
FS4		25.0 $\pm$ 2.2	48.7 $\pm$ 4.4	10.09**	4.88*	106.33**
FS5		24.5 $\pm$ 0.7	40.4 $\pm$ 1.4	--	--	108.68**
<u>Female Longevity (days)</u>						
FS1		35.9 $\pm$ 1.1	53.8 $\pm$ 4.9	3.52*	3.10	9.64
FS3		32.1 $\pm$ 3.3	49.6 $\pm$ 2.7	4.09*	3.78	14.28
FS4		33.9 $\pm$ 0.9	50.9 $\pm$ 1.7	8.49**	11.15**	123.46**
FS5		36.3 $\pm$ 1.4	46.2 $\pm$ 1.9	--	--	17.98**
<u>Male Longevity (days)</u>						
FS1		34.4 $\pm$ 2.2	53.9 $\pm$ 2.1	6.36*	8.68**	74.91*
FS3		31.6 $\pm$ 1.3	47.5 $\pm$ 0.4	15.08**	23.59**	556.63**
FS4		32.2 $\pm$ 2.7	52.9 $\pm$ 1.1	7.08**	5.76*	33.33*
FS5		31.8 $\pm$ 1.3	49.0 $\pm$ 1.9	--	--	55.39**

Table 9.3 : F and S Maternal Effects

Character	Mean $\pm$ S.E.		T-TEST		ANOVA
	FS	SF	Indep. T	Paired T	F
<u>Fecundity (eggs / 24 hours)</u>					
FS1	68.4 $\pm$ 4.5	65.5 $\pm$ 5.1	0.43	2.39	0.14
FS2	85.2 $\pm$ 6.6	88.2 $\pm$ 3.0	0.41	0.69	0.49
FS3	101.2 $\pm$ 3.7	101.1 $\pm$ 4.5	0.04	0.09	0.01
FS4	76.2 $\pm$ 6.8	76.7 $\pm$ 3.4	0.08	0.17	0.03
FS5	116.6 $\pm$ 4.4	114.0 $\pm$ 3.9	--	--	0.20
<u>Conditional Fecundity (eggs / 24 hours)</u>					
FS1	68.4 $\pm$ 4.5	66.0 $\pm$ 5.0	0.37	3.04	9.23
FS2	87.0 $\pm$ 6.0	89.6 $\pm$ 3.5	0.37	0.90	0.49
FS3	103.0 $\pm$ 3.8	101.0 $\pm$ 4.5	0.34	0.93	0.88
FS4	77.3 $\pm$ 6.1	77.4 $\pm$ 4.0	0.01	0.04	0.00
FS5	119.5 $\pm$ 3.4	114.0 $\pm$ 3.9	--	--	1.15
<u>Female Starvation (hours)</u>					
FS1	47.7 $\pm$ 3.5	46.9 $\pm$ 1.6	0.20	0.36	0.13
FS2	30.6 $\pm$ 2.0	31.3 $\pm$ 3.2	0.17	0.55	0.31
FS3	34.0 $\pm$ 4.8	35.6 $\pm$ 4.2	0.81	1.51	2.21
FS4	51.4 $\pm$ 2.5	55.4 $\pm$ 4.7	0.75	1.75	3.08
FS5	35.4 $\pm$ 1.3	34.1 $\pm$ 1.4	--	--	0.48

Table 9.3 continued : F and S Maternal Effects

Character	Mean $\pm$ S.E.		T-TEST		ANOVA
	FS	SF	Indep. T	Paired T	F
<u>Male Starvation (hours)</u>					
FS1	36.1 $\pm$ 2.5	37.0 $\pm$ 1.9	0.52	2.23	4.99
FS2	20.7 $\pm$ 2.2	26.2 $\pm$ 2.8	1.65	5.61*	30.39*
FS3	24.5 $\pm$ 2.9	30.0 $\pm$ 2.7	1.40	6.09*	38.29*
FS4	34.2 $\pm$ 3.2	39.2 $\pm$ 4.6	0.89	2.10	4.35
FS5	33.6 $\pm$ 1.9	28.7 $\pm$ 1.2	--	--	4.75
<u>Female Longevity (days)</u>					
FS4	44.4 $\pm$ 0.9	42.3 $\pm$ 2.1	0.92	1.75	3.04
FS5	42.0 $\pm$ 1.5	41.5 $\pm$ 2.3	--	--	0.09
<u>Male Longevity (days)</u>					
FS4	41.2 $\pm$ 2.9	42.7 $\pm$ 4.1	0.27	1.23	1.49
FS5	38.5 $\pm$ 2.0	40.9 $\pm$ 1.9	--	--	0.74

Table 9.4 : F and S Average Dominance Effects

<u>Character</u>	<u>Mean <math>\pm</math> S.E.</u>		<u>T-TEST</u>		<u>ANOVA</u>
	<u>Parentals</u>	<u>Crosses</u>	<u>Indep. T</u>	<u>Paired T</u>	<u>F</u>
<u>Fecundity (eggs / 24 hours)</u>					
FS1	65.7 $\pm$ 2.2	66.9 $\pm$ 4.7	0.23	0.47	0.22
FS2	82.2 $\pm$ 5.8	86.7 $\pm$ 4.7	0.60	1.73	2.93
FS3	91.6 $\pm$ 4.0	101.1 $\pm$ 4.0	1.69	2.08	4.49
FS4	80.7 $\pm$ 3.1	76.5 $\pm$ 5.0	0.73	0.10	4.39
FS5	111.0 $\pm$ 2.3	115.3 $\pm$ 2.9	--	--	1.24
<u>Conditional Fecundity (eggs / 24 hours)</u>					
FS1	67.8 $\pm$ 2.0	67.2 $\pm$ 4.7	0.13	0.25	0.06
FS2	84.0 $\pm$ 4.8	88.3 $\pm$ 4.7	0.63	1.91	3.67
FS3	94.7 $\pm$ 3.4	102.0 $\pm$ 4.0	1.38	2.14	4.71
FS4	82.0 $\pm$ 3.3	77.3 $\pm$ 5.0	0.78	2.75	7.54
FS5	113.9 $\pm$ 1.9	116.7 $\pm$ 2.6	--	--	0.81
<u>Female Starvation (hours)</u>					
FS1	51.6 $\pm$ 2.8	47.3 $\pm$ 2.5	1.13	1.37	1.87
FS2	36.3 $\pm$ 3.7	30.9 $\pm$ 2.6	1.19	1.56	2.37
FS3	38.3 $\pm$ 4.2	34.8 $\pm$ 4.5	0.58	1.37	2.00
FS4	51.3 $\pm$ 4.4	53.4 $\pm$ 3.6	0.38	0.92	0.86
FS5	41.4 $\pm$ 1.2	34.8 $\pm$ 1.0	--	--	13.43**

Table 9.4 continued : F and S Average Dominance Effects

<u>Character</u>		Mean $\pm$ S.E.		T-TEST		ANOVA
Expt.		Parentals	Crosses	Indep. T	Paired T	F
<u>Male Starvation (hours)</u>						
FS1		37.9 $\pm$ 2.7	36.9 $\pm$ 2.2	0.30	1.51	2.27
FS2		29.0 $\pm$ 2.2	23.5 $\pm$ 2.4	1.68	1.77	3.06
FS3		30.7 $\pm$ 3.7	27.2 $\pm$ 2.8	0.76	1.71	2.94
FS4		35.9 $\pm$ 3.1	36.8 $\pm$ 3.7	0.18	0.80	0.63
FS5		32.5 $\pm$ 1.0	31.1 $\pm$ 1.1	--	--	0.68
<u>Female Longevity (days)</u>						
FS1		45.0 $\pm$ 2.2	45.3 $\pm$ 4.1	0.08	0.16	0.03
FS3		40.7 $\pm$ 2.0	47.6 $\pm$ 2.9	1.93	3.85	14.83
FS4		42.5 $\pm$ 1.2	43.3 $\pm$ 1.5	0.44	3.08	9.43
FS5		41.2 $\pm$ 1.2	42.0 $\pm$ 1.5	--	--	0.70
<u>Male Longevity (days)</u>						
FS1		44.2 $\pm$ 1.9	43.5 $\pm$ 1.5	0.32	1.57	2.46
FS3		36.9 $\pm$ 0.9	42.8 $\pm$ 2.0	2.21	4.29	18.29
FS4		42.5 $\pm$ 1.0	41.9 $\pm$ 3.5	0.15	0.20	0.04
FS5		40.3 $\pm$ 1.3	39.7 $\pm$ 1.4	--	--	0.77

## CHAPTER 10

### Gene Number Analysis of F and S Populations

## 10.1 Introduction

Experiments were performed to estimate the number of "effective factors" (Lande 1981) involved in postponed aging. Effective factors are loci of "equivalent effect" that are responsible for the differentiation of a quantitative character between two populations.

## 10.2 Experimental Procedure

The basic estimators and design principles described in Chapter 5 were used again. As before, inverse effective factor estimates were used for hypothesis testing, because they do not have the problem of misleading biases when the  $F_2$  variance is less than the  $F_1$  variance. Table 10.1 outlines the experiments that were performed to estimate the number of effective factors, or  $n_e$ . These experiments are coded as GFSi, i giving the number of the experiment. In experiments GFS1 and GFS3, the larvae were reared at a density of 90/vial. In experiment GFS2, the larvae were reared at a density of 30/vial.

## 10.3 Results and Discussion

The summary statistics for each character in each experiment are given in Appendix K, Tables K1 through K18, following the order of Table 10.1.

Table 10.1 : F and S Gene Number Experiments

Experiment	Character Assayed	Populations Assayed per Character	Mean Number Assayed per Population	Total Number Assayed
<u>GFS1</u>				
	Fecundity	4x3 = 12	88.9	1,067
	Conditional Fecund.	4x3 = 12	87.3	1,048
	Female Starvation	4x3 = 12	95.5	1,146
	Male Starvation	4x3 = 12	95.9	1,151
	Female Longevity	4x3 = 12	98.5	1,182
	Male Longevity	4x3 = 12	98.0	1,176
<u>GFS2</u>				
	Fecundity	4x3 = 12	105.3	1,264
	Conditional Fecund.	4x3 = 12	102.4	1,229
	Female Starvation	4x3 = 12	108.8	1,305
	Male Starvation	4x3 = 12	108.6	1,303
	Female Longevity	4x3 = 12	98.1	1,177
	Male Longevity	4x3 = 12	97.4	1,169
<u>GFS3</u>				
	Fecundity	4x3 = 12	115.5	1,386
	Conditional Fecund.	4x3 = 12	113.9	1,367
	Female Starvation	4x3 = 12	117.8	1,414
	Male Starvation	4x3 = 12	117.9	1,415
	Female Longevity	4x3 = 12	97.3	1,167
	Male Longevity	4x3 = 12	96.7	1,160
Total		216		22,125



Figure 10.1 is a set of frequency histograms of fecundity for one of the replicates,  $F_2 \times S_2$ , of experiment GFS2. Shown are, from top to bottom, the  $F_2$  parental histogram, the  $S_2$  parental histogram, the  $F_1$  hybrid histogram, and the  $F_2$  hybrid histogram. It is clear that there is not a trimodal distribution in the histogram of the  $F_2$  hybrid, which is evidence against the existence of only one gene being responsible for the differentiation of the parental populations. Figures 10.2 through 10.5 are similar sets of histograms for female starvation time, male starvation time, female longevity, and male longevity, respectively. All of these are from the same replicate,  $F_2 \times S_2$ , of experiment GFS2 and are intended to be representative of the patterns found in all of the crosses. There are a total of 54 of these sets of histograms in the present experiments. In none of the  $F_2$  histograms is there a trimodal distribution, again evidence against the existence of only one gene differentiating the parental populations. Further, the distributions of the  $F_2$ 's does not appear to be very different from the distributions of their paired  $F_1$ 's; evidence for a large number of genes being involved in the differentiation of the parental populations. The distributions of the parental populations, while not being completely discrete, are quite well separated. These  $F \times S$  histograms are, therefore, stronger evidence for the existence of many genes affecting

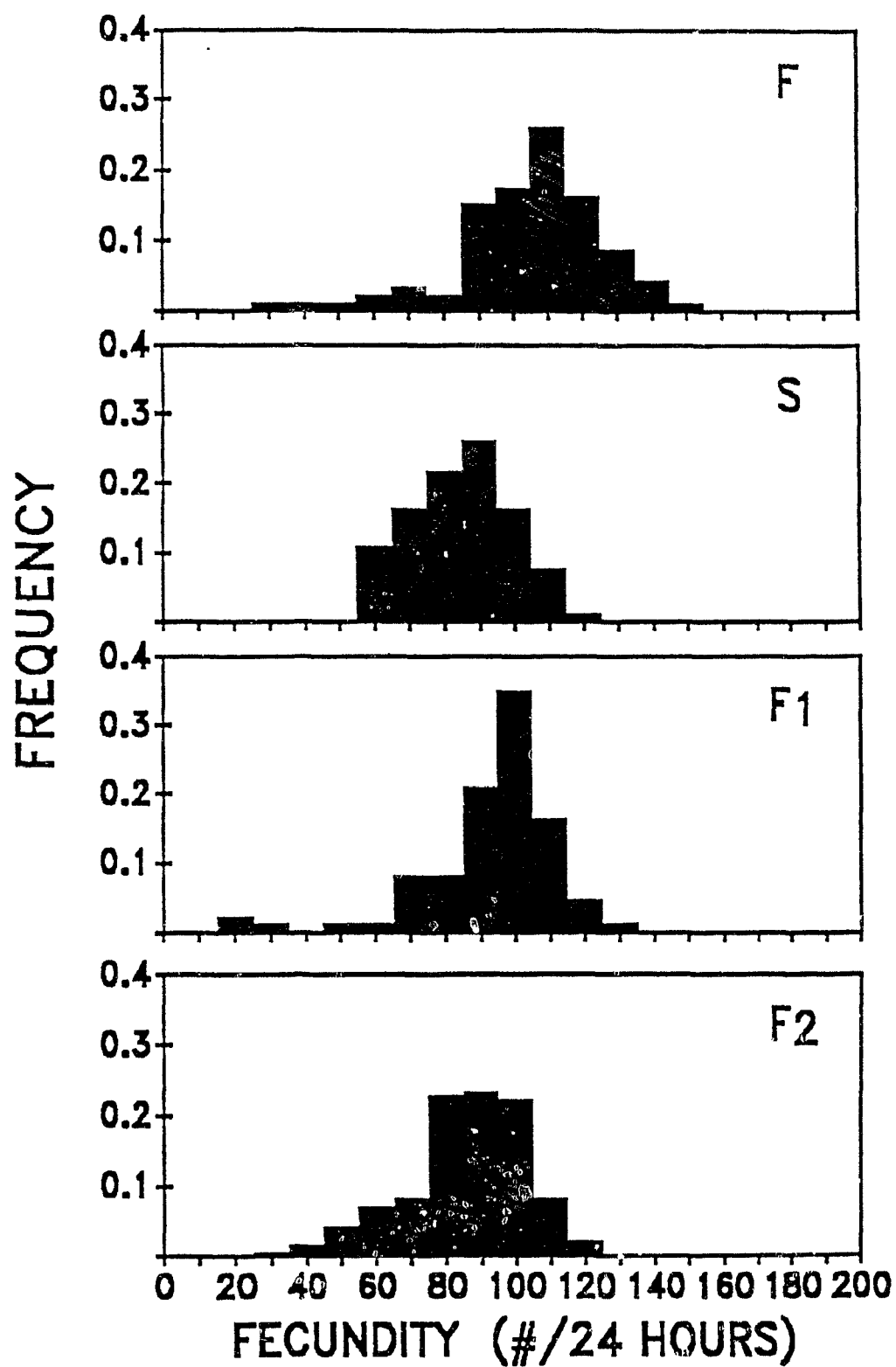


Figure 10.1. Frequency histograms of fecundity in replicate  $F_2 \times S_2$  of experiment GFS2.

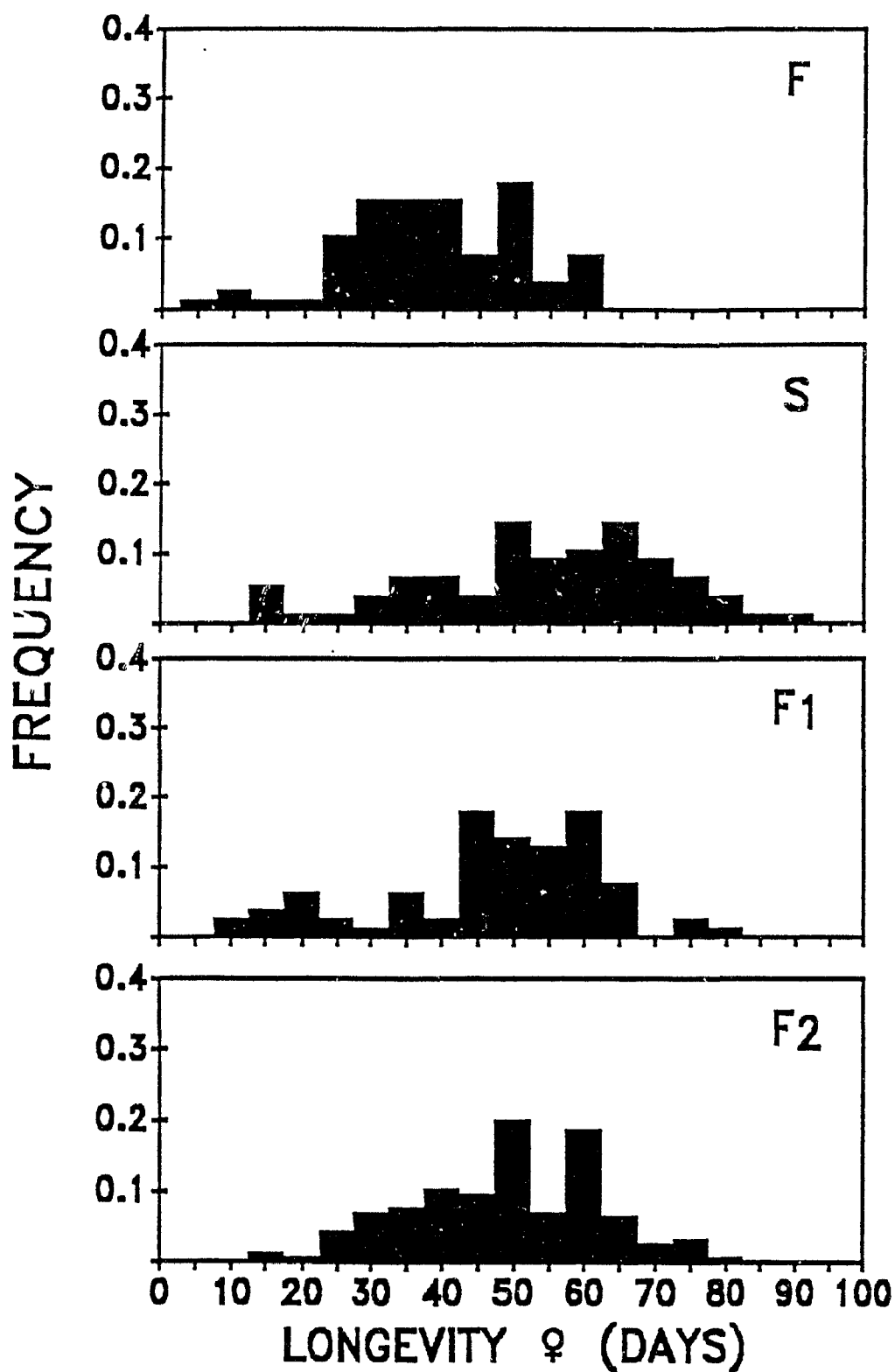


Figure 10.4. Frequency histograms of female longevity in replicate  $F_2 \times S_2$  of experiment GFS2.

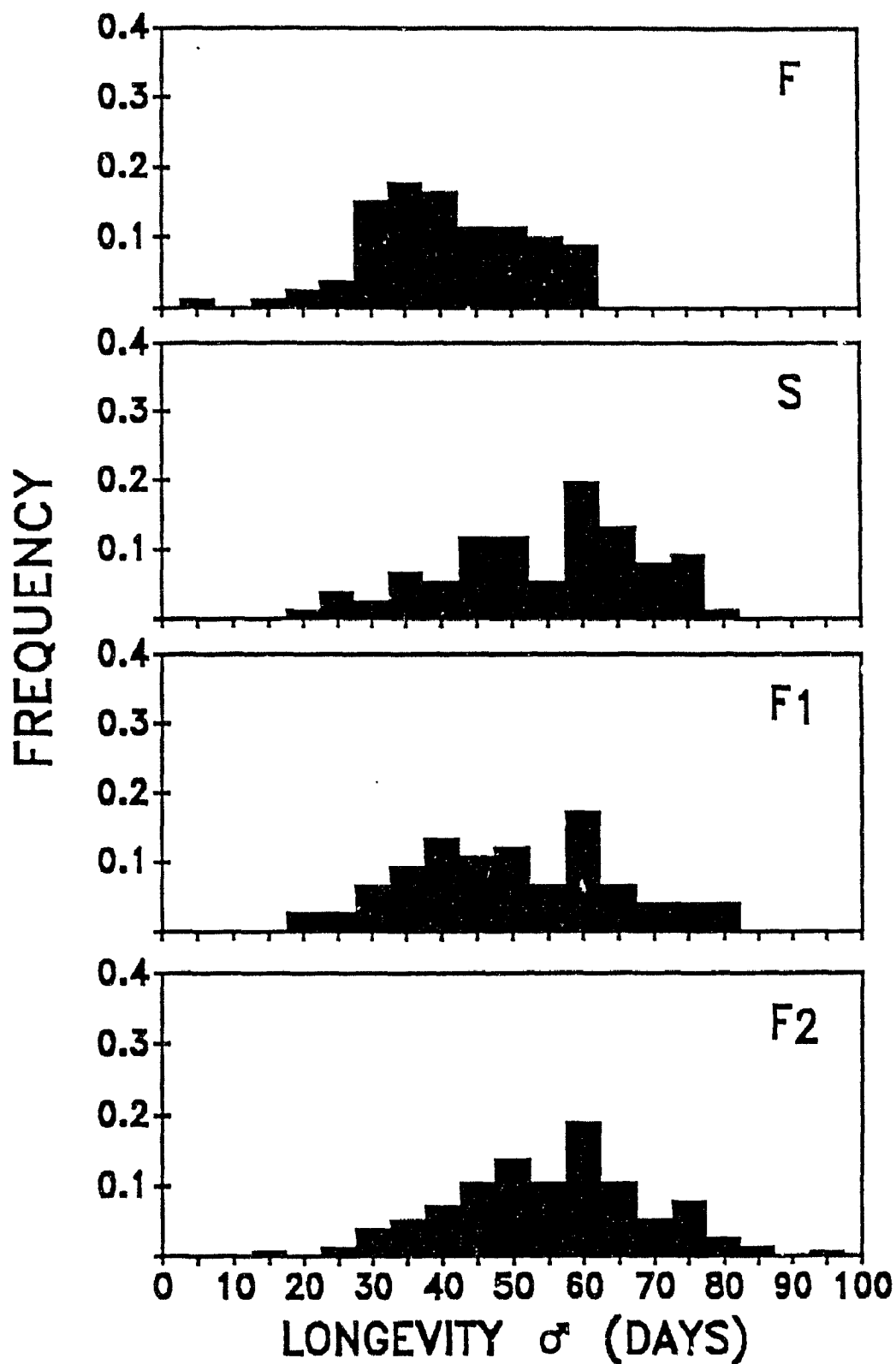


Figure 10.5. Frequency histograms of male longevity in replicate  $F_2 \times S_2$  of experiment GFS2.

senescence than were the B x O crosses of Chapter 5.

Table 10.2 gives the effective factor estimates from crosses of F and S lines. It is apparent that many of the gene number estimates are now negative or take on positive values greater than one, unlike the data from the B and O populations. Table 10.3 gives the inverse effective factor estimates from crosses of F and S lines. These data are more appropriate for the analysis, for the reasons discussed in Chapter 5, particularly because negative  $n_e$  estimates indicate large numbers of loci, yet bias averages of  $n_e$  estimates downward. In only three cases, fecundity in experiment GFS1, female starvation in experiment GFS2, and female starvation in experiment GFS3, was there statistical evidence for fewer than an arbitrarily large number of loci involved in the differentiation of F and S stocks. In these cases, the effective factor estimates indicate the involvement of at least two loci. [It should be borne in mind that this is a systematic underestimate (cf. Lande 1981).] Whatever is made of the three cases having a significantly small number of contributing loci, in general the results of this study do not indicate a small number of loci contributing to the differentiation of the F and S populations.

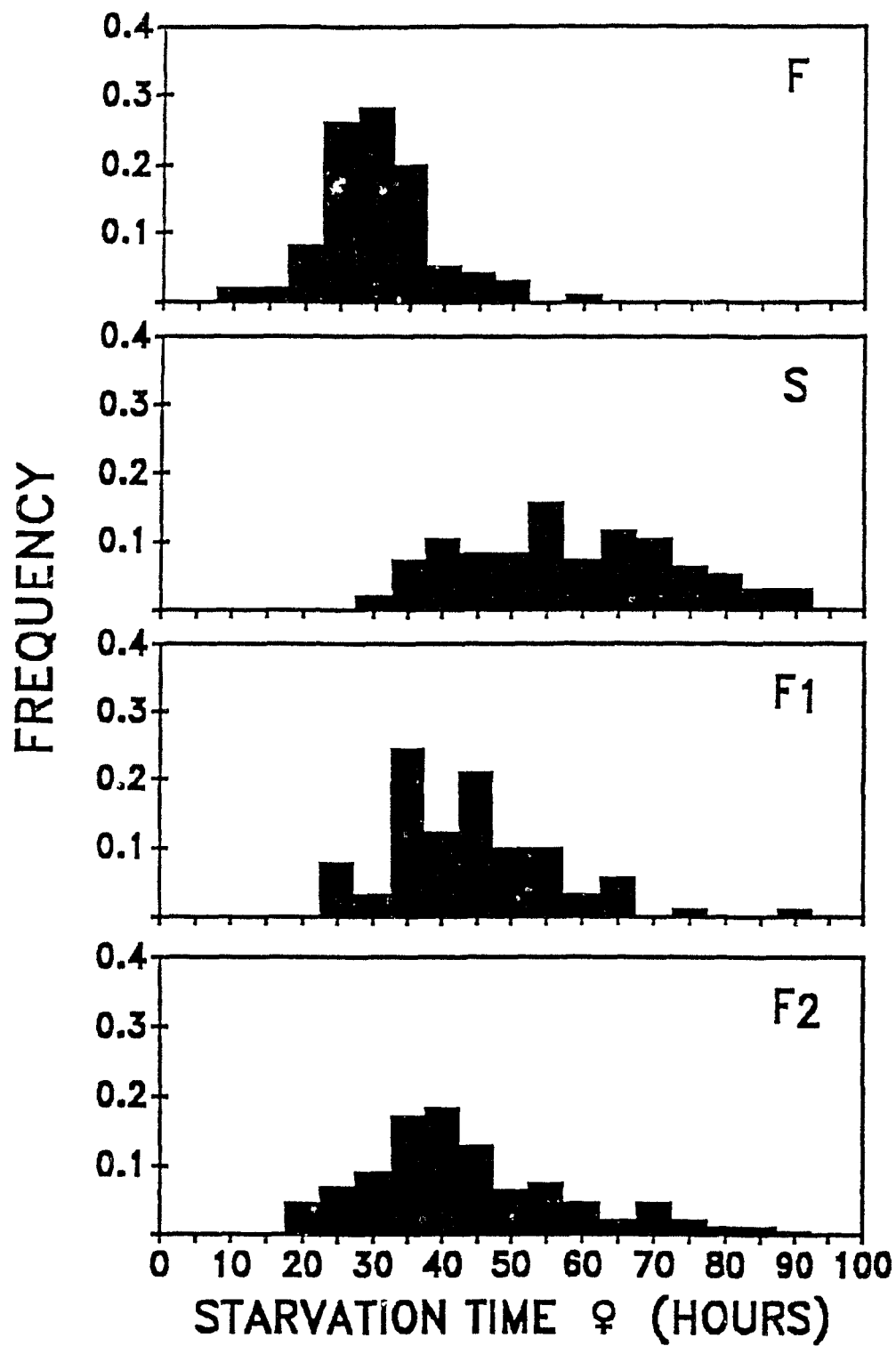


Figure 10.2. Frequency histograms of female starvation time in replicate  $F_2 \times S_2$  of experiment GFS2.

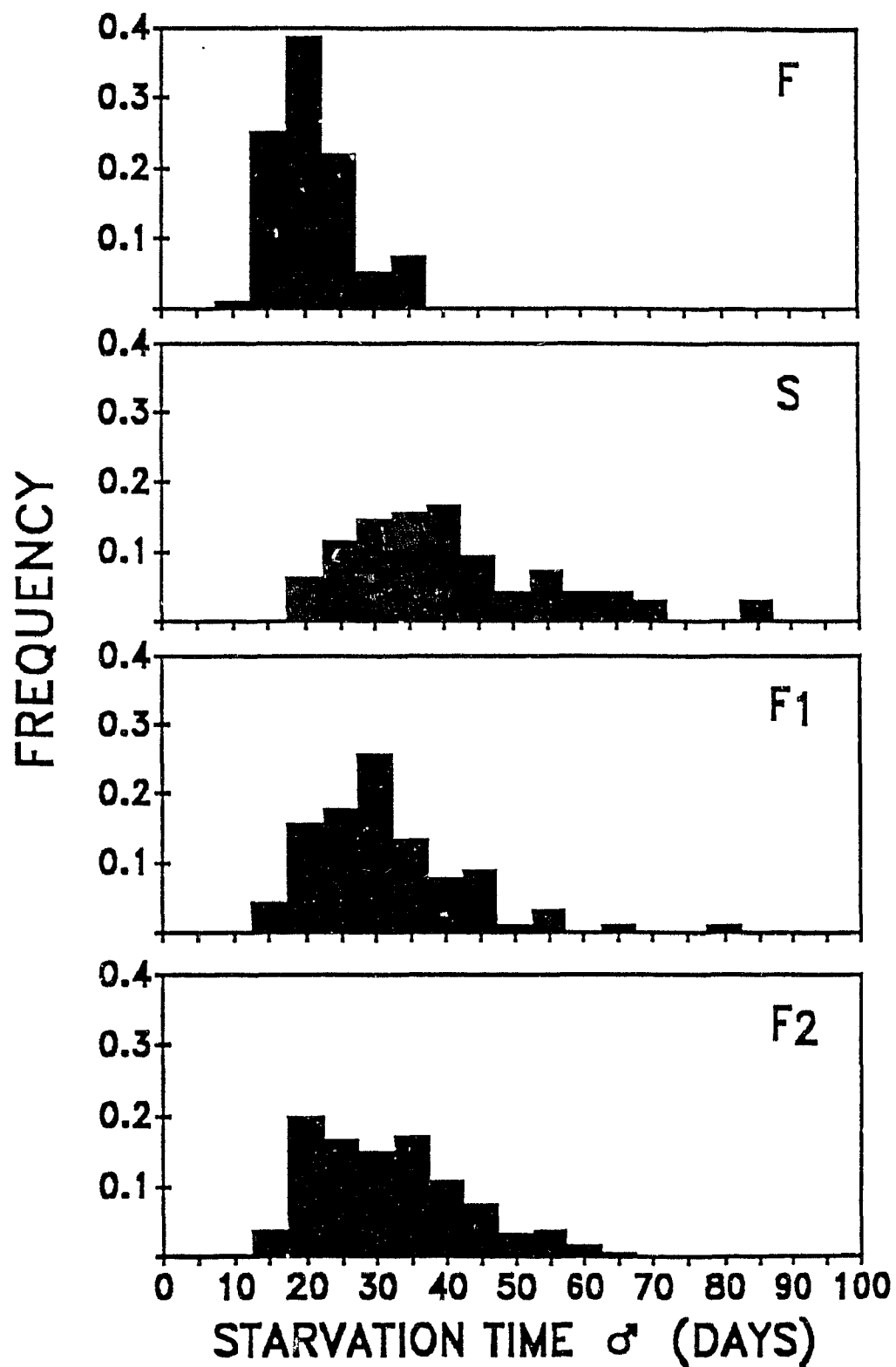


Figure 10.3. Frequency histograms of male starvation time in replicate  $F_2 \times S_2$  of experiment GFS3.

Table 10.2 : F and S Effective Factor Estimates

<u>Character</u> Experiment	1	Line 2	3	Mean $\pm$ SEM
<u>Fecundity</u>				
GFS1	2.01	0.89	3.46	2.12 $\pm$ 0.74
GFS2	0.49	0.19	-0.71	-0.01 $\pm$ 0.36
GFS3	-0.43	-0.18	0.27	-0.11 $\pm$ 0.21
<u>Conditional Fecundity</u>				
GFS1	-4.06	1.31	0.93	-0.59 $\pm$ 1.74
GFS2	0.90	0.29	-0.64	0.19 $\pm$ 0.45
GFS3	-0.61	-0.40	0.86	-0.05 $\pm$ 0.46
<u>Female Starvation</u>				
GFS1	18.93	-36.76	0.66	-5.72 $\pm$ 16.39
GFS2	1.27	0.94	3.03	1.75 $\pm$ 0.65
GFS3	1.57	4.22	0.95	2.25 $\pm$ 1.00
<u>Male Starvation</u>				
GFS1	2.87	2.73	0.40	2.00 $\pm$ 0.80
GFS2	-2.97	1.69	0.86	-0.14 $\pm$ 1.43
GFS3	-4.00	228.14	1.35	75.16 $\pm$ 76.5
<u>Female Longevity</u>				
GFS1	-0.99	0.31	-2.76	-1.15 $\pm$ 0.89
GFS2	-13.48	-0.37	0.27	-4.53 $\pm$ 4.48
GFS3	-0.42	-0.73	3.67	0.84 $\pm$ 1.42
<u>Male Longevity</u>				
GFS1	-2.36	-4.71	1.46	-1.87 $\pm$ 1.80
GFS2	0.50	33.50	-1.80	9.14 $\pm$ 12.04
GFS3	-1.85	-1.96	1.51	-0.77 $\pm$ 1.14



Table 10.3 : F and S Inverse Effective Factor Estimates

<u>Character</u> Experiment	1	Line 2	3	Mean $\pm$ SEM
<u>Fecundity</u>				
GFS1	0.50	1.12	0.29	0.64 $\pm$ 0.25*
GFS2	2.03	5.26	-1.42	1.96 $\pm$ 1.93
GFS3	-2.30	-5.48	3.66	-1.38 $\pm$ 2.68
<u>Conditional Fecundity</u>				
GFS1	-0.25	0.76	1.08	0.53 $\pm$ 0.40
GFS2	1.11	3.45	-1.57	1.00 $\pm$ 1.45
GFS3	-1.65	-2.52	1.17	-1.00 $\pm$ 1.11
<u>Female Starvation</u>				
GFS1	0.05	-0.03	1.51	0.51 $\pm$ 0.50
GFS2	0.79	1.06	0.33	0.73 $\pm$ 0.21*
GFS3	0.64	0.24	1.05	0.64 $\pm$ 0.24*
<u>Male Starvation</u>				
GFS1	0.35	0.37	2.50	1.07 $\pm$ 0.71
GFS2	-0.34	0.59	1.16	0.47 $\pm$ 0.44
GFS3	-0.25	0.00	0.741	0.17 $\pm$ 0.30
<u>Female Longevity</u>				
GFS1	-1.01	3.21	-0.36	0.61 $\pm$ 1.31
GFS2	-0.07	-2.71	3.73	0.31 $\pm$ 1.87
GFS3	-2.37	-1.36	0.27	-1.15 $\pm$ 0.77
<u>Male Longevity</u>				
GFS1	-0.43	-0.21	0.69	0.02 $\pm$ 0.34
GFS2	1.98	0.03	-0.56	0.49 $\pm$ 0.77
GFS3	-0.54	-0.51	0.66	-0.13 $\pm$ 0.40

## CHAPTER 11

### Discussion of Analysis of Selected Populations

### 11.1 Discussion

The results of this part of the study conform to those reported in Part II on the B and O populations, in Clare and Luckinbill (1985), and in Luckinbill et al. (1987). The only point of difference between any of these studies is in the interpretation of their results by Luckinbill et al. (1987), who argued for a single major factor producing postponed aging in their D. melanogaster stocks, even though there was no evidence of trimodality in their F<sub>2</sub> populations. The present study is probably the clearest of the four; there are fewer instances of significant maternal and dominance effects than there were in Part II. However, the four studies together are simple in their implications: Aging in laboratory cultures of D. melanogaster cultured from older females only, for a number of generations, appears to be postponed as a result of allele frequency changes at at least a moderate number of loci, those alleles having additive effects on average. There is no reproducible evidence for any type of maternal, or other non-genetic, effect.

These findings fit those of Luckinbill et al. (1988b), who found clear evidence in at least some of their experiments for a hereditary contribution of all three major D. melanogaster chromosomes to postponed aging. This conclusion, as noted by Luckinbill et al. (1988b), is incompatible with the gene number experiments of Luckinbill

et al. (1987), in that it suggests that there are **at least** three contributory loci for postponed aging, and probably many more. The evidence for a predominant effect of chromosome III on aging in Luckinbill et al. (1988b) does not necessarily indicate a small number of loci, because it makes up a large proportion of the D. melanogaster genome. In any case, it is not known how reproducible this particular chromosomal-effect result would be over a number of lines having postponed aging, since only one line was analyzed by Luckinbill et al. (1988b).

PART V

GENERAL DISCUSSION

CHAPTER 12  
General Discussion

## 12.1 Discussion

One of the outstanding problems affecting research on aging has been the persistence of disbelief that aging is made up of normal phenotypes amenable to genetic analysis and selection (e.g. Lints and Hoste 1974, 1977; Lints 1978; Lints et al. 1979). The present results together with those of Luckinbill and his colleagues (Clare and Luckinbill 1985; Luckinbill and Clare 1985) indicate that aging phenotypes are quite ordinary, at the level of quantitative genetics.

A more technical point is that of inbreeding depression. While a number of *Drosophila* stocks exhibit different aging patterns, upon crossing there is often extensive heterosis (Gowen and Johnson 1946; Clarke and Maynard Smith 1955), indicating inbreeding depression. [This has made the study of *Caenorhabditis elegans* aging particularly attractive, because self-fertilization in that species appears to prevent inbreeding depression for aging (Johnson and Wood 1982).] The lack of inbreeding depression in the extensive **within-type** crosses performed in the present study indicates that stocks with postponed aging created using the methods of Rose (1984) will not suffer from the problem. Thus, they can be used as material for the investigation of physiological hypotheses concerning mechanisms for the postponement of normal aging (see Rose et al. 1984; Service et al. 1985; Service 1987; Luckinbill et al. 1988a).

What is the significance of all of these *Drosophila* results for our understanding of the genetics of aging in general? Firstly, what of the many known alleles, from that which causes Huntington's chorea in man to those aberrant mutants in *Drosophila* with shortened lifespan? These alleles are often supposed to cause "accelerated aging", and are taken as evidence for few controlling elements for the aging process. In both man (e.g. Martin 1978) and *Drosophila* (Hutchinson and Rose 1987), it is doubtful that alleles of this kind are related to aging. These alleles may kill adults, and induce chronic pathologies, but that is not evidence that they affect aging itself. Close inspection of their pathophysiology reveals a number of disparities with "normal aging" (Martin 1978). Therefore, the existence of such alleles does not clash with the present conclusions, because they are of no genuine relevance to the genetic dissection of aging.

Secondly, are there any known alleles which can postpone aging in any model system? Such alleles are known in both *D. subobscura* (Maynard Smith 1958) and *C. elegans* (Friedman and Johnson 1988). In both these cases, lifespan is increased by homozygosity of a single allele as much or more than it is in the *D. melanogaster* stocks of Rose (1984) or Luckinbill et al. (1984). Interestingly, in both these cases, reproduction is greatly decreased in the longer-lived mutant strain. The *D. subobscura* mutants are in fact completely sterile (Maynard Smith 1958). In a physiological



sense, these other studies corroborate the results of Rose and Charlesworth (1981a,b), Rose (1984), and Luckinbill and Clare (1985) in finding a clear association between postponed aging and reduced early reproduction.

Thirdly, is there any likelihood that the D. melanogaster results will prove to be universally applicable to the genetics of aging in general? The finding of quantitative inheritance is indeed quite likely to hold. Many loci should affect later survival and reproduction, because survival and reproduction are the ends toward which natural selection strives. Loci which do not have alleles that directly or indirectly foster survival or reproduction are not going to be preserved, because natural selection will not oppose the accumulation of silencing mutations at those loci. Maintenance of polymorphism at those loci affecting aging is likely, because both of the population genetic mechanisms of aging, antagonistic pleiotropy (Williams 1957; Rose 1985) and mutation-accumulation (Medawar 1952; Edney and Gill 1968; Charlesworth 1980), act to maintain genetic polymorphism. Antagonistic pleiotropy does so by generating overdominance and its higher-order analogues (Rose 1982, 1985). Mutation-accumulation maintains genetic polymorphism by allowing mutations affecting later survival and reproduction to drift to high frequencies, due to the weakness of natural selection at later ages (Charlesworth 1980). Therefore, almost all outbred species are likely to have allelic variation

affecting aging at a great many loci, allelic variation which could be selected so as to postpone aging.

APPENDIX A

Summary Statistics of B and O Diallels

Table A1 : Experiment DB1 - Ovary Weight

Male Parent	Mean Dry Ovary Weight (mg.) (Standard Error) Number of Individuals					Mean
	1	2	3	4	5	
1	0.124 (0.006) 28	0.134 (0.009) 28	0.129 (0.009) 28	0.133 (0.006) 36	0.150 (0.009) 28	0.134 (0.004) 5
2	0.142 (0.007) 28	0.111 (0.008) 28	0.139 (0.008) 28	0.144 (0.007) 36	0.140 (0.010) 28	0.135 (0.006) 5
3	0.153 (0.008) 28	0.123 (0.006) 28	0.173 (0.008) 28	0.154 (0.008) 36	0.139 (0.007) 28	0.148 (0.008) 5
4	0.146 (0.008) 28	0.145 (0.009) 28	0.160 (0.006) 28	0.144 (0.005) 36	0.150 (0.011) 28	0.149 (0.003) 5
5	0.143 (0.009) 28	0.158 (0.008) 28	0.104 (0.008) 28	0.146 (0.007) 36	0.127 (0.010) 28	0.136 (0.009) 5
Mean	0.142 (0.005) 5	0.134 (0.008) 5	0.141 (0.012) 5	0.144 (0.003) 5	0.141 (0.004) 5	0.141 (0.002) 740

Table A2 : Experiment DB1 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals						
Male Parent	Female Parent					Mean
	1	2	3	4	5	
1	40.02 (1.50) 52	37.90 (1.36) 56	34.68 (1.21) 56	34.05 (1.12) 52	37.78 (1.97) 56	36.89 (1.11) 5
2	36.96 (1.46) 56	44.97 (1.39) 56	41.40 (1.34) 52	39.69 (1.44) 56	45.95 (1.65) 56	41.79 (1.66) 5
3	35.84 (0.90) 56	39.64 (1.13) 56	33.92 (1.21) 56	38.19 (1.39) 56	41.12 (2.23) 56	37.74 (1.29) 5
4	35.98 (1.22) 56	38.64 (1.13) 48	34.94 (1.38) 52	37.82 (1.25) 56	34.74 (1.47) 52	36.42 (0.78) 5
5	36.94 (1.45) 56	39.79 (1.19) 52	35.33 (1.87) 56	43.06 (1.81) 56	32.91 (0.93) 56	37.61 (1.76) 5
Mean	37.15 (0.76) 5	40.19 (1.24) 5	36.05 (1.36) 5	38.56 (1.46) 5	39.90 (2.40) 5	38.10 (0.30) 1368

Table A3 : Experiment DB2 - Ovary Weight

Mean Dry Ovary Weight (mg.) (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	0.183 (0.016) 22	0.171 (0.006) 32	0.134 (0.008) 19	0.163 (0.015) 3
2	0.170 (0.009) 28	0.177 (0.010) 23	0.186 (0.009) 27	0.178 (0.005) 3
3	0.186 (0.008) 31	0.131 (0.007) 32	0.157 (0.011) 21	0.158 (0.016) 3
Mean	0.180 (0.005) 3	0.160 (0.014) 3	0.384 (0.015) 3	0.167 (0.003) 235

Table A4 : Experiment D01 - Ovary Weight

Mean Dry Ovary Weight (mg.) (Standard Error) Number of Individuals						
Male Parent	Female Parent					Mean
	1	2	3	4	5	
1	0.069 (0.006) 28	0.092 (0.008) 28	0.102 (0.006) 28	0.106 (0.011) 28	0.062 (0.006) 28	0.086 (0.009) 5
2	0.057 (0.009) 28	0.054 (0.005) 28	0.086 (0.007) 28	0.099 (0.011) 28	0.049 (0.011) 28	0.069 (0.010) 5
3	0.081 (0.010) 28	0.093 (0.005) 28	0.123 (0.012) 28	0.117 (0.010) 28	0.049 (0.005) 28	0.093 (0.013) 5
4	0.095 (0.010) 28	0.078 (0.006) 28	0.110 (0.009) 28	0.052 (0.006) 28	0.039 (0.004) 28	0.075 (0.013) 5
5	0.075 (0.006) 28	0.123 (0.008) 28	0.063 (0.006) 28	0.093 (0.012) 28	0.044 (0.005) 28	0.080 (0.013) 5
Mean	0.075 (0.006) 5	0.088 (0.011) 5	0.097 (0.010) 5	0.093 (0.011) 5	0.049 (0.004) 5	0.080 (0.002) 700

Table A5 : Experiment D01 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals						
Male Parent	Female Parent					Mean
	1	2	3	4	5	
1	38.17 (1.72) 56	33.79 (1.51) 56	36.36 (1.40) 56	37.20 (1.72) 56	41.37 (2.45) 52	37.38 (1.24) 5
2	33.85 (1.47) 56	39.88 (2.20) 56	37.63 (1.73) 56	31.14 (1.42) 56	37.17 (1.86) 56	35.93 (1.54) 5
3	35.05 (1.37) 56	43.75 (1.87) 56	33.33 (1.44) 56	31.74 (1.27) 56	36.26 (1.47) 56	36.03 (2.08) 5
4	37.13 (1.41) 56	33.60 (1.85) 56	35.09 (1.37) 56	31.08 (1.62) 56	37.03 (1.50) 56	34.79 (1.13) 5
5	40.64 (2.34) 52	38.93 (1.72) 56	46.42 (1.68) 52	34.85 (1.57) 52	37.95 (1.55) 56	39.76 (1.91) 5
Mean	36.97 (1.19) 5	37.99 (1.93) 5	37.77 (2.28) 5	33.20 (1.22) 5	37.96 (0.89) 5	36.73 (0.35) 1384



Table A6 : Experiment D02 - Female Starvation

Mean Survival Time (hours)  
 (Standard Error)  
 Number of Individuals

Male Parent	Female Parent					Mean
	1	2	3	4	5	
1	55.10 (3.12) 52	61.69 (3.27) 60	60.18 (2.73) 56	48.85 (2.51) 56	61.63 (3.16) 36	57.49 (2.47) 5
2	60.15 (2.68) 56	69.18 (3.12) 56	60.79 (3.05) 56	58.52 (2.28) 56	62.35 (4.03) 48	62.20 (1.85) 5
3	58.02 (2.67) 52	67.90 (2.89) 56	77.92 (4.09) 36	50.59 (2.19) 52	60.58 (2.89) 52	63.00 (4.64) 5
4	51.40 (1.95) 56	52.31 (2.07) 48	54.18 (2.33) 56	59.26 (3.10) 56	53.24 (2.35) 52	54.08 (1.38) 5
5	69.00 (3.71) 56	72.49 (3.17) 60	66.20 (3.40) 52	64.79 (3.18) 52	65.13 (2.34) 56	67.52 (1.45) 5
Mean	58.73 (2.96) 5	64.71 (3.56) 5	63.85 (4.00) 5	56.40 (2.95) 5	60.59 (1.99) 5	60.85 (0.61) 1321

Table A7 : Experiment D03 - Ovary Weight

Male Parent	Mean Dry Ovary Weight (mg.) (Standard Error) Number of Individuals			Mean
	1	2	3	
1	0.156 (0.009) 23	0.093 (0.010) 24	0.164 (0.006) 27	0.138 (0.022) 3
2	0.168 (0.009) 31	0.094 (0.009) 23	0.146 (0.009) 32	0.136 (0.022) 3
3	0.148 (0.010) 28	0.099 (0.010) 24	0.157 (0.013) 22	0.135 (0.018) 3
Mean	0.157 (0.006) 3	0.095 (0.002) 3	0.156 (0.005) 3	0.138 (0.004) 234

Table A8 : Experiment D04 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals						
Male Parent	Female Parent					Mean
	1	2	3	4	5	
1	35.25 (1.42) 39	35.86 (1.87) 21	37.44 (2.57) 21	32.50 (1.57) 21	38.19 (3.43) 18	35.85 (0.99) 5
2	34.07 (1.58) 18	39.04 (2.21) 48	35.95 (2.77) 24	40.60 (3.30) 21	35.25 (2.07) 24	36.98 (1.22) 5
3	37.36 (2.89) 21	30.80 (0.88) 24	33.59 (1.33) 42	34.26 (3.17) 21	32.90 (1.57) 21	33.78 (1.07) 5
4	36.23 (2.68) 18	32.60 (1.66) 24	29.11 (1.28) 21	31.06 (0.95) 42	36.79 (3.43) 21	33.16 (1.48) 5
5	34.15 (1.63) 24	36.96 (2.54) 21	28.33 (0.87) 18	31.26 (2.82) 21	38.53 (2.60) 45	33.85 (1.86) 5
Mean	35.41 (0.63) 5	35.05 (1.49) 5	32.88 (1.81) 5	33.94 (1.76) 5	36.33 (1.04) 5	34.89 (0.46) 639

Table A9 : Experiment D04 - Male Starvation

Mean Survival Time (hours)  
 (Standard Error)  
 Number of Individuals

Male Parent	Female Parent					Mean
	1	2	3	4	5	
1	27.72 (1.50) 39	29.57 (1.60) 21	30.01 (2.12) 21	25.93 (1.21) 21	26.47 (1.50) 18	27.94 (0.81) 5
2	33.40 (1.75) 18	28.48 (1.12) 48	29.77 (1.92) 21	29.17 (1.69) 21	28.25 (1.39) 24	29.81 (0.94) 5
3	25.64 (1.28) 21	26.80 (1.14) 24	24.87 (0.86) 42	29.11 (1.52) 21	26.33 (1.70) 21	26.55 (0.72) 5
4	30.23 (1.65) 18	28.35 (1.75) 24	27.69 (1.78) 21	30.20 (1.45) 42	29.36 (1.53) 21	29.17 (0.50) 5
5	29.65 (1.63) 24	29.81 (1.34) 21	26.33 (1.14) 18	26.11 (1.44) 21	25.60 (1.19) 45	27.50 (0.92) 5
Mean	29.33 (1.30) 5	28.60 (0.53) 5	27.73 (0.99) 5	28.10 (0.87) 5	27.20 (0.69) 5	28.04 (0.30) 636

## APPENDIX B

### Analysis of B and O Population Diallels

Table B1 : Experiment DB1 - Ovary Weight

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	0.008	4	0.002	0.279	0.887
MPAR	0.034	4	0.008	1.148	0.370
FPAR & MPAR	0.042	8	0.005	0.713	0.677
FPAR x MPAR	0.117	16	0.007		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	0.008	4	0.002	0.243	0.900
MPAR	0.034	4	0.008		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	0.014	4	0.003	0.983	0.506
MPAR	0.014	4	0.004		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	0.136	0.142
Standard Deviation	0.024	0.01
N	5	20

SEPARATE VAR	T = 0.539	DF = 4.6	Probability = 0.619
POOLED VAR	T = 0.778	DF = 23	Probability = 0.444

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.004	1	0.004	0.624	0.438
REP within TRT	0.154	23	0.007		

Table B2 : Experiment DB1 - Female Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	2655.26	4	663.81	1.396	0.280
MPAR	5009.89	4	1252.47	2.634	0.073
FPAR & MPAR	7771.00	8	971.38	2.043	0.107
FPAR x MPAR	7607.31	16	475.46		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	2655.26	4	663.81	0.530	0.723
MPAR	5009.89	4	1252.47		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	3113.65	4	778.41	0.671	0.646
MPAR	4643.00	4	1160.75		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	37.927	38.130
Standard Deviation	4.879	3.110
N	5	20

SEPARATE VAR	T = 0.089	DF = 4.3	Probability = 0.934
POOLED VAR	T = 0.117	DF = 23	Probability = 0.908

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	9.06	1	9.06	0.014	0.908
REP within TRT	15394.43	23	669.32		

Table B3 : Experiment DB2 - Ovary Weight

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
F <sub>PAR</sub>	0.021	2	0.010	0.746	0.530
M <sub>PAR</sub>	0.016	2	0.008	0.565	0.608
F <sub>PAR</sub> & M <sub>PAR</sub>	0.037	4	0.009	0.666	0.648
F <sub>PAR</sub> x M <sub>PAR</sub>	0.056	4	0.014		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
F <sub>PAR</sub>	0.021	2	0.010	1.319	0.431
M <sub>PAR</sub>	0.016	2	0.008		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
F <sub>PAR</sub>	0.014	2	0.007	2.454	0.290
M <sub>PAR</sub>	0.006	2	0.003		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	0.172	0.163
Standard Deviation	0.013	0.024
N	3	6

SEPARATE VAR	T = 0.752	DF = 6.8	Probability = 0.480
POOLED VAR	T = 0.613	DF = 7	Probability = 0.559

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.004	1	0.004	0.333	0.582
REP within TRT	0.089	7	0.013		



Table B4 : Experiment D01 - Ovary Weigh

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	0.216	4	0.054	4.723	0.010
MPAR	0.048	4	0.012	1.058	0.409
FPAR & MPAR	0.264	8	0.033	2.891	0.034
FPAR x MPAR	0.183	16	0.011		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	0.216	4	0.054	4.463	0.088
MPAR	0.048	4	0.012		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	0.194	4	0.048	14.782	0.012
MPAR	0.013	4	0.003		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	0.068	0.083
Standard Deviation	0.032	0.024
N	5	20

SEPARATE VAR	T = 0.989	DF = 5.2	Probability = 0.368
POOLED VAR	T = 1.184	DF = 23	Probability = 0.249

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.026	1	0.026	1.402	0.249
REP within TRT	0.421	23	0.018		

Table B5 : Experiment D01 - Female Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	4597.75	4	1149.44	1.859	0.167
MPAR	3946.77	4	986.69	1.596	0.224
FPAR & MPAR	8597.97	8	1074.75	1.738	0.165
FPAR x MPAR	9894.49	16	618.41		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	4597.75	4	1149.44	1.165	0.443
MPAR	3946.77	4	986.69		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	4359.94	4	1089.99	0.961	0.515
MPAR	4538.23	4	1134.56		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	36.082	36.950
Standard Deviation	3.703	3.823
N	5	20

SEPARATE VAR	T = 0.465	DF = 6.3	Probability = 0.658
POOLED VAR	T = 0.456	DF = 23	Probability = 0.652

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	168.03	1	168.03	0.213	0.648
REP within TRT	18107.95	23	787.30		

Table B6 : Experiment D02 - Female Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	13300.13	4	3325.03	2.442	0.089
MPAR	28717.63	4	7179.41	5.273	0.007
FPAR & MPAR	42532.90	8	5316.61	3.905	0.010
FPAR x MPAR	21783.54	16	1361.47		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	13300.13	4	3325.03	0.463	0.763
MPAR	28717.63	4	7179.41		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	13273.78	4	3318.44	0.410	0.795
MPAR	32369.17	4	8092.29		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	65.316	59.933
Standard Deviation	8.873	6.575
N	5	20

SEPARATE VAR	T = 1.272	DF = 5.2	Probability = 0.259
POOLED VAR	T = 1.532	DF = 23	Probability = 0.139

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	5826.35	1	5826.35	2.275	0.145
REP within TRT	58904.56	23	2561.07		

Table B7 : Experiment D03 - Ovary Weight

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	0.181	2	0.091	34.029	0.003
MPAR	0.000	2	0.000	0.059	0.944
FPAR & MPAR	0.182	4	0.046	17.095	0.009
FPAR x MPAR	0.011	4	0.003		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	0.181	2	0.091	576.84	0.002
MPAR	0.000	2	0.000		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	0.092	2	0.046	40.983	0.024
MPAR	0.002	2	0.001		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	0.136	0.136
Standard Deviation	0.036	0.032
N	3	6

SEPARATE VAR	T = 0.032	DF = 3.7	Probability = 0.976
POOLED VAR	T = 0.034	DF = 7	Probability = 0.974

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.000	1	0.000	0.001	0.974
REP within TRT	0.193	7	0.028		

Table B8 : Experiment D04 - Female Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	830.28	4	207.57	0.977	0.448
MPAR	1235.34	4	308.84	1.453	0.263
FPAR & MPAR	2124.53	8	265.57	1.249	0.334
FPAR x MPAR	3400.64	16	212.54		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	830.28	4	207.57	0.672	0.645
MPAR	1235.34	4	308.84		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	521.66	4	130.41	0.542	0.716
MPAR	962.04	4	240.51		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	35.494	34.530
Standard Deviation	3.361	3.147
N	5	20

SEPARATE VAR	T = 0.581	DF = 5.9	Probability = 0.587
POOLED VAR	T = 0.605	DF = 23	Probability = 0.551

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	131.88	1	131.88	0.519	0.478
REP within TRT	5843.74	23	254.08		

Table B9 : Experiment D04 - Male Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	302.72	4	75.68	1.034	0.420
MPAR	803.17	4	200.79	2.743	0.065
FPAR & MPAR	1124.17	8	140.52	1.919	0.127
FPAR x MPAR	1171.43	16	73.22		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	302.72	4	75.68	0.377	0.816
MPAR	803.17	4	200.79		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	271.34	4	67.84	0.574	0.698
MPAR	472.61	4	118.15		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	27.372	28.400
Standard Deviation	2.164	1.975
N	5	20

SEPARATE VAR	T = 0.966	DF = 5.8	Probability = 0.378
POOLED VAR	T = 1.023	DF = 23	Probability = 0.317

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	149.69	1	149.69	1.522	0.230
REP within TRT	2232.70	23	98.38		

## APPENDIX C

### Summary Statistics of B and O Transmission Patterns

Table C1 : Experiment B01 - Ovary Weight

Mean Dry Ovary Weight (mg.)  
 (Standard Error)  
 Number of Individuals

Replicate	BB	BO	OB
1	0.112 (0.007) 43	0.100 (0.009) 22	0.141 (0.012) 22
2	0.147 (0.009) 43	0.109 (0.010) 24	0.104 (0.009) 16
3	0.126 (0.008) 46	0.139 (0.013) 24	0.127 (0.008) 25
4	0.142 (0.007) 47	0.125 (0.010) 25	0.131 (0.009) 21
5	0.125 (0.008) 46	0.135 (0.009) 23	0.119 (0.011) 16
Mean	0.130 (0.006) 5	0.122 (0.007) 5	0.124 (0.006) 5



Table C2 : Experiment B01 - Female Starvation

Replicate	Mean Survival Time (hours)			
	(Standard Error)			
	Number of Individuals			
	BB	BO	OB	OO
1	30.33 (1.20) 48	33.10 (1.72) 24	30.05 (1.36) 24	31.60 (1.41) 33
2	27.79 (0.81) 42	31.17 (1.96) 24	34.83 (2.08) 18	34.50 (1.40) 30
3	29.60 (1.16) 48	34.50 (2.16) 24	28.1 (1.32) 24	31.88 (0.82) 36
4	30.20 (1.03) 48	32.10 (2.01) 24	28.31 (1.27) 21	32.06 (1.06) 33
5	25.43 (0.90) 45	28.20 (0.88) 27	31.22 (2.88) 15	33.63 (1.37) 36
Mean	28.67 (0.93) 5	31.81 (1.06) 5	30.50 (1.23) 5	32.74 (0.57) 5

Table C3 : Experiment B01 - Male Starvation

Replicate	Mean Survival Time (hours) (Standard Error) Number of Individuals			
	BB	BO	OB	OO
1	19.14 (0.96) 48	23.01 (1.33) 21	22.05 (1.40) 24	24.15 (1.19) 33
2	22.02 (1.04) 42	23.00 (1.19) 24	24.17 (1.74) 18	28.86 (1.08) 33
3	18.98 (0.74) 48	22.75 (1.49) 24	22.85 (1.13) 24	25.60 (1.06) 36
4	21.20 (1.01) 48	20.85 (1.56) 24	23.07 (1.54) 21	25.16 (0.75) 33
5	17.97 (1.31) 45	20.20 (1.32) 27	19.22 (1.17) 15	24.30 (1.28) 36
Mean	19.86 (0.75) 5	21.96 (0.60) 5	22.27 (0.83) 5	25.61 (0.85) 5

Table C4 : Experiment B02 - Ovary Weight

Mean Dry Ovary Weight (mg.) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	0.128 (0.011) 30	0.085 (0.005) 30	0.104 (0.005) 30	0.051 (0.003) 30
2	0.101 (0.006) 30	0.072 (0.004) 30	0.075 (0.006) 30	0.041 (0.003) 30
3	0.135 (0.012) 30	0.124 (0.006) 30	0.111 (0.006) 30	0.051 (0.008) 30
4	0.098 (0.010) 30	0.100 (0.008) 30	0.064 (0.005) 30	0.070 (0.006) 30
5	0.084 (0.006) 30	0.110 (0.009) 30	0.098 (0.009) 30	0.072 (0.006) 30
Mean	0.109 (0.009) 5	0.098 (0.009) 5	0.090 (0.009) 5	0.057 (0.006) 5

Table C5 : Experiment B02 - Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	88.8 (1.4) 60	79.9 (1.7) 59	84.0 (1.7) 59	70.3 (1.5) 60
2	100.8 (1.7) 54	95.8 (2.2) 60	95.5 (2.0) 58	89.8 (2.1) 59
3	106.9 (1.7) 59	102.4 (1.5) 60	104.9 (1.4) 59	97.5 (1.4) 60
4	111.5 (1.7) 60	105.4 (1.9) 59	100.1 (2.9) 56	105.1 (2.5) 59
5	102.4 (1.3) 59	105.8 (1.7) 59	100.2 (2.2) 60	98.8 (1.9) 59
Mean	102.1 (3.8) 5	97.9 (4.8) 5	97.0 (3.6) 5	92.3 (6.0) 5

Table C6 : Experiment B02 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	BB	B0	OB	00
1	88.8 (1.4) 60	79.9 (1.7) 59	84.0 (1.7) 59	70.3 (1.5) 60
2	101.0 (1.7) 54	95.8 (2.2) 60	95.5 (2.0) 58	89.8 (2.1) 59
3	106.9 (1.7) 59	102.4 (1.5) 60	104.9 (1.4) 59	97.5 (1.4) 60
4	111.5 (1.7) 60	105.4 (1.9) 59	100.1 (2.9) 56	105.1 (2.5) 59
5	102.4 (1.3) 59	105.8 (1.7) 59	101.9 (1.4) 59	98.8 (1.9) 59
Mean	102.1 (3.8) 5	97.9 (4.8) 5	97.3 (3.6) 5	92.3 (6.0) 5

Table C7 : Experiment B02 - Female Starvation

Replicate	Mean Survival Time (hours) (Standard Error) Number of Individuals			
	BB	B0	OB	00
1	50.49 (1.79) 55	71.00 (4.00) 55	53.00 (2.17) 80	83.55 (3.20) 65
2	43.96 (2.15) 50	65.73 (3.22) 45	58.60 (2.27) 60	75.85 (2.90) 80
3	43.65 (1.98) 40	46.00 (3.10) 30	37.92 (1.41) 50	50.17 (2.27) 65
4	42.04 (2.09) 50	49.45 (1.93) 40	46.60 (1.97) 45	56.47 (2.69) 45
5	56.16 (2.88) 50	60.90 (2.36) 60	56.51 (2.14) 55	75.00 (1.65) 60
Mean	47.25 (2.65) 5	58.62 (4.76) 5	50.53 (3.75) 5	68.21 (6.34) 5

Table C8 : Experiment B02 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals				
Replicate	BB	B0	OB	00
1	60.7 (1.7) 60	66.6 (1.9) 60	56.4 (2.4) 60	71.3 (2.0) 60
2	46.7 (1.4) 60	53.4 (1.9) 60	50.0 (1.7) 60	55.1 (1.7) 60
3	49.5 (1.7) 60	54.6 (1.7) 60	51.9 (1.9) 60	64.4 (2.3) 60
4	47.2 (1.9) 60	59.5 (2.1) 60	58.0 (2.8) 30	59.6 (2.8) 30
5	44.3 (1.8) 60	54.5 (2.0) 60	63.3 (2.4) 60	62.2 (2.3) 60
Mean	50.08 (2.43) 5	57.72 (2.20) 5	55.92 (2.10) 5	62.52 (2.40) 5

Table C9 : Experiment B03 - Ovary Weight

Mean Dry Ovary Weight (mg.) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	0.183 (0.016) 22	0.156 (0.011) 47	0.166 (0.008) 55	0.148 (0.007) 46
2	0.177 (0.007) 46	0.113 (0.007) 45	0.174 (0.008) 48	0.072 (0.006) 47
3	0.170 (0.010) 45	0.159 (0.009) 48	0.143 (0.008) 48	0.115 (0.010) 45
Mean	0.177 (0.003) 3	0.143 (0.015) 3	0.161 (0.009) 3	0.112 (0.022) 3



Table C10 : Experiment B03 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	45.83 (1.79) 40	52.58 (2.20) 40	48.33 (1.16) 40	53.70 (1.54) 40
2	46.93 (1.46) 40	52.55 (1.39) 40	57.83 (1.63) 40	57.95 (2.09) 40
3	41.68 (1.43) 40	47.23 (1.84) 40	50.35 (1.43) 40	54.70 (1.62) 40
Mean	44.81 (1.60) 3	50.78 (1.78) 3	52.17 (2.89) 3	55.45 (1.28) 3

Table C11 : Experiment B03 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	29.0 (1.9) 50	39.6 (1.6) 50	37.4 (1.9) 50	44.2 (1.3) 50
2	19.5 (1.7) 50	34.6 (2.2) 50	35.6 (2.4) 50	47.2 (1.8) 49
3	27.0 (1.6) 50	34.6 (2.0) 50	40.6 (1.7) 50	53.5 (1.7) 50
Mean	25.2 (2.9) 3	36.3 (1.7) 3	37.9 (1.5) 3	48.3 (2.7) 3

Table C12 : Experiment B04 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	38.07 (2.23) 36	53.59 (3.36) 36	34.63 (1.74) 36	46.81 (2.96) 36
2	44.41 (3.84) 16	46.30 (2.89) 32	54.40 (3.48) 40	50.78 (2.57) 40
3	36.35 (3.06) 20	41.18 (2.98) 36	39.50 (2.67) 36	43.88 (2.88) 40
Mean	39.61 (2.45) 3	47.02 (3.60) 3	42.84 (5.95) 3	47.15 (2.00) 3

Table C13 : Experiment B05 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

Replicate	BB	BO	OB	OO
1	80.2 (2.1) 104	84.4 (1.7) 64	79.3 (2.7) 59	85.2 (1.8) 99
2	88.3 (2.1) 100	95.3 (3.2) 39	96.4 (2.7) 58	88.4 (2.4) 98
3	73.6 (2.0) 97	84.2 (3.0) 59	80.1 (1.9) 59	81.4 (2.0) 82
Mean	80.7 (4.3) 3	88.0 (3.7) 3	85.3 (5.6) 3	85.0 (2.0) 3

Table C14 : Experiment B05 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	82.5 (1.6) 101	84.4 (1.7) 64	82.1 (1.9) 57	85.2 (1.8) 99
2	88.3 (2.1) 100	95.3 (3.2) 39	96.4 (2.7) 58	91.1 (1.9) 95
3	75.9 (1.6) 94	87.2 (2.2) 57	81.5 (1.3) 58	82.4 (1.7) 81
Mean	82.2 (3.6) 3	88.9 (3.2) 3	86.7 (4.9) 3	86.2 (2.6) 3

Table C15 : Experiment B05 - Female Starvation

Replicate	Mean Survival Time (hours)			
	(Standard Error)			
	Number of Individuals			
	BB	BO	OB	OO
1	25.46 (0.64) 98	27.75 (0.79) 64	27.80 (1.10) 56	33.64 (0.82) 100
2	28.10 (0.88) 96	27.85 (1.07) 52	31.68 (1.06) 60	37.78 (1.02) 100
3	30.09 (0.84) 100	32.03 (1.19) 60	36.93 (1.06) 60	36.10 (1.06) 94
Mean	27.88 (1.34) 3	29.21 (1.41) 3	32.14 (2.65) 3	35.84 (1.20) 3

Table C16 : Experiment B05 - Male Starvation

Mean Survival Time (hours)  
 (Standard Error)  
 Number of Individuals

Replicate	BB	BO	OB	OO
1	18.84 (0.48) 98	22.55 (0.82) 64	26.57 (0.97) 56	27.49 (0.80) 100
2	16.94 (0.44) 96	20.07 (0.79) 52	24.28 (1.20) 60	26.14 (0.86) 100
3	17.46 (0.58) 100	20.03 (0.88) 60	24.88 (0.84) 60	26.56 (1.14) 94
Mean	17.75 (0.57) 3	20.88 (0.83) 3	25.25 (0.69) 3	26.73 (0.40) 3

Table C17 : Experiment B06 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

Replicate	BB	BO	OB	OO
1	97.7 (2.6) 95	87.5 (1.9) 58	82.5 (2.4) 60	97.8 (2.5) 100
2	91.0 (1.5) 100	88.3 (3.4) 42	89.0 (2.3) 75	93.0 (2.4) 99
3	93.8 (2.8) 94	97.6 (2.3) 60	92.9 (3.9) 49	89.1 (2.9) 97
Mean	94.2 (1.9) 3	91.1 (3.2) 3	88.1 (3.1) 3	93.3 (2.5) 3



Table C18 : Experiment B06 - Conditional Fecundity

Mean 24 Hour Fecundity  
 (Standard Error)  
 Number of Individuals

Replicate	BB	BO	OB	OO
1	100.8 (1.9) 92	87.5 (1.9) 58	83.9 (2.0) 59	97.8 (2.5) 100
2	91.0 (1.5) 100	90.5 (2.8) 41	90.2 (2.0) 74	95.9 (1.8) 96
3	96.9 (2.2) 91	97.6 (2.3) 60	96.9 (2.8) 47	92.9 (2.3) 93
Mean	96.3 (2.9) 3	91.8 (3.0) 3	90.3 (3.8) 3	95.6 (1.4) 3

Table C19 : Experiment E06 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	27.41 (0.65) 100	27.32 (0.95) 59	29.72 (0.87) 60	33.50 (0.95) 60
2	28.98 (0.60) 100	29.42 (1.02) 42	31.59 (0.78) 78	37.47 (0.82) 100
3	25.45 (0.54) 100	26.35 (0.70) 62	24.73 (0.74) 46	30.49 (1.01) 100
Mean	27.28 (1.02) 3	27.70 (0.98) 3	28.68 (2.04) 3	33.82 (2.02) 3

Table C20 : Experiment B06 - Male Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	22.46 (0.53) 100	26.45 (0.67) 60	30.22 (1.01) 60	33.96 (0.94) 98
2	21.12 (0.52) 100	24.40 (0.90) 42	27.44 (0.86) 78	33.18 (1.19) 100
3	16.42 (0.43) 100	24.51 (0.87) 62	23.49 (0.09) 46	25.87 (0.93) 99
Mean	20.00 (1.83) 3	25.12 (0.67) 3	27.05 (1.95) 3	31.00 (2.58) 3

Table C21 : Experiment B06 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals			
Replicate	BB	BO & OB	OO
1	43.7 (1.2) 99	49.0 (1.5) 97	49.1 (1.7) 100
2	41.5 (1.2) 100	45.8 (1.3) 98	49.4 (1.6) 100
3	36.0 (1.2) 99	46.8 (1.1) 97	55.7 (1.5) 100
Mean	40.4 (2.3) 3	47.2 (0.9) 3	51.4 (2.2) 3

Table C22 : Experiment BO6 - Male Longevity

Mean Longevity (days) (Standard Error) Number of Individuals			
Replicate	BB	BO & OB	OO
1	32.3 (1.2) 98	39.0 (1.2) 97	49.4 (1.4) 95
2	31.4 (0.9) 100	40.7 (1.2) 100	54.3 (1.4) 100
3	32.2 (0.9) 96	37.7 (1.0) 100	52.3 (1.6) 100
Mean	31.9 (0.3) 3	39.1 (0.9) 3	52.0 (1.4) 3

Table C23 : Experiment B07 - Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	94.4 (2.5) 92	96.3 (2.0) 48	93.0 (2.9) 48	99.9 (2.4) 95
2	88.4 (1.8) 93	82.6 (2.6) 46	79.9 (1.7) 45	82.4 (1.7) 91
3	62.9 (1.4) 93	84.3 (2.3) 44	80.5 (2.1) 51	79.8 (2.0) 95
Mean	81.9 (9.7) 3	87.7 (4.3) 3	84.5 (4.3) 3	87.3 (6.3) 3

Table C24 : Experiment B07 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	97.5 (1.8) 89	96.3 (2.0) 48	94.9 (2.1) 47	102.0 (1.9) 93
2	88.4 (1.8) 93	82.6 (2.6) 46	79.9 (1.7) 45	82.4 (1.7) 91
3	63.6 (1.3) 92	84.3 (2.3) 44	80.5 (2.1) 51	82.3 (1.5) 92
Mean	83.2 (10.1) 3	87.7 (4.3) 3	85.1 (4.9) 3	88.9 (6.6) 3

Table C25 : Experiment B07 - Female Starvation

Replicate	Mean Survival Time (hours)			
	(Standard Error)			
	Number of Individuals			
	BB	BO	OB	OO
1	32.20 (0.88) 96	36.95 (1.52) 48	40.03 (1.74) 48	47.46 (1.44) 96
2	35.05 (0.97) 96	38.50 (1.03) 48	42.06 (2.01) 48	51.52 (1.36) 95
3	35.56 (0.84) 96	39.45 (1.11) 45	39.92 (1.17) 51	45.26 (1.08) 96
Mean	34.27 (1.05) 3	38.30 (0.73) 3	40.67 (0.70) 3	48.08 (1.84) 3



Table C26 : Experiment B07 - Male Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	23.48 (0.67) 96	32.26 (1.27) 48	40.03 (1.74) 48	37.46 (1.01) 96
2	25.89 (0.71) 96	30.81 (1.08) 48	32.14 (1.21) 48	36.25 (1.03) 94
3	23.47 (0.60) 96	29.92 (1.31) 45	32.09 (1.17) 51	35.58 (0.98) 95
Mean	24.28 (0.80) 3	31.00 (0.68) 3	32.04 (0.07) 3	36.43 (0.55) 3

Table C27 : Experiment B07 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	37.8 (1.4) 71	45.8 (2.3) 39	44.7 (2.0) 39	47.1 (1.8) 79
2	34.4 (1.2) 83	36.6 (2.5) 41	42.0 (2.6) 38	48.5 (1.8) 79
3	37.7 (1.4) 78	42.1 (2.9) 39	37.6 (2.0) 39	50.2 (2.0) 77
Mean	36.6 (1.1) 3	41.5 (2.7) 3	41.4 (2.1) 3	48.6 (0.9) 3

Table C28 : Experiment B07 - Male Longevity

Mean Longevity (days) (Standard Error) Number of Individuals				
Replicate	BB	BO	OB	OO
1	34.2 (1.5) 77	40.2 (1.9) 40	41.2 (2.4) 39	47.3 (1.8) 75
2	31.5 (1.1) 77	33.8 (1.8) 39	42.1 (2.2) 40	48.5 (1.9) 79
3	29.7 (1.1) 68	32.9 (2.1) 40	34.9 (1.6) 39	48.3 (2.0) 81
Mean	31.8 (1.3) 3	35.6 (2.3) 3	39.4 (2.3) 3	48.0 (0.4) 3

Table C29 : Experiment B08 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

BB	B0	OB	00
95.2 (4.0) 79	98.0 (5.2) 58	102.9 (3.7) 20	98.6 (2.2) 79

Table C30 : Experiment B08 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals			
BB	BO	OB	OO
98.9 (3.5) 76	99.7 (5.0) 57	102.9 (3.7) 20	98.6 (2.2) 79

Table C31 : Experiment B08 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals			
BB	BO	OB	OO
27.21 (0.80) 80	29.62 (1.01) 60	29.65 (1.26) 20	35.41 (0.91) 80

Table C32 : Experiment B08 - Male Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals			
BB	BO	OB	OO
21.33 (0.77) 80	23.57 (0.60) 60	22.90 (0.97) 20	26.05 (0.55) 00

Table C33 : Experiment B08 - Female Longevity

Mean Survival Time (hours) (Standard Error) Number of Individuals			
BB	BO	OB	OO
34.85 (1.46) 72	41.41 (2.03) 44	40.63 (2.15) 40	44.86 (1.96) 77



Table C34 : Experiment B08 - Male Longevity

Mean Survival Time (hours) (Standard Error) Number of Individuals			
BB	BO	OB	OO
31.14 (1.17) 79	37.14 (1.72) 36	38.40 (1.56) 40	44.96 (1.57) 74

APPENDIX D

Analysis of B and O Transmission Patterns

Table D1 : Experiment B01 - Ovary Weight

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	0.122	0.124	-0.003
Standard Deviation	0.017	0.014	0.023
N	5	5	5

INDEPENDENT	T = 0.278	DF = 8	Probability = 0.788
PAIRED	T = 0.265	DF = 4	Probability = 0.804

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.000	1	0.000	0.069	0.806
TRT x REP	0.023	4	0.006		

Table D2 : Experiment B01 - Female Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	28.67	32.74	- 4.07
Standard Deviation	2.07	1.27	3.16
N	5	5	5

INDEPENDENT	T = 3.743	DF = 8	Probability = 0.006
PAIRED	T = 2.877	DF = 4	Probability = 0.045

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1601.92	1	1601.92	8.245	0.045
TRT x REP	777.20	4	194.30		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	31.81	30.50	1.31
Standard Deviation	2.37	2.74	4.43
N	5	5	5

INDEPENDENT	T = 0.809	DF = 8	Probability = 0.442
PAIRED	T = 0.661	DF = 4	Probability = 0.545

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	94.01	1	94.01	0.444	0.542
TRT x REP	846.56	4	211.64		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	30.41	31.05	- 0.64
Standard Deviation	0.76	1.31	1.01
N	5	5	5

INDEPENDENT	T = 0.940	DF = 8	Probability = 0.375
PAIRED	T = 1.404	DF = 4	Probability = 0.233

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	58.07	1	58.07	2.054	0.225
TRT x REP	113.11	4	28.28		

Table D3 : Experiment B01 - Male Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	19.86	25.61	- 5.75
Standard Deviation	1.69	1.91	1.23
N	5	5	5

INDEPENDENT	T = 5.047	DF = 8	Probability = 0.001
PAIRED	T = 10.457	DF = 4	Probability = 0.000

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3241.82	1	3241.82	109.94	0.00
TRT x REP	117.95	4	29.49		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	21.96	22.27	- 0.31
Standard Deviation	1.34	1.87	1.39
N	5	5	5

INDEPENDENT	T = 0.301	DF = 8	Probability = 0.771
PAIRED	T = 0.497	DF = 4	Probability = 0.645

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	5.15	1	5.15	0.248	0.645
TRT x REP	83.21	4	20.80		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	22.32	22.11	0.22
Standard Deviation	1.70	1.39	1.28
N	5	5	5

INDEPENDENT	T = 0.220	DF = 8	Probability = 0.832
PAIRED	T = 0.377	DF = 4	Probability = 0.726

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	6.63	1	6.63	0.141	0.726
TRT x REP	187.46	4	46.87		

Table D4 : Experiment B02 - Ovary Weight

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	0.109	0.057	0.052
Standard Deviation	0.021	0.014	0.031
N	5	5	5

INDEPENDENT	T = 4.614	DF = 8	Probability = 0.002
PAIRED	T = 3.753	DF = 4	Probability = 0.020

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.204	1	0.204	14.088	0.020
TRT x REP	0.058	4	0.204		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	0.098	0.090	0.008
Standard Deviation	0.020	0.020	0.020
N	5	5	5

INDEPENDENT	T = 0.437	DF = 8	Probability = 0.556
PAIRED	T = 0.863	DF = 4	Probability = 0.437

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.005	1	0.005	0.745	0.437
TRT x REP	0.024	4	0.006		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	0.083	0.094	-0.011
Standard Deviation	0.009	0.017	0.013
N	5	5	5

INDEPENDENT	T = 1.265	DF = 8	Probability = 0.241
PAIRED	T = 1.892	DF = 4	Probability = 0.131

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.018	1	0.018	3.579	0.131
TRT x REP	0.020	4	0.005		

Table 75 : Experiment B02 - Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	102.13	92.28	9.85
Standard Deviation	8.52	13.48	5.70
N	5	5	5

INDEPENDENT	T = 1.381	DF = 8	Probability = 0.204
PAIRED	T = 3.864	DF = 4	Probability = 0.018

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	14281.86	1	14281.86	14.743	0.018
TRT x REP	3874.79	4	968.70		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	97.87	96.95	0.92
Standard Deviation	10.77	7.94	4.39
N	5	5	5

INDEPENDENT	T = 0.154	DF = 8	Probability = 0.881
PAIRED	T = 0.470	DF = 4	Probability = 0.663

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	125.30	1	125.30	0.221	0.663
TRT x REP	2267.30	4	566.83		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	97.15	97.42	- 0.27
Standard Deviation	10.92	9.21	3.34
N	5	5	5

INDEPENDENT	T = 0.042	DF = 8	Probability = 0.967
PAIRED	T = 0.181	DF = 4	Probability = 0.865

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	21.53	1	21.53	0.033	0.865
TRT x REP	2624.20	4	656.05		

Table D6 : Experiment B02 - Conditional Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	102.13	92.28	9.85
Standard Deviation	8.52	13.48	5.70
N	5	5	5

INDEPENDENT	T = 1.381	DF = 8	Probability = 0.204
PAIRED	T = 3.864	DF = 4	Probability = 0.018

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	14281.86	1	14281.86	14.743	0.018
TRT x REP	3874.79	4	968.70		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	97.87	97.29	0.58
Standard Deviation	10.77	8.15	3.99
N	5	5	5

INDEPENDENT	T = 0.097	DF = 8	Probability = 0.925
PAIRED	T = 0.327	DF = 4	Probability = 0.760

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	49.93	1	49.93	0.107	0.760
TRT x REP	1862.04	4	465.51		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	97.15	97.59	- 0.45
Standard Deviation	10.92	9.35	3.50
N	5	5	5

INDEPENDENT	T = 0.069	DF = 8	Probability = 0.947
PAIRED	T = 0.284	DF = 4	Probability = 0.790

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	58.24	1	58.24	0.081	0.790
TRT x REP	2875.74	4	718.94		



Table D7 : Experiment B02 - Female Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	47.26	68.21	-20.95
Standard Deviation	5.93	14.17	11.42
N	5	5	5

INDEPENDENT	T = 3.049	DF = 8	Probability = 0.016
PAIRED	T = 4.102	DF = 4	Probability = 0.015

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	59189.74	1	59189.74	16.651	0.015
TRT x REP	14219.16	4	3554.79		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	58.62	50.53	8.09
Standard Deviation	10.64	8.39	5.92
N	5	5	5

INDEPENDENT	T = 1.336	DF = 8	Probability = 0.218
PAIRED	T = 3.055	DF = 4	Probability = 0.038

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	7984.13	1	7984.13	7.702	0.050
TRT x REP	4146.69	4	1036.67		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	59.00	53.94	5.06
Standard Deviation	9.94	9.07	3.37
N	5	5	5

INDEPENDENT	T = 0.841	DF = 8	Probability = 0.425
PAIRED	T = 3.361	DF = 4	Probability = 0.028

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	6732.98	1	6732.98	11.214	0.029
TRT x REP	2401.73	4	600.43		

Table D8 : Experiment B02 - Female Longevity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	50.08	62.52	-12.44
Standard Deviation	6.06	6.00	3.04
N	5	5	5

INDEPENDENT	T = 3.261	DF = 8	Probability = 0.012
PAIRED	T = 9.147	DF = 4	Probability = 0.001

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	21114.07	1	21114.07	76.069	0.001
TRT x REP	1110.26	4	277.56		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	57.73	55.92	1.81
Standard Deviation	5.48	5.25	6.81
N	5	5	5

INDEPENDENT	T = 0.532	DF = 8	Probability = 0.609
PAIRED	T = 0.593	DF = 4	Probability = 0.585

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	445.10	1	445.10	0.320	0.602
TRT x REP	5561.07	4	1390.27		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	55.89	56.87	- 0.99
Standard Deviation	6.16	4.18	5.25
N	5	5	5

INDEPENDENT	T = 0.297	DF = 8	Probability = 0.774
PAIRED	T = 0.421	DF = 4	Probability = 0.695

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	274.73	1	274.73	0.186	0.689
TRT x REP	5910.31	4	1477.588		

Table D9 : Experiment B03 - Ovary Weight

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	0.177	0.112	0.065
Standard Deviation	0.006	0.038	0.036
N	3	3	3

INDEPENDENT	T = 2.938	DF = 4	Probability = 0.042
PAIRED	T = 3.140	DF = 2	Probability = 0.088

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.245	1	0.245	9.645	0.090
TRT x REP	0.051	2	0.025		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	0.143	0.161	-0.018
Standard Deviation	0.025	0.016	0.039
N	3	3	3

INDEPENDENT	T = 1.043	DF = 4	Probability = 0.356
PAIRED	T = 0.807	DF = 2	Probability = 0.504

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.024	1	0.024	0.668	0.500
TRT x REP	0.071	2	0.035		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	0.142	0.152	-0.010
Standard Deviation	0.017	0.008	0.009
N	3	3	3

INDEPENDENT	T = 0.918	DF = 4	Probability = 0.411
PAIRED	T = 1.908	DF = 2	Probability = 0.197

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.014	1	0.014	3.659	0.196
TRT x REP	0.008	2	0.004		

Table D10 : Experiment BO3 - Female Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	44.81	55.45	-10.64
Standard Deviation	2.77	2.22	2.60
N	3	3	3

INDEPENDENT	T = 5.192	DF = 4	Probability = 0.007
PAIRED	T = 7.099	DF = 2	Probability = 0.019

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	6794.70	1	6794.70	50.400	0.019
TRT x REP	269.63	2	134.82		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	50.78	52.17	- 1.38
Standard Deviation	3.08	5.00	5.00
N	3	3	3

INDEPENDENT	T = 0.408	DF = 4	Probability = 0.704
PAIRED	T = 0.480	DF = 2	Probability = 0.679

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	114.82	1	114.82	0.230	0.679
TRT x REP	998.26	2	499.13		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	50.13	51.48	- 1.35
Standard Deviation	2.15	3.32	1.22
N	3	3	3

INDEPENDENT	T = 0.589	DF = 4	Probability = 0.587
PAIRED	T = 1.916	DF = 2	Probability = 0.195

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	217.35	1	217.35	3.670	0.195
TRT x REP	118.45	2	59.23		

Table D11 : Experiment B03 - Female Longevity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	25.17	48.32	-23.14
Standard Deviation	4.97	4.70	6.39
N	3	3	3

INDEPENDENT	T = 5.863	DF = 4	Probability = 0.004
PAIRED	T = 5.867	DF = 2	Probability = 0.028

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	40028.98	1	40028.98	34.324	0.028
TRT x REP	2332.42	2	1166.21		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	36.25	37.87	- 1.61
Standard Deviation	2.86	2.55	4.09
N	3	3	3

INDEPENDENT	T = 0.729	DF = 4	Probability = 0.506
PAIRED	T = 0.684	DF = 2	Probability = 0.565

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	195.21	1	195.21	0.467	0.565
TRT x REP	835.17	2	417.58		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	36.70	37.06	- 0.36
Standard Deviation	3.50	1.78	2.59
N	3	3	3

INDEPENDENT	T = 0.160	DF = 4	Probability = 0.881
PAIRED	T = 0.242	DF = 2	Probability = 0.831

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	19.68	1	19.68	0.059	0.831
TRT x REP	671.26	2	335.63		

Table D12 : Experiment B04 - Female Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	39.61	47.15	- 7.54
Standard Deviation	4.25	3.46	1.19
N	3	3	3

INDEPENDENT	T = 2.384	DF = 4	Probability = 0.076
PAIRED	T = 10.993	DF = 2	Probability = 0.008

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2347.81	1	2347.81	116.653	0.008
TRT x REP	40.25	2	20.13		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	47.02	42.84	4.18
Standard Deviation	6.24	10.30	13.70
N	3	3	3

INDEPENDENT	T = 0.601	DF = 4	Probability = 0.580
PAIRED	T = 0.528	DF = 2	Probability = 0.650

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	939.43	1	939.43	0.279	0.650
TRT x REP	6726.09	2	3363.04		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	44.26	45.08	- 0.83
Standard Deviation	4.11	5.30	1.61
N	3	3	3

INDEPENDENT	T = 0.214	DF = 4	Probability = 0.841
PAIRED	T = 0.892	DF = 2	Probability = 0.467

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	68.68	1	68.68	0.804	0.464
TRT x REP	170.78	2	85.39		

Table D13 : Experiment B05 - Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	80.67	85.00	- 4.33
Standard Deviation	7.39	3.49	3.92
N	3	3	3

INDEPENDENT	T = 0.917	DF = 4	Probability = 0.411
PAIRED	T = 1.909	DF = 2	Probability = 0.196

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2697.25	1	2697.25	3.696	0.194
TRT x REP	1459.51	2	729.75		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	CB Lines	DIF
Mean	87.98	85.26	2.72
Standard Deviation	6.35	9.65	3.33
N	3	3	3

INDEPENDENT	T = 0.407	DF = 4	Probability = 0.705
PAIRED	T = 1.412	DF = 2	Probability = 0.294

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	607.29	1	607.29	2.151	0.280
TRT x REP	564.60	2	282.30		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	82.70	86.69	- 3.99
Standard Deviation	5.60	8.03	4.23
N	3	3	3

INDEPENDENT	T = 0.706	DF = 4	Probability = 0.519
PAIRED	T = 1.635	DF = 2	Probability = 0.244

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3370.32	1	3370.32	2.624	0.247
TRT x REP	2568.55	2	1284.27		

Table D14 : Experiment B05 - Conditional Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	82.25	86.23	- 3.99
Standard Deviation	6.20	4.46	2.18
N	3	3	3

INDEPENDENT	T = 0.903	DF = 4	Probability = 0.417
PAIRED	T = 3.162	DF = 2	Probability = 0.087

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2251.00	1	2251.00	10.417	0.084
TRT x REP	432.16	2	216.08		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	88.96	86.65	2.31
Standard Deviation	5.67	8.45	3.39
N	3	3	3

INDEPENDENT	T = 0.394	DF = 4	Probability = 0.714
PAIRED	T = 1.182	DF = 2	Probability = 0.359

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	434.81	1	434.81	1.464	0.350
TRT x REP	594.11	2	297.05		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	84.14	87.86	- 3.71
Standard Deviation	5.39	7.04	3.71
N	3	3	3

INDEPENDENT	T = 0.726	DF = 4	Probability = 0.508
PAIRED	T = 1.734	DF = 2	Probability = 0.225

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2880.32	1	2880.32	2.906	0.230
TRT x REP	1982.59	2	991.29		



Table D15 : Experiment B05 - Female Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	27.88	35.84	- 7.96
Standard Deviation	2.33	2.08	1.84
N	3	3	3

INDEPENDENT	T = 4.417	DF = 4	Probability = 0.012
PAIRED	T = 7.474	DF = 2	Probability = 0.017

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	9306.58	1	9306.58	56.192	0.017
TRT x REP	331.24	2	165.62		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	29.21	32.14	- 2.93
Standard Deviation	2.44	4.58	2.53
N	3	3	3

INDEPENDENT	T = 0.977	DF = 4	Probability = 0.384
PAIRED	T = 1.992	DF = 2	Probability = 0.185

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	751.05	1	751.05	3.891	0.187
TRT x REP	386.04	2	193.02		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	31.88	30.72	1.16
Standard Deviation	1.98	3.43	2.38
N	3	3	3

INDEPENDENT	T = 0.506	DF = 4	Probability = 0.640
PAIRED	T = 0.842	DF = 2	Probability = 0.488

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	293.88	1	293.88	0.711	0.488
TRT x REP	826.15	2	413.08		

Table D16 : Experiment B05 - Male Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	17.75	26.73	- 8.98
Standard Deviation	0.98	0.69	0.29
N	3	3	3

INDEPENDENT	T = 12.956	DF = 4	Probability = 0.000
PAIRED	T = 53.067	DF = 2	Probability = 0.000

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	11850.06	1	11850.06	2799.130	0.000
TRT x REP	8.47	2	4.23		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	20.88	25.25	- 4.36
Standard Deviation	1.44	1.19	0.43
N	3	3	3

INDEPENDENT	T = 4.048	DF = 4	Probability = 0.016
PAIRED	T = 17.509	DF = 2	Probability = 0.003

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1668.86	1	1668.86	300.159	0.003
TRT x REP	11.12	2	5.56		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	22.24	23.07	- 0.83
Standard Deviation	0.85	1.18	0.34
N	3	3	3

INDEPENDENT	T = 0.992	DF = 4	Probability = 0.377
PAIRED	T = 4.283	DF = 2	Probability = 0.050

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	152.00	1	152.00	18.124	0.051
TRT x REP	16.77	2	8.39		

Table D17 : Experiment B06 - Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	94.17	93.33	0.84
Standard Deviation	3.33	4.36	3.48
N	3	3	3

INDEPENDENT	T = 0.264	DF = 4	Probability = 0.805
PAIRED	T = 0.419	DF = 2	Probability = 0.716

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	103.08	1	103.08	0.176	0.715
TRT x REP	1170.21	2	585.10		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	91.13	88.15	2.98
Standard Deviation	5.62	5.28	3.22
N	3	3	3

INDEPENDENT	T = 0.669	DF = 4	Probability = 0.540
PAIRED	T = 1.604	DF = 2	Probability = 0.250

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	737.55	1	737.55	2.602	0.248
TRT x REP	566.87	2	283.44		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	93.73	89.74	3.99
Standard Deviation	3.50	5.35	8.47
N	3	3	3

INDEPENDENT	T = 1.082	DF = 4	Probability = 0.340
PAIRED	T = 0.816	DF = 2	Probability = 0.500

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3451.34	1	3451.34	0.671	0.449
TRT x REP	10285.54	2	5142.77		

Table D18 : Experiment B06 - Conditional Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	96.26	95.56	0.70
Standard Deviation	4.97	2.46	4.88
N	3	3	3

INDEPENDENT	T = 0.217	DF = 4	Probability = 0.839
PAIRED	T = 0.247	DF = 2	Probability = 0.828

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	69.15	1	69.15	0.060	0.829
TRT x REP	2294.97	2	1147.49		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	91.85	90.34	1.51
Standard Deviation	5.20	6.51	1.83
N	3	3	3

INDEPENDENT	T = 0.314	DF = 4	Probability = 0.769
PAIRED	T = 1.430	DF = 2	Probability = 0.289

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	186.32	1	186.32	1.978	0.295
TRT x REP	188.41	2	94.20		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	95.86	91.09	4.77
Standard Deviation	3.06	5.85	8.14
N	3	3	3

INDEPENDENT	T = 1.252	DF = 4	Probability = 0.279
PAIRED	T = 1.015	DF = 2	Probability = 0.417

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	4839.39	1	4839.39	1.034	0.416
TRT x REP	9364.12	2	4682.06		

Table D19 : Experiment B06 - Female Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	27.28	33.82	- 6.54
Standard Deviation	1.77	3.50	1.77
N	3	3	3

INDEPENDENT	T = 2.888	DF = 4	Probability = 0.045
PAIRED	T = 6.407	DF = 2	Probability = 0.024

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	6395.32	1	6395.32	40.923	0.024
TRT x REP	312.56	2	156.28		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	27.70	28.68	- 0.98
Standard Deviation	1.57	3.55	2.25
N	3	3	3

INDEPENDENT	T = 0.439	DF = 4	Probability = 0.683
PAIRED	T = 0.756	DF = 2	Probability = 0.529

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	80.50	1	80.50	0.584	0.525
TRT x REP	275.59	2	137.79		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	30.54	28.34	2.20
Standard Deviation	2.63	2.59	0.27
N	3	3	3

INDEPENDENT	T = 1.032	DF = 4	Probability = 0.005
PAIRED	T = 14.332	DF = 2	Probability = 0.360

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1061.54	1	1061.54	202.540	0.005
TRT x REP	10.48	2	5.24		

Table D20 : Experiment B06 - Male Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	20.00	31.00	-11.00
Standard Deviation	3.17	4.46	1.38
N	3	3	3

INDEPENDENT	T = 3.480	DF = 4	Probability = 0.025
PAIRED	T = 13.860	DF = 2	Probability = 0.005

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	18069.03	1	18069.03	191.881	0.005
TRT x REP	188.34	2	94.17		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	25.12	27.05	- 1.93
Standard Deviation	1.15	3.38	2.58
N	3	3	3

INDEPENDENT	T = 0.936	DF = 4	Probability = 0.402
PAIRED	T = 1.297	DF = 2	Probability = 0.324

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	310.89	1	310.89	1.712	0.321
TRT x REP	363.11	2	181.56		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	25.47	26.26	- 0.79
Standard Deviation	3.80	2.13	1.94
N	3	3	3

INDEPENDENT	T = 0.312	DF = 4	Probability = 0.770
PAIRED	T = 0.703	DF = 2	Probability = 0.555

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	135.76	1	135.76	0.504	0.551
TRT x REP	538.50	2	269.25		

Table D21 : Experiment B06 - Female Longevity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	40.43	51.39	-10967
Standard Deviation	3.95	3.76	7.66
N	3	3	3

INDEPENDENT	T = 3.481	DF = 4	Probability = 0.025
PAIRED	T = 2.479	DF = 2	Probability = 0.131

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	17971.46	1	17971.46	6.153	0.131
TRT x REP	5841.29	2	2920.65		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	45.93	47.18	- 1.25
Standard Deviation	0.47	1.63	1.18
N	3	3	3

INDEPENDENT	T = 1.281	DF = 4	Probability = 0.269
PAIRED	T = 1.842	DF = 2	Probability = 0.207

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	306.81	1	306.81	3.393	0.207
TRT x REP	180.85	2	90.43		

Table D22 : Experiment B06 - Male Longevity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	31.94	51.99	-20.04
Standard Deviation	0.50	2.46	2.91
N	3	3	3

INDEPENDENT	T = 13.826	DF = 4	Probability = 0.000
PAIRED	T = 11.923	DF = 2	Probability = 0.007

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	59122.08	1	59122.08	142.153	0.007
TRT x REP	831.81	2	415.91		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	41.99	39.14	2.85
Standard Deviation	1.13	1.49	1.63
N	3	3	3

INDEPENDENT	T = 2.644	DF = 4	Probability = 0.057
PAIRED	T = 3.029	DF = 2	Probability = 0.094

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1606.90	1	1606.90	9.164	0.094
TRT x REP	350.71	2	175.35		



Table D23 : Experiment B07 - Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	81.91	87.35	- 5.44
Standard Deviation	16.74	10.94	11.46
N	3	3	3

INDEPENDENT	T = 0.471	DF = 4	Probability = 0.662
PAIRED	T = 0.822	DF = 2	Probability = 0.497

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	4131.00	1	4131.00	0.677	0.497
TRT x REP	12201.13	2	6100.57		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	87.74	84.45	3.29
Standard Deviation	7.47	7.37	0.54
N	3	3	3

INDEPENDENT	T = 0.542	DF = 4	Probability = 0.616
PAIRED	T = 10.638	DF = 2	Probability = 0.009

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	759.13	1	759.13	114.702	0.009
TRT x REP	13.24	2	6.62		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	84.69	86.05	- 1.37
Standard Deviation	13.91	7.45	8.23
N	3	3	3

INDEPENDENT	T = 0.159	DF = 4	Probability = 0.881
PAIRED	T = 0.288	DF = 2	Probability = 0.801

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	350.77	1	350.77	0.083	0.801
TRT x REP	8487.74	2	4243.87		

Table D24 : Experiment B07 - Conditional Fecundity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	83.17	88.89	- 5.73
Standard Deviation	17.57	11.37	12.41
N	3	3	3

INDEPENDENT	T = 0.474	DF = 4	Probability = 0.660
PAIRED	T = 0.799	DF = 2	Probability = 0.508

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	4506.94	1	4506.94	0.636	0.509
TRT x REP	14176.23	2	7088.12		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	87.74	85.11	2.63
Standard Deviation	7.47	8.51	1.21
N	3	3	3

INDEPENDENT	T = 0.402	DF = 4	Probability = 0.709
PAIRED	T = 3.772	DF = 2	Probability = 0.064

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	483.35	1	483.35	14.035	0.064
TRT x REP	68.88	2	34.44		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	86.06	86.39	- 0.33
Standard Deviation	13.46	8.02	7.79
N	3	3	3

INDEPENDENT	T = 0.036	DF = 4	Probability = 0.973
PAIRED	T = 0.073	DF = 2	Probability = 0.948

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	350.77	1	350.77	0.083	0.801
TRT x REP	8487.74	2	4243.87		

Table D25 : Experiment B07 - Female Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	34.27	48.08	-13.81
Standard Deviation	1.81	3.18	3.61
N	3	3	3

INDEPENDENT	T = 6.537	DF = 4	Probability = 0.003
PAIRED	T = 6.618	DF = 2	Probability = 0.022

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	27403.18	1	27403.18	43.782	0.022
TRT x REP	1251.80	2	625.90		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	38.30	40.67	- 2.37
Standard Deviation	1.26	1.22	1.67
N	3	3	3

INDEPENDENT	T = 2.343	DF = 4	Probability = 0.079
PAIRED	T = 2.459	DF = 2	Probability = 0.133

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	404.38	1	404.38	6.054	0.133
TRT x REP	133.60	2	66.80		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	41.16	39.49	1.67
Standard Deviation	1.83	0.92	1.16
N	3	3	3

INDEPENDENT	T = 1.413	DF = 4	Probability = 0.230
PAIRED	T = 2.495	DF = 2	Probability = 0.130

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	534.07	1	534.07	6.229	0.130
TRT x REP	171.48	2	85.74		

Table D26 : Experiment B07 - Male Starvation

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	24.28	36.43	-12.15
Standard Deviation	1.40	0.95	1.81
N	3	3	3

INDEPENDENT	T = 12.453	DF = 4	Probability = 0.000
PAIRED	T = 11.623	DF = 2	Probability = 0.007

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	21135.62	1	21135.62	135.079	0.007
TRT x REP	312.94	2	156.47		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	31.00	32.04	- 1.05
Standard Deviation	1.18	0.13	1.29
N	3	3	3

INDEPENDENT	T = 1.523	DF = 4	Probability = 0.202
PAIRED	T = 1.403	DF = 2	Probability = 0.296

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	78.60	1	78.60	1.967	0.296
TRT x REP	79.91	2	39.95		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	30.33	31.54	- 1.218
Standard Deviation	0.77	0.51	0.658
N	3	3	3

INDEPENDENT	T = 2.284	DF = 4	Probability = 0.084
PAIRED	T = 3.206	DF = 2	Probability = 0.085

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	284.18	1	284.18	10.285	0.085
TRT x REP	55.26	2	27.63		

Table D27 : Experiment B07 - Female Longevity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	36.61	48.60	-11.99
Standard Deviation	1.92	1.59	2.47
N	3	3	3

INDEPENDENT	T = 8.333	DF = 4	Probability = 0.001
PAIRED	T = 8.406	DF = 2	Probability = 0.014

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	16742.31	1	16742.31	71.217	0.014
TRT x REP	470.18	2	235.09		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	41.51	41.41	0.10
Standard Deviation	4.63	3.60	5.00
N	3	3	3

INDEPENDENT	T = 0.030	DF = 4	Probability = 0.978
PAIRED	T = 0.035	DF = 2	Probability = 0.975

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.59	1	0.59	0.001	0.975
TRT x REP	980.49	2	490.24		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	42.61	41.43	1.19
Standard Deviation	1.31	3.34	3.44
N	3	3	3

INDEPENDENT	T = 0.573	DF = 4	Probability = 0.598
PAIRED	T = 0.598	DF = 2	Probability = 0.611

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	220.26	1	220.26	0.361	0.609
TRT x REP	1220.31	2	610.16		

Table D28 : Experiment B07 - Male Longevity

BB - OO DIFFERENCESMethod 1 - t-test

	BB Lines	OO Lines	DIF
Mean	31.83	48.03	-16.20
Standard Deviation	2.27	0.65	2.84
N	3	3	3

INDEPENDENT	T = 11.867	DF = 4	Probability = 0.000
PAIRED	T = 9.896	DF = 2	Probability = 0.010

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	29901.63	1	29901.63	98.666	0.010
TRT x REP	606.12	2	303.06		

MATERNAL EFFECTSMethod 1 - t-test

	BO Lines	OB Lines	DIF
Mean	35.62	39.42	- 3.79
Standard Deviation	4.01	3.94	3.96
N	3	3	3

INDEPENDENT	T = 1.169	DF = 4	Probability = 0.307
PAIRED	T = 1.659	DF = 2	Probability = 0.239

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	852.93	1	852.93	2.751	0.239
TRT x REP	620.07	2	310.04		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	40.21	37.53	2.68
Standard Deviation	0.44	3.46	3.03
N	3	3	3

INDEPENDENT	T = 1.331	DF = 4	Probability = 0.254
PAIRED	T = 1.528	DF = 2	Probability = 0.266

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1117.88	1	1117.87	2.346	0.265
TRT x REP	953.00	2	476.50		

Table D29 : Experiment B08 - Fecundity

BB - OO DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	468.25	1	468.25	0.571	0.451
ERROR	127905.70	156	819.91		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	354.81	1	354.81	0.280	0.598
ERROR	96266.48	76	1266.66		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	283.96	1	283.96	0.295	0.587
ERROR	224995.24	234	961.52		

Table D30 : Experiment B08 - Conditional Fecundity

BB - OO DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3.81	1	3.81	0.006	0.939
ERROR	99664.36	153	651.40		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	148.38	1	148.38	0.129	0.721
ERROR	86500.87	75	1153.35		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	156.69	1	156.69	0.193	0.660
ERROR	186317.41	230	810.08		



Table D31 : Experiment B08 - Female Starvation

BB - OO DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2689.60	1	2689.60	45.507	0.000
ERROR	9338.38	158	59.10		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.017	1	0.02	0.000	0.986
ERROR	4228.53	78	54.21		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	151.88	1	151.88	2.223	0.137
ERROR	16256.53	238	68.31		

Table D32 : Experiment B08 - Male Starvation

BB - OO DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	893.03	1	893.03	25.017	0.000
ERROR	5640.15	158	35.70		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	6.67	1	6.67	0.319	0.574
ERROR	1630.33	78	20.90		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	4.41	1	4.41	0.128	0.720
ERROR	8070.18	238	34.33		

Table D33 : Experiment B08 - Female Longevity

BB - OO DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3728.19	1	3728.19	16.461	0.000
ERROR	33292.75	147	226.48		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	30.13	1	354.81	0.280	0.598
ERROR	7501.91	74	101.38		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	55.40	1	55.40	0.246	0.620
ERROR	52049.83	231	225.32		

Table D34 : Experiment B08 - Male Longevity

BB - OO DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3728.19	1	3728.19	16.461	0.000
ERROR	33292.75	147	226.48		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	30.13	1	30.13	0.297	0.587
ERROR	7501.91	74	101.38		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.02	1	0.02	0.000	0.991
ERROR	36536.28	227	160.95		

## APPENDIX E

### Summary Statistics of B and O Gene Number Estimates

Table E1 : Experiment GBO1 - Ovary Weight

Replicate	Mean Dry Ovary Weight (mg.) (Variance) Number of Individuals			
	Generation 1		Generation 2	
	BB	BO	BB	BO
1	0.112 (0.002) 43	0.120 (0.003) 44	0.111 (0.003) 41	0.103 (0.003) 48
2	0.147 (0.003) 43	0.107 (0.002) 40	0.122 (0.002) 43	0.120 (0.003) 39
3	0.126 (0.003) 46	0.133 (0.003) 49	0.096 (0.002) 39	0.106 (0.003) 43
4	0.142 (0.003) 47	0.128 (0.002) 46	0.118 (0.002) 36	0.114 (0.002) 48
5	0.125 (0.003) 46	0.128 (0.002) 39	0.103 (0.003) 43	0.116 (0.002) 41
Mean	0.130 (0.006) 5	0.123 (0.005) 5	0.110 (0.005) 5	0.112 (0.003) 5

Table E2-A : Experiment GBO1 - Female Starvation

Replicate	Mean Survival Time (hours) (Variance) Number of Individuals				
	Generation 1			Generation 2	
	BB	OO	BO	BB	BO
1	30.33 (68.83) 48	31.60 (65.63) 33	31.58 (58.93) 48	24.66 (50.03) 42	25.64 (63.90) 51
2	27.75 (27.58) 42	34.50 (59.02) 30	32.74 (87.17) 42	27.59 (28.45) 42	29.86 (79.88) 42
3	29.60 (64.94) 48	31.88 (24.40) 36	31.30 (85.57) 48	26.78 (82.47) 39	26.90 (44.84) 45
4	30.20 (51.31) 48	32.06 (36.70) 33	30.33 (69.68) 45	28.49 (51.06) 39	29.60 (57.96) 48
5	25.43 (36.36) 45	33.63 (67.66) 36	29.28 (57.90) 42	25.44 (39.49) 42	27.13 (48.84) 42
Mean	28.67	32.74	31.05	26.59	27.83
Std Error	(0.93)	(0.57)	(0.59)	(0.70)	(0.82)
N	5	5	5	5	5

Table E2-B : Experiment GB01 - Female Starvation

Replicate	Mean Survival Time (hours) (Variance) Number of Individuals			
	Generation 3		Generation 4	
	BB	BO	BB	BO
1	28.57 (106.07) 45	25.61 (51.28) 42	31.17 (41.38) 45	33.47 (45.32) 42
2	27.99 (79.19) 39	33.39 (95.19) 42	31.38 (38.58) 33	38.54 (78.13) 42
3	25.33 (61.17) 42	31.63 (132.26) 45	29.17 (34.07) 45	32.23 (73.26) 36
4	28.40 (97.28) 48	31.07 (102.91) 45	33.52 (54.56) 39	35.67 (53.53) 51
5	29.60 (148.11) 36	29.65 (82.40) 39	31.63 (87.50) 39	34.61 (61.82) 42
Mean	27.98	30.27	31.37	34.91
Std Error	(0.71)	(1.31)	(0.69)	(1.08)
N	5	5	5	5



Table E2-C : Experiment GBO1 - Female Starvation

Replicate	Mean Survival Time (hours) (Variance) Number of Individuals			
	Generation 5		Generation 6	
	BB	BO	BB	BO
1	36.44 (58.42) 45	34.93 (73.00) 36	28.89 (35.04) 42	31.46 (54.86) 42
2	33.10 (52.62) 27	36.30 (57.47) 39	27.67 (33.23) 36	35.59 (90.27) 33
3	32.47 (73.42) 42	32.67 (73.46) 45	27.07 (44.01) 42	31.56 (48.27) 42
4	34.50 (49.02) 42	38.27 (57.91) 36	30.53 (49.77) 48	32.27 (66.84) 42
5	33.13 (93.18) 39	37.10 (93.34) 36	26.80 (41.56) 42	32.65 (54.07) 33
Mean	33.93	35.85	28.19	32.70
Std error	(0.71)	(0.96)	(0.69)	(0.76)
N	5	5	5	5

Table F3-A : Experiment GBO1 - Male Starvation

Replicate	Mean Survival Time (hours) (Variance) Number of Individuals				
	Generation 1			Generation 2	
	BB	OO	BO	BB	BO
1	19.14 (44.46) 48	24.15 (47.03) 33	22.50 (41.53) 45	17.80 (36.73) 42	21.88 (54.75) 51
2	22.02 (45.43) 42	28.86 (38.73) 33	23.50 (41.99) 42	20.87 (48.84) 42	23.57 (65.08) 42
3	18.98 (26.35) 48	25.60 (40.72) 36	22.80 (41.05) 48	17.60 (21.47) 39	21.43 (53.16) 45
4	21.20 (48.83) 48	25.16 (18.06) 33	21.89 (54.46) 45	20.65 (78.61) 39	25.48 (60.11) 48
5	17.97 (57.53) 45	24.30 (59.34) 36	19.85 (36.96) 42	16.73 (30.11) 42	23.27 (65.08) 42
Mean	19.86	25.61	22.11	18.73	23.13
Std Error	(0.754)	(0.854)	(0.621)	(0.849)	(0.713)
N	5	5	5	5	5

Table E3-B : Experiment GB01 - Male Starvation

Replicate	Mean Survival Time (hours) (Variance) Number of Individuals			
	Generation 3		Generation 4	
	BB	BO	BB	BO
1	20.10 (31.91) 45	24.76 (50.03) 42	20.77 (41.16) 45	25.90 (65.42) 42
2	22.91 (41.59) 39	27.93 (50.34) 42	20.66 (18.70) 33	26.97 (41.81) 42
3	19.47 (36.98) 42	24.70 (48.44) 45	19.30 (34.36) 45	24.04 (55.88) 42
4	22.65 (39.77) 48	26.93 (56.98) 45	23.82 (33.86) 39	25.40 (67.96) 50
5	20.93 (47.54) 36	22.87 (41.44) 39	17.94 (18.41) 39	22.61 (54.79) 42
Mean	21.21	25.44	20.50	24.99
Std Error	(0.681)	(0.895)	(0.978)	(0.757)
N	5	5	5	5

Table E3-C : Experiment GB01 - Male Starvation

Replicate	Mean Survival Time (hours) (Variance) Number of Individuals			
	Generation 5		Generation 6	
	BB	BO	BB	BO
1	20.80 (28.09) 48	20.93 (27.06) 36	19.89 (38.99) 42	20.87 (32.66) 45
2	24.01 (67.77) 33	26.30 (110.53) 39	19.21 (22.75) 42	23.96 (56.32) 33
3	20.19 (32.11) 42	22.80 (38.80) 45	18.64 (30.86) 42	20.84 (28.52) 42
4	23.08 (40.25) 38	22.77 (38.29) 36	21.65 (30.57) 48	25.56 (41.39) 42
5	22.52 (45.09) 39	23.43 (33.91) 36	18.66 (20.17) 42	22.65 (42.82) 33
Mean	22.12	23.25	19.61	22.77
Std error	(0.712)	(0.870)	(0.558)	(0.909)
N	5	5	5	5

Table E4 : Experiment GB02 - Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	97.70 (638.2) 95	97.82 (604.8) 100	84.94 (278.6) 118	82.46 (486.9) 143
2	91.00 (234.7) 100	93.05 (584.0) 99	88.78 (437.6) 117	89.94 (385.7) 143
3	93.81 (719.0) 94	89.11 (831.1) 97	95.51 (507.8) 109	84.19 (548.7) 138
Mean	94.17	93.33	89.74	85.53
Std Error	(1.94)	(2.52)	(3.09)	(2.26)
N	3	3	3	3

Table E5 : Experiment GB02 - Conditional Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	100.9 (334.3) 92	97.82 (604.8) 100	85.67 (218.3) 117	84.84 (298.3) 139
2	91.00 (234.7) 100	95.92 (328.4) 96	90.32 (304.6) 115	90.57 (330.6) 142
3	96.89 (442.1) 91	92.95 (507.1) 93	97.29 (342.0) 107	86.70 (345.7) 134
Mean	96.26	95.56	91.09	87.37
Std Error	(2.87)	(1.42)	(3.38)	(1.69)
N	3	3	3	3

Table E6 : Experiment GB02 - Female Starvation

Replicate	Mean Survival Time (hours) (Variance) Number of Individuals			
	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	27.41 (41.67) 100	33.50 (87.88) 98	28.53 (50.34) 119	30.46 (75.16) 142
2	28.98 (36.31) 100	37.47 (67.64) 100	30.83 (46.79) 120	29.82 (75.18) 142
3	25.45 (28.92) 100	30.49 (101.0) 100	25.66 (28.61) 108	27.64 (69.00) 142
Mean	27.28	33.82	28.34	29.31
Std Error	(1.02)	(2.02)	(1.50)	(0.86)
N	3	3	3	3

Table E7 : Experiment GB02 - Male Starvation

Mean Survival Time (hours) (Variance) Number of Individuals				
Replicate	BB	00	F <sub>1</sub>	F <sub>2</sub>
1	22.46 (28.01) 100	33.96 (85.76) 98	28.33 (47.23) 120	30.37 (52.86) 142
2	21.12 (26.95) 100	33.18 (142.5) 100	26.38 (50.79) 120	26.32 (36.87) 142
3	16.42 (18.04) 100	25.87 (86.25) 99	24.07 (42.94) 108	23.96 (63.74) 142
Mean	20.00	31.00	26.26	26.88
Std Error	(1.83)	(2.58)	(1.23)	(1.87)
N	3	3	3	3



Table E8 : Experiment GB02 - Female Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	43.71 (125.3) 99	49.05 (277.5) 100	48.97 (216.0) 97	43.47 (155.7) 153
2	41.53 (146.0) 100	49.39 (268.7) 100	45.80 (169.0) 98	43.90 (179.3) 158
3	36.04 (138.0) 99	55.73 (233.6) 100	46.77 (118.7) 97	42.51 (201.1) 159
Mean	40.42	51.39	47.18	43.29
Std Error	(2.28)	(2.17)	(0.94)	(0.41)
N	3	3	3	3

Table E9 : Experiment GBO2 - Male Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	32.31 (146.2) 98	49.37 (191.3) 95	38.98 (141.8) 97	40.94 (134.8) 158
2	31.37 ( 86.0) 100	54.25 (184.8) 100	40.70 (133.1) 100	39.94 (148.2) 160
3	32.15 ( 86.0) 96	53.34 (258.8) 100	37.73 ( 97.9) 100	36.46 (117.0) 160
Mean	31.94	52.32	39.14	39.11
Std Error	(0.29)	(1.50)	(0.86)	(1.36)
N	3	3	3	3

Table F10 : Experiment GBO3 - Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	94.40 (565.2) 92	99.90 (561.6) 95	94.64 (294.2) 96	81.22 (420.1) 191
2	88.44 (289.0) 93	82.40 (262.7) 91	81.29 (219.2) 91	85.66 (204.8) 181
3	62.89 (193.8) 93	79.76 (384.4) 95	82.24 (223.6) 95	72.94 (263.7) 185
Mean	81.91	87.35	86.05	79.94
Std Error	(9.66)	(6.34)	(4.30)	(3.73)
N	3	3	3	3

Table E11 : Experiment GB03 - Conditional Fecundity

Replicate	Mean 24 Hour Fecundity (Variance) Number of Individuals			
	PB	OO	F <sub>1</sub>	F <sub>2</sub>
1	97.49 (287.4) 89	102.0 (356.6) 93	95.63 (201.0) 95	83.80 (220.6) 185
2	88.44 (289.0) 93	82.40 (262.7) 91	81.29 (219.2) 91	85.66 (204.8) 181
3	63.57 (153.4) 92	82.26 (195.9) 92	82.24 (223.6) 95	73.29 (242.7) 184
Mean	83.17	88.89	86.39	80.92
Std Error	(10.14)	(6.57)	(4.63)	(3.85)
N	3	3	3	3

Table E12 : Experiment GB03 - Female Starvation

Mean Survival Time (hours) (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	32.20 (73.97) 96	47.46 (199.8) 96	38.49 (129.5) 96	44.65 (118.3) 179
2	35.05 (90.92) 96	51.52 (175.0) 95	40.28 (130.8) 96	41.56 (99.31) 192
3	35.56 (67.01) 96	45.26 (111.2) 96	39.70 (62.62) 96	38.61 (113.3) 186
Mean	34.27	48.08	39.49	41.61
Std Error	(1.05)	(1.84)	(0.53)	(1.75)
N	3	3	3	3

Table E13 : Experiment GBO3 - Male Starvation

Mean Survival Time (hours) (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	23.48 (43.22) 96	37.46 (97.79) 96	32.08 (76.63) 96	33.17 (118.3) 179
2	25.89 (48.21) 96	36.25 (98.88) 94	31.48 (63.00) 96	32.32 (76.58) 192
3	23.47 (34.10) 96	35.58 (92.07) 95	31.08 (69.68) 96	29.00 (67.98) 185
Mean	24.28	36.43	31.54	31.50
Std Error	(0.81)	(0.55)	(0.29)	(1.27)
N	3	3	3	3

Table E14 : Experiment GB03 - Female Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	37.78 (143.6) 71	47.05 (254.9) 79	45.27 (180.8) 78	42.71 (208.3) 158
2	34.40 (129.2) 83	48.51 (268.7) 79	39.20 (260.5) 79	38.13 (210.8) 154
3	37.65 (160.2) 78	50.23 (282.3) 77	39.81 (239.5) 78	40.79 (195.8) 158
Mean Std Error N	36.61 (1.11) 3	48.60 (0.92) 3	41.43 (1.93) 3	40.54 (1.33) 3

Table E15 : Experiment GB03 - Male Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	BB	OO	F <sub>1</sub>	F <sub>2</sub>
1	34.25 (180.5) 77	47.29 (253.5) 75	40.72 (187.2) 79	42.83 (192.9) 160
2	31.51 ( 96.5) 77	48.53 (293.1) 79	38.01 (175.4) 79	41.10 (170.9) 157
3	29.74 ( 81.5) 68	48.27 (322.4) 81	33.86 (145.3) 79	38.11 (161.9) 160
Mean	31.83	48.03	37.43	40.68
Std Error	(1.31)	(0.38)	(1.92)	(1.38)
N	3	3	3	3



APPENDIX F

Analysis of Heritability and Selection Experiments

Table F1 : Analysis of Heritability Changes

B -> F COMPARISONFemale Starvation

	B Lines	F Lines	DIF
Mean	0.750	0.487	0.265
Standard Deviation	0.565	0.032	0.600
N	3	3	3

INDEPENDENT	T = 0.806	DF = 4	Probability = 0.465
PAIRED	T = 0.765	DF = 2	Probability = 0.524

Male Starvation

	B Lines	F Lines	DIF
Mean	0.180	0.310	-0.130
Standard Deviation	0.203	0.098	0.185
N	3	3	3

INDEPENDENT	T = 0.998	DF = 4	Probability = 0.375
PAIRED	T = 1.216	DF = 2	Probability = 0.348

O -> S COMPARISONFemale Starvation

	O Lines	S Lines	DIF
Mean	0.840	0.513	0.327
Standard Deviation	0.471	0.355	0.809
N	3	3	3

INDEPENDENT	T = 0.959	DF = 4	Probability = 0.392
PAIRED	T = 0.699	DF = 2	Probability = 0.557

Male Starvation

	O Lines	S Lines	DIF
Mean	0.593	0.463	0.130
Standard Deviation	0.486	0.101	0.563
N	3	3	3

INDEPENDENT	T = 0.453	DF = 4	Probability = 0.674
PAIRED	T = 0.400	DF = 2	Probability = 0.728

Table F2 : Analysis of Direct Response to Selection for  
Early Fecundity In Last 6 Generations of B -> F Populations

Fecundity

SOURCE	SS	DF	MS	F	P
TRT	132815.467	1	132815.467	199.869	0.000
TRT x REP x GEN	6645.108	10	664.511		

Conditional Fecundity

SOURCE	SS	DF	MS	F	P
TRT	146941.388	1	146941.388	275.640	0.000
TRT x REP x GEN	5330.912	10	533.091		

Table F3 : Analysis of Indirect Response to Selection for  
Early Fecundity In Last 6 Generations of B -> F Populations

Female Starvation

SOURCE	SS	DF	MS	F	P
TRT	2815.761	1	2815.761	15.838	0.003
TRT x REP x GEN	1777.799	10	177.780		

Table F4 : Analysis of Direct Response to Selection for  
Starvation Time In Last 6 Generations of O -> S Populations

Female Starvation

SOURCE	SS	DF	MS	F	P
TRT	208193.230	1	208193.230	584.932	0.000
TRT x REP x GEN	3559.273	10	355.927		

Male Starvation

SOURCE	SS	DF	MS	F	P
TRT	342119.839	1	342119.839	679.879	0.000
TRT x REP x GEN	5054.368	10	505.437		

Starvation

SOURCE	SS	DF	MS	F	P
TRT	271067.820	1	271067.827	841.413	0.000
TRT x REP x GEN	3221.580	10	322.158		

Table F5 · Analysis of Indirect Response to Selection for  
Starvation Time In Last 6 Generations of O -> S Populations

Fecundity

SOURCE	SS	DF	MS	F	P
TRT	21681.823	1	21681.823	36.839	0.000
TRT x REP x GEN	5884.148	10	588.715		

Conditional Fecundity

SOURCE	SS	DF	MS	F	P
TRT	16989.981	1	16989.981	39.116	0.000
TRT x REP x GEN	4343.541	10	434.354		

APPENDIX G

Summary Statistics of F and S Diallels

Table G1 : Experiment DF1 - Fecundity

Male Parent	Mean 24 Hour Fecundity (Standard Error) Number of Individuals			Mean
	1	2	3	
1	48.75 (2.24) 60	---	---	
2	48.32 (2.07) 60	42.80 (1.51) 60	---	
3	47.97 (1.91) 60	45.83 (1.49) 60	46.97 (1.62) 60	
Mean				46.77 (0.75) 360



Table G2 : Experiment DF1 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	50.40 (2.00) 58	---	---	
2	48.32 (2.07) 60	42.80 (1.51) 60	---	
3	47.97 (1.91) 60	45.83 (1.49) 60	47.71 (1.47) 59	
Mean				47.15 (0.72) 357

Table G3 : Experiment DF2 - Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	88.64 (7.82) 14	96.50 (7.75) 8	96.89 (6.60) 9	94.01 (2.69) 3
2	79.36 (10.59) 11	94.44 (2.93) 70	77.33 (4.41) 39	83.71 (5.40) 3
3	89.08 (8.58) 12	81.13 (4.62) 38	81.70 (2.07) 77	83.97 (2.56) 3
Mean	85.69 (3.17) 3	90.69 (4.82) 3	85.31 (5.93) 3	85.71 (1.52) 278

Table G4 : Experiment DF2 - Conditional Fecundity

	Mean 24 Hour Fecundity (Standard Error) Number of Individuals			
Male Parent	Female Parent			Mean
	1	2	3	
1	95.31 (4.42) 13	96.50 (7.75) 8	96.89 (6.60) 9	96.23 (0.48) 3
2	87.10 (8.00) 10	97.19 (2.26) 68	83.78 (2.73) 36	89.36 (4.03) 3
3	97.18 (3.11) 11	88.09 (2.68) 35	81.70 (2.07) 77	88.99 (4.49) 3
Mean	93.20 (3.10) 3	93.93 (2.93) 3	87.46 (4.75) 3	89.22 (1.16) 267

Table G5 : Experiment DF2 - Female Starvation

Mean Starvation Time (hours) (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	25.14 (1.01) 26	29.28 (1.60) 8	25.55 (1.30) 12	26.66 (1.32) 3
2	25.75 (1.67) 12	28.35 (0.78) 79	26.16 (1.12) 38	26.75 (0.81) 3
3	29.15 (1.18) 12	27.33 (1.07) 39	25.48 (0.82) 80	27.32 (1.06) 3
Mean	26.68 (1.25) 3	28.32 (0.56) 3	25.73 (0.22) 3	26.77 (0.38) 306

Table G6 : Experiment DF2 - Male Starvation

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	18.91 (0.93) 26	23.65 (1.58) 8	25.30 (2.35) 12	22.62 (1.92) 3
2	19.75 (1.01) 12	22.44 (0.82) 79	21.85 (0.83) 37	21.35 (0.82) 3
3	24.15 (2.23) 12	21.40 (0.83) 40	19.85 (0.67) 80	21.80 (1.26) 3
Mean	20.94 (1.62) 3	22.50 (0.65) 3	22.33 (1.59) 3	21.36 (0.36) 306

Table G7 : Experiment DF3 - Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	90.26 (1.70) 78	47.53 (2.57) 40	80.82 (2.37) 33	72.87 (12.96) 3
2	39.67 (1.56) 39	39.01 (1.77) 80	76.20 (1.85) 40	51.63 (12.29) 3
3	66.28 (4.35) 39	77.00 (2.21) 40	80.67 (1.96) 78	74.65 (4.32) 3
Mean	65.40 (14.61) 3	54.51 (11.51) 3	79.23 (1.52) 3	66.98 (1.17) 467

Table G8 : Experiment DF3 -- Conditional Fecundity

Male Parent	Mean 24 Hour Fecundity (Standard Error) Number of Individuals			Mean
	1	2	3	
1	90.26 (1.70) 78	48.74 (2.32) 39	80.82 (2.37) 33	73.27 (12.57) 3
2	39.67 (1.56) 39	42.12 (1.38) 74	76.20 (1.85) 40	52.66 (11.79) 3
3	69.57 (3.89) 37	77.00 (2.21) 40	82.71 (1.36) 76	76.43 (3.80) 3
Mean	66.50 (14.68) 3	55.95 (10.70) 3	79.91 (1.93) 3	68.55 (1.10) 456

Table G9 : Experiment DF3 - Female Starvation

Mean Starvation Time (hours) (Standard Error) Number of Individuals				
Male Parent 1	Female Parent		Mean	
	2	3		
1	30.81 (0.77) 80	28.45 (1.10) 40	28.15 (1.08) 34	29.14 (0.84) 3
2	29.43 (1.23) 40	31.99 (0.79) 80	27.55 (0.99) 40	29.66 (1.29) 3
3	31.20 (1.20) 38	26.75 (1.07) 40	30.61 (0.87) 80	29.52 (1.40) 3
Mean	30.48 (0.54) 3	29.06 (1.54) 3	28.77 (0.94) 3	29.88 (0.33) 472



Table G10 : Experiment DF3 - Male Starvation

Male Parent	Mean 24 Hour Fecundity (Standard Error) Number of Individuals			Mean
	1	2	3	
1	22.29 (0.93) 80	21.20 (1.11) 39	21.80 (1.02) 34	21.76 (0.32) 3
2	25.53 (1.78) 40	20.93 (0.75) 80	22.75 (1.04) 40	23.07 (1.34) 3
3	22.43 (1.42) 38	19.10 (0.78) 40	20.41 (0.67) 80	20.65 (0.97) 3
Mean	23.42 (1.06) 3	20.41 (0.66) 3	21.65 (0.68) 3	21.67 (0.35) 471

Table G11 : Experiment DS1 - Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	28.05 (1.47) 60	---	---	
2	29.42 (1.30) 60	25.05 (1.13) 60	---	
3	31.32 (1.40) 59	29.83 (1.03) 60	28.39 (1.30) 59	
Mean				28.67 (0.53) 358

Table G12 : Experiment DS1 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	29.33 (1.35) 57	---	---	
2	30.43 (1.13) 58	26.23 (0.95) 57	---	
3	31.32 (1.40) 59	30.34 (0.91) 59	28.88 (1.23) 58	
Mean				29.44 (0.48) 348

Table G13 : Experiment DS2 - Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	78.35 (2.28) 74	74.40 (3.66) 38	74.16 (3.89) 38	75.64 (1.36) 3
2	85.23 (3.23) 39	72.81 (2.60) 72	81.36 (4.80) 22	79.80 (3.67) 3
3	78.16 (3.42) 37	78.68 (3.47) 40	69.64 (3.98) 55	75.49 (1.73) 3
Mean	80.58 (2.33) 3	75.30 (1.75) 3	75.05 (3.43) 3	76.31 (1.13) 415

Table G14 : Experiment DS2 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	79.41 (2.04) 73	78.53 (2.38) 36	78.28 (2.78) 36	78.74 (0.34) 3
2	87.47 (2.38) 38	77.00 (1.70) 68	85.24 (2.97) 21	83.24 (3.18) 3
3	80.33 (2.71) 36	80.69 (2.90) 39	79.79 (1.89) 48	80.27 (0.26) 3
Mean	82.47 (2.55) 3	78.74 (1.07) 3	81.10 (2.11) 3	80.15 (0.79) 395

Table G15 : Experiment DS2 - Female Starvation

Mean Starvation Time (hours) (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	31.34 (1.35) 80	38.35 (1.96) 40	49.64 (2.49) 38	39.78 (5.33) 3
2	28.63 (1.93) 40	48.74 (1.34) 74	50.98 (2.25) 22	42.78 (7.11) 3
3	51.73 (2.01) 36	46.60 (1.28) 40	41.84 (1.59) 60	46.72 (2.86) 3
Mean	37.23 (7.29) 3	44.56 (3.17) 3	47.49 (2.85) 3	41.95 (0.70) 430

Table G16 : Experiment DS2 - Male Starvation

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Male Parent	Female Parent			Mean
	1	2	3	
1	26.01 (1.41) 78	28.13 (2.47) 40	41.91 (1.42) 38	32.02 (4.98) 3
2	22.48 (2.07) 40	43.43 (1.45) 74	41.98 (1.42) 38	35.96 (6.75) 3
3	35.23 (1.73) 36	36.40 (1.55) 40	31.36 (1.14) 60	34.33 (1.52) 3
Mean	27.91 (3.80) 3	35.99 (4.42) 3	38.42 (3.53) 3	33.62 (0.66) 428

## APPENDIX II

### Analysis of F and S Population Diallels



Table H1 : Experiment DF1 - Fecundity

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	878.01	2	439.01	7.150	0.123
MPAR	122.81	2	61.40		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	46.172	47.37 2
Standard Deviation	3.054	1.34 4
N	3	3

POOLED VAR      T = 0.623    DF = 4      Probability = 0.567

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	129.60	1	129.60	0.388	0.567
REP within TRT	1335.69	4	333.92		

Table H2 : Experiment DF1 - Conditional Fecundity

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	903.91	2	451.95	2.946	0.253
MPAR	306.81	2	153.41		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	46.969	47.37 2
Standard Deviation	3.852	1.34 4
N	3	3

POOLED VAR      T = 0.171    DF = 4      Probability = 0.873

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	14.48	1	14.48	0.029	0.872
REP within TRT	1973.28	4	493.32		

Table H3 : Experiment DF2 - Fecundity

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	957.60	2	478.80	0.341	0.730
MPAR	2509.41	2	1254.71	0.895	0.477
FPAR & MPAR	3257.92	4	814.48	0.581	0.694
FPAR x MPAR	5610.49	4	1402.62		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	957.60	2	478.80	0.382	0.724
MPAR	2509.41	2	1254.71		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	546.46	2	273.23	0.113	0.898
MPAR	4833.32	2	2416.66		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	88.262	86.717
Standard Deviation	6.379	8.696
N	3	6

SEPARATE VAR	T = 0.302	DF = 5.5	Probability = 0.775
POOLED VAR	T = 0.270	DF = 7	Probability = 0.795

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	100.33	1	100.33	0.063	0.809
REP within TRT	11125.37	7	1589.34		

Table H4 : Experiment DF2 - Conditional Fecundity

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	1361.39	2	680.69	1.149	0.403
MPAR	1181.68	2	590.84	1.998	0.445
FPAR & MPAR	2940.17	4	735.04	1.241	0.420
FPAR x MPAR	2368.98	4	592.24		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	1361.39	2	680.69	1.152	0.465
MPAR	1181.68	2	590.84		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	719.52	2	359.76	0.331	0.751
MPAR	2171.14	2	1085.57		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	91.400	91.589
Standard Deviation	8.452	5.949
N	3	6

SEPARATE VAR	T = 0.035	DF = 3.0	Probability = 0.975
POOLED VAR	T = 0.040	DF = 7	Probability = 0.970

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1.43	1	1.43	0.001	0.978
REP within TRT	11934.70	7	1704.96		

Table H5 : Experiment DF2 - Female Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	212.08	2	106.04	2.578	0.191
MPAR	16.06	2	8.03	0.195	0.830
FPAR & MPAR	241.55	4	60.39	1.468	0.360
FPAR x MPAR	164.56	4	41.14		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	212.08	2	106.04	13.205	0.070
MPAR	16.06	2	8.03		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	15.41	2	7.70	1.044	0.489
MPAR	14.76	2	7.38		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	26.321	27.20 3
Standard Deviation	1.764	1.6875
N	3	6

SEPARATE VAR	T = 0.720	DF = 3.9	Probability = 0.524
POOLED VAR	T = 0.734	DF = 7	Probability = 0.487

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	41.16	2	41.16	0.506	0.500
REP within TRT	568.94	2	81.28		

Table H6 : Experiment DF2 - Male Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	71.22	2	35.61	0.259	0.784
MPAR	39.58	2	19.79	0.144	0.870
FPAR & MPAR	83.49	4	20.87	0.152	0.953
FPAR x MPAR	550.80	4	137.70		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	71.22	2	35.61	1.799	0.357
MPAR	39.58	2	19.79		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	98.76	2	49.38	0.422	0.703
MPAR	234.10	2	117.05		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	20.399	222.683
Standard Deviation	1.828	12.044
N	3	6

SEPARATE VAR	T = 1.698	DF = 4.6	Probability = 0.165
POOLED VAR	T = 1.628	DF = 7	Probability = 0.148

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	275.59	2	275.59	2.936	0.130
REP within TRT	657.16	2	93.88		

Table H7 : Experiment DF3 - Fecundity

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	42170.77	2	21085.39	1.599	0.390
MPAR	46270.27	2	23135.13	1.754	0.284
FPAR & MPAR	10544.74	4	26361.18	1.999	0.259
FPAR x MPAR	52759.23	4	13189.81		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	42170.77	2	21085.39	0.911	0.523
MPAR	46270.27	2	23125.13		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	48310.05	2	24155.02	1.548	0.393
MPAR	31217.44	2	15608.72		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	69.379	64.582
Standard Deviation	27.243	17.131
N	3	6

SEPARATE VAR	T = 0.314	DF = 2.8	Probability = 0.784
POOLED VAR	T = 0.372	DF = 7	Probability = 0.721

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3391.30	1	3391.30	0.137	0.723
REP within TRT	173870.56	7	24838.65		

Table H8 : Experiment DF3 - Conditional Fecundity

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	39042.34	2	19521.17	1.63 <sub>2</sub>	0.303
MPAR	46223.79	2	23111.89	1.934	0.258
FPAR & MPAR	100604.22	4	25151.06	2.105	0.244
FPAR x MPAR	47799.31	4	11949.83		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	39042.34	2	19521.17	0.845	0.542
MPAR	46223.79	2	23111.89		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	45751.25	2	22875.63	1.383	0.420
MPAR	33071.71	2	16535.86		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	71.696	65.333
Standard Deviation	25.889	817.005
N	3	6

SEPARATE VAR	T = 0.386	DF = 2.9	Probability = 0.737
POOLED VAR	T = 0.451	DF = 7	Probability = 0.666

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	4604.83	1	4604.83	0.207	0.663
REP within TRT	155915.86	7	22273.70		



Table H9 : Experiment DF3 - Female Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	232.35	2	116.17	0.406	0.691
MPAR	19.71	2	9.86	0.034	0.966
FPAR & MPAR	236.24	4	59.06	0.207	0.922
FPAR x MPAR	1143.56	4	285.89		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	232.35	2	116.17	11.788	0.078
MPAR	19.71	2	9.86		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	404.14	2	202.07	5.556	0.153
MPAR	72.74	2	36.37		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	31.138	228.587
Standard Deviation	0.743	11.559
N	3	6

SEPARATE VAR	T = 3.322	DF = 7.0	Probability = 0.016
POOLED VAR	T = 2.620	DF = 7	Probability = 0.034

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	765.91	2	765.91	9.575	0.017
REP within TRT	559.93	2	79.99		

Table H10 : Experiment DF3 - Male Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	646.05	2	323.02	7.368	0.046
MPAR	417.83	2	208.92	4.765	0.087
FPAR & MPAR	1022.50	4	255.63	5.830	0.058
FPAR x MPAR	175.37	4	43.84		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	646.05	2	323.02	1.546	0.393
MPAR	417.83	2	208.92		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	376.78	2	188.39	1.298	0.435
MPAR	290.35	2	145.18		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	21.208	222.135
Standard Deviation	0.969	12.105
N	3	6

SEPARATE VAR	T = 0.904	DF = 7.0	Probability = 0.401
POOLED VAR	T = 0.707	DF = 7	Probability = 0.502

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	100.87	2	100.87	0.683	0.436
REP within TRT	1034.56	2	147.80		

Table H11 : Experiment DS1 - Fecundity

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	701.97	2	350.99	0.794	0.557
MPAR	883.79	2	441.89		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	27.163	30.191
Standard Deviation	1.838	1.002
N	3	3

POOLED VAR      T = 2.505    DF = 4      Probability = 0.066

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	820.23	1	820.23	6.273	0.066
REP within TRT	523.00	4	130.75		

Table H12 : Experiment DS1 - Conditional Fecundity

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	533.43	2	266.72	1.175	0.460
MPAR	453.94	2	226.97		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	28.147	30.697
Standard Deviation	1.677	0.543
N	3	3

POOLED VAR      T = 2.506   DF = 4      Probability = 0.066

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	565.80	1	565.80	6.359	0.065
REP within TRT	355.93	4	88.98		

Table H13 : Experiment DS2 - Fecundity

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	2517.98	2	1258.99	1.316	0.364
MPAR	1357.27	2	678.64	0.710	0.545
FPAR & MPAR	3995.21	4	998.80	1.044	0.484
FPAR x MPAR	3825.53	4	956.38		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	2517.98	2	1258.99	1.855	0.350
MPAR	1357.27	2	678.64		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	118.80	2	59.40	0.062	0.942
MPAR	1931.49	2	965.74		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	73.598	78.664
Standard Deviation	4.411	4.224
N	3	6

SEPARATE VAR	T = 1.647	DF = 3.9	Probability = 0.198
POOLED VAR	T = 1.675	DF = 7	Probability = 0.138

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2580.40	1	2580.40	3.082	0.123
REP within TRT	5860.60	7	837.23		

Table H14 : Experiment DS2 - Conditional Fecundity

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	908.96	2	454.48	0.969	0.454
MPAR	1168.80	2	584.40	1.246	0.380
FPAR & MPAR	1766.10	4	441.53	0.941	0.523
FPAR x MPAR	1875.95	4	468.99		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	1766.10	2	454.48	0.778	0.563
MPAR	1168.80	2	584.40		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	41.08	2	20.54	0.025	0.976
MPAR	1642.73	2	821.36		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	78.734	81.757
Standard Deviation	1.514	3.755
N	3	6

SEPARATE VAR	T = 1.713	DF = 6.9	Probability = 0.138
POOLED VAR	T = 1.305	DF = 7	Probability = 0.233

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	866.05	1	866.05	2.241	0.178
REP within TRT	2705.27	7	386.47		

Table H15 : Experiment DS2 - Female Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	6948.00	2	3474.00	0.923	0.468
MPAR	3269.29	2	1634.64	0.434	0.675
FPAR & MPAR	12367.24	4	3091.81	0.822	0.573
FPAR x MPAR	15051.98	4	3763.00		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	6948.00	2	3474.00	2.125	0.320
MPAR	3269.29	2	1634.64		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	8575.27	2	4287.64	0.857	0.538
MPAR	10000.88	2	5000.44		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	40.640	244.322
Standard Deviation	8.762	19.109
N	3	6

SEPARATE VAR	T = 0.587	DF = 4.2	Probability = 0.589
POOLED VAR	T = 0.578	DF = 7	Probability = 0.581

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1413.93	2	1413.93	0.363	0.566
REP within TRT	27237.57	2	3891.08		

Table H16 : Experiment DS2 - Male Starvation

LINE EFFECTS

SOURCE	SS	DF	MS	F	P
FPAR	7605.56	2	3802.78	1.350	0.356
MPAR	977.82	2	488.91	0.174	0.847
FPAR & MPAR	9266.41	4	2316.60	0.822	0.573
FPAR x MPAR	11267.04	4	2816.76		

MATERNAL EFFECTSMethod 1 - ANOVA of Diallel with Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	7605.56	2	3802.78	7.778	0.114
MPAR	977.82	2	488.91		

Method 2 - ANOVA of Diallel without Diagonal

SOURCE	SS	DF	MS	F	P
FPAR	9008.07	2	4504.04	2.078	0.325
MPAR	4334.63	2	2167.32		

HETEROSIS / INBREEDING EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines
Mean	33.600	234.353
Standard Deviation	8.920	17.747
N	3	6

SEPARATE VAR	T = 0.125	DF = 3.6	Probability = 0.909
POOLED VAR	T = 0.131	DF = 7	Probability = 0.899

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	58.91	2	58.91	0.018	0.896
REP within TRT	22661.66	2	3237.38		



APPENDIX I.

Summary Statistics of F and S Transmission Patterns

Table II : Experiment FS1 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

Replicate	FF	FS	SF	SS
1	82.5 (1.4) 90	76.8 (2.3) 45	75.7 (1.5) 44	57.7 (2.0) 90
2	74.3 (1.6) 88	61.7 (1.6) 45	59.3 (1.3) 44	51.7 (1.7) 88
3	74.3 (2.0) 88	66.7 (1.4) 45	61.4 (2.0) 45	54.0 (1.7) 89
Mean	77.0 (2.7) 3	68.4 (4.5) 3	65.5 (5.1) 3	54.5 (1.8) 3

Table I2 : Experiment FS1 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	82.5 (1.4) 90	76.8 (2.3) 45	75.7 (1.5) 44	60.4 (1.6) 86
2	75.0 (1.4) 87	61.7 (1.6) 45	59.3 (1.3) 44	54.1 (1.2) 84
3	76.9 (1.3) 85	66.7 (1.4) 45	62.7 (1.5) 44	57.0 (1.1) 84
Mean	78.1 (2.2) 3	68.4 (4.5) 3	66.0 (5.0) 3	57.2 (1.8) 3

Table I3 : Experiment FS1 - Female Starvation

Replicate	Mean Survival Time (hours)			
	(Standard Error)			
	Number of Individuals			
	FF	FS	SF	SS
1	32.02 (0.91) 90	46.55 (1.67) 48	47.73 (1.61) 48	80.00 (1.61) 96
2	35.04 (0.87) 96	54.29 (1.72) 48	49.28 (1.85) 48	66.23 (1.34) 96
3	38.75 (1.25) 96	42.28 (1.53) 48	43.80 (1.66) 48	55.86 (1.39) 96
Mean	35.27 (1.95) 3	47.71 (3.52) 3	46.93 (1.63) 3	67.36 (6.99) 3

Table I4 : Experiment FS1 - Male Starvation

Replicate	Mean Survival Time (hours)			
	(Standard Error)			
	FF	FS	SF	SS
1	21.06 (0.64) 96	38.43 (1.24) 48	38.73 (1.52) 48	57.17 (1.23) 96
2	26.84 (0.83) 95	38.63 (1.46) 48	40.40 (1.09) 48	56.91 (1.42) 96
3	24.56 (0.96) 96	31.15 (1.04) 48	33.97 (1.08) 48	40.93 (0.10) 96
Mean	24.15 (1.68) 3	36.07 (2.46) 3	37.03 (1.93) 3	51.67 (5.37) 3

Table I5 : Experiment FS1 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals			
Replicate	FF	FS & SF	SS
1	33.9 (1.4) 95	50.0 (1.7) 100	62.8 (1.6) 99
2	36.2 (1.1) 99	37.1 (1.2) 97	45.8 (1.7) 98
3	37.7 (1.4) 98	49.0 (1.6) 97	52.9 (1.6) 99
Mean	35.9 (1.1) 3	45.4 (4.1) 3	53.8 (4.9) 3

Table I6 : Experiment FS1 - Male Longevity

Mean Longevity (days) (Standard Error) Number of Individuals			
Replicate	FF	FS & SF	SS
1	38.5 (1.4) 95	46.4 (1.4) 98	57.2 (1.8) 99
2	33.9 (1.4) 97	42.1 (1.7) 97	50.0 (1.9) 99
3	30.8 (0.9) 100	41.8 (1.4) 95	54.6 (1.8) 98
Mean	34.4 (2.2) 3	43.4 (1.5) 3	53.9 (2.1) 3

Table I7 : Experiment FS2 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

Replicate	FF	FS	SF	SS
1	87.2 (2.9) 88	88.6 (2.7) 43	86.6 (3.0) 48	69.4 (1.9) 92
2	86.6 (3.6) 78	72.4 (3.0) 44	84.1 (1.5) 43	65.4 (1.6) 95
3	104.1 (1.9) 97	94.6 (2.8) 50	94.0 (3.1) 45	83.0 (1.6) 97
Mean	92.6 (5.7) 3	85.2 (6.6) 3	88.2 (3.0) 3	72.6 (5.3) 3



Table I8 : Experiment FS2 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	90.3 (2.4) 85	88.6 (2.7) 43	88.4 (2.4) 47	70.1 (1.7) 91
2	93.9 (2.3) 72	75.8 (1.8) 42	84.1 (1.5) 43	66.8 (1.2) 93
3	104.1 (1.9) 97	96.5 (2.2) 43	96.1 (2.4) 44	83.1 (1.6) 97
Mean	96.1 (4.1) 3	87.0 (6.0) 3	89.6 (3.5) 3	73.3 (5.0) 3

Table I9 : Experiment FS2 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	20.37 (0.48) 90	27.89 (1.14) 46	27.13 (0.93) 52	37.55 (1.11) 96
2	26.51 (0.63) 74	34.61 (1.54) 44	37.61 (1.99) 44	46.94 (1.19) 100
3	49.03 (0.74) 100	29.36 (0.99) 50	29.06 (1.19) 50	33.89 (0.76) 99
Mean	31.97 (8.71) 3	30.62 (2.04) 3	31.27 (3.22) 3	39.46 (3.89) 3

Table I10 : Experiment FS2 - Male Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	15.40 (0.45) 90	18.95 (0.70) 46	25.63 (1.12) 52	33.23 (1.14) 96
2	17.91 (0.69) 74	25.00 (1.03) 44	31.20 (1.38) 44	40.37 (0.86) 100
3	38.50 (0.38) 100	18.20 (0.56) 50	21.74 (0.71) 50	24.82 (0.75) 100
Mean	23.94 (7.32) 3	20.72 (2.15) 3	26.19 (2.75) 3	32.81 (4.50) 3

Table I11 : Experiment FS3 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

Replicate	FF	FS	SF	SS
1	96.5 (5.6) 49	99.7 (3.1) 53	103.8 (2.2) 51	78.1 (2.5) 100
2	110.5 (2.2) 66	95.74 (2.5) 58	92.2 (2.3) 59	80.1 (1.8) 98
3	113.0 (2.3) 96	108.2 (3.2) 57	107.1 (3.0) 58	83.4 (3.1) 97
Mean	106.7 (5.1) 3	101.2 (3.7) 3	101.1 (4.5) 3	80.6 (1.5) 3

Table I12 : Experiment FS3 - Conditional Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

Replicate	FF	FS	SF	SS
1	105.1 (4.1) 45	101.6 (2.5) 52	103.8 (2.2) 51	82.2 (1.9) 95
2	110.5 (2.2) 66	97.3 (2.0) 57	92.2 (2.3) 59	81.8 (1.4) 96
3	114.2 (2.0) 95	110.2 (2.6) 56	107.1 (3.0) 58	87.7 (2.6) 92
Mean	109.9 (2.6) 3	103.0 (3.8) 3	100.0 (4.5) 3	83.9 (1.9) 3

Table I13 : Experiment FS3 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	23.30 (0.62) 52	30.96 (0.85) 54	31.58 (0.58) 52	50.76 (1.35) 80
2	27.67 (0.81) 66	43.47 (1.21) 60	43.95 (1.52) 58	55.80 (1.66) 100
3	25.58 (0.80) 100	27.57 (1.06) 60	31.40 (0.85) 60	35.33 (0.71) 100
Mean	25.51 (1.26) 3	34.00 (4.84) 3	35.64 (4.15) 3	47.30 (6.16) 3

Table I14 : Experiment FS3 - Male Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	16.79 (0.47) 52	21.12 (0.82) 54	28.47 (1.42) 52	41.16 (1.26) 80
2	19.74 (0.97) 65	30.27 (0.89) 60	35.26 (1.19) 58	47.52 (1.33) 100
3	18.83 (0.71) 100	22.02 (0.72) 60	26.35 (0.88) 60	29.15 (0.71) 100
Mean	18.45 (0.87) 3	24.47 (2.9 ) 3	30.03 (2.69) 3	39.28 (5.39) 3

Table I15 : Experiment FS3 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals			
Replicate	FF	FS & SF	SS
1	27.8 (1.4) 100	51.1 (1.8) 100	54.3 (1.9) 96
2	29.9 (1.3) 99	41.7 (1.7) 96	44.9 (2.0) 95
3	38.6 (1.6) 100	49.8 (1.5) 100	49.6 (1.9) 100
Mean	32.1 (3.3) 3	47.5 (2.9) 3	49.6 (2.7) 3



Table I16 : Experiment FS3 - Male Longevity

Mean Longevity (days) (Standard Error) Number of Individuals			
Replicate	FF	FS & SF	SS
1	29.2 (1.0) 100	45.9 (1.5) 100	48.3 (2.0) 98
2	25.1 (0.9) 100	39.9 (1.7) 97	47.1 (2.0) 95
3	25.5 (1.3) 100	39.7 (1.4) 96	47.0 (1.6) 99
Mean	26.6 (1.3) 3	41.8 (2.0) 3	47.5 (0.4) 3

Table I17 : Experiment FS4 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

Replicate	FF	FS	SF	SS
1	97.0 (2.6) 94	89.5 (3.3) 41	83.3 (3.2) 46	77.5 (1.8) 102
2	84.2 (1.8) 113	67.1 (3.5) 42	72.0 (2.2) 47	69.0 (1.5) 93
3	83.8 (2.3) 92	72.0 (2.2) 47	74.9 (1.7) 48	69.9 (1.6) 67
Mean	88.4 (4.3) 3	76.2 (6.8) 3	76.7 (3.4) 3	72.1 (2.7) 3

Table I18 : Experiment FS4 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	99.1 (2.2) 92	89.5 (3.3) 41	85.2 (2.6) 45	79.0 (1.4) 100
2	85.7 (1.5) 111	70.4 (2.8) 40	72.0 (2.2) 47	69.7 (1.4) 92
3	85.7 (1.9) 90	72.0 (2.2) 47	74.9 (1.7) 48	69.9 (1.6) 67
Mean	90.2 (4.5) 3	77.3 (6.1) 3	77.4 (4.0) 3	72.9 (3.1) 3

Table I19 : Experiment FS4 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	33.53 (1.05) 96	49.07 (1.95) 42	49.40 (2.34) 48	66.31 (1.90) 106
2	46.45 (1.14) 116	56.48 (2.41) 48	64.59 (2.38) 48	75.68 (2.08) 89
3	36.18 (0.92) 96	48.78 (1.49) 48	52.20 (1.65) 48	55.12 (1.54) 66
Mean	38.72 (3.94) 3	51.44 (2.52) 3	55.40 (4.67) 3	65.70 (4.35) 3

Table I20 : Experiment FS4 - Male Starvation

Mean Survival Time (hours)  
 (Standard Error)  
 Number of Individuals

Replicate	FF	FS	SF	SS
1	23.02 (0.66) 95	30.50 (1.12) 42	38.09 (2.39) 48	47.01 (1.83) 106
2	29.33 (0.77) 116	40.54 (1.67) 48	47.59 (2.06) 48	56.93 (1.57) 90
3	22.68 (0.63) 96	31.59 (1.37) 48	31.83 (0.94) 48	42.16 (1.29) 66
Mean	25.01 (2.16) 3	34.21 (3.18) 3	39.17 (4.58) 3	48.70 (4.35) 3

Table I21 : Experiment FS4 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	35.6 (1.4) 78	45.1 (2.6) 39	43.7 (2.5) 39	51.0 (2.0) 76
2	32.4 (1.0) 77	42.6 (2.2) 40	38.2 (2.4) 40	47.9 (1.8) 77
3	33.8 (1.5) 77	45.4 (2.5) 40	44.9 (2.4) 36	53.9 (1.7) 80
Mean	33.9 (0.9) 3	44.4 (0.9) 3	42.3 (2.1) 3	50.9 (1.7) 3

Table I22 : Experiment FS4 - Male Longevity

Mean Longevity (days) (Standard Error) Number of Individuals				
Replicate	FF	FS	SF	SS
1	37.5 (1.2) 79	45.6 (2.6) 40	48.7 (2.0) 35	51.6 (1.6) 76
2	28.6 (1.2) 79	42.3 (2.4) 36	44.4 (3.2) 37	55.1 (1.8) 78
3	30.4 (1.4) 79	35.7 (2.0) 41	34.9 (1.9) 37	52.0 (1.8) 79
Mean	32.2 (2.7) 3	41.2 (2.9) 3	42.7 (4.1) 3	52.9 (1.1) 3

Table I23 : Experiment FS5 - Fecundity

Mean 24 Hour Fecundity  
(Standard Error)  
Number of Individuals

FF	FS	SF	SS
122.3 (3.3) 77	116.6 (4.4) 40	114.0 (3.9) 40	100.0 (2.7) 79



Table I24 : Experiment FS5 - Conditional Fecundity

Mean 24 Hour Fecundity (Standard Error) Number of Individuals			
FF	FS	SF	SS
125.5 (2.4) 75	119.5 (3.4) 39	114.0 (3.9) 40	102.5 (2.1) 77

Table I25 : Experiment FS5 - Female Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals			
FF	FS	SF	SS
31.68 (0.85) 80	35.43 (1.27) 40	34.10 (1.44) 40	51.19 (1.61) 80

Table I26 : Experiment FS5 - Male Starvation

Mean Survival Time (hours) (Standard Error) Number of Individuals			
FF	FS	SF	SS
24.51 (0.69) 80	33.55 (1.88) 40	28.70 (1.18) 40	40.39 (1.36) 80

Table I27 : Experiment FS5 - Female Longevity

Mean Longevity (days) (Standard Error) Number of Individuals			
FF	FS	SF	SS
36.3 (1.4) 81	42.0 (1.5) 40	41.5 (2.3) 40	46.2 (1.9) 79

Table I28 : Experiment FS5 - Male Longevity

Mean Longevity (days)  
 (Standard Error)  
 Number of Individuals

FF	FS	SF	SS
31.8 (1.3) 81	38.5 (2.0) 40	40.9 (1.9) 40	49.0 (1.9) 79

## APPENDIX J

### Analysis of F and S Transmission Patterns

Table J1 : Experiment FS1 - Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	77.03	54.46	22.57
Standard Deviation	4.73	3.05	2.21
N	3	3	3

INDEPENDENT	T = 6.946	DF = 4	Probability = 0.002
PAIRED	T = 17.664	DF = 2	Probability = 0.0003

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	67870.74	1	67870.74	310.581	0.003
TRT x REP	437.06	2	218.53		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	68.39	65.48	2.91
Standard Deviation	7.74	8.92	2.11
N	3	3	3

INDEPENDENT	T = 0.427	DF = 4	Probability = 0.691
PAIRED	T = 2.390	DF = 2	Probability = 0.139

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	567.67	1	567.67	5.696	0.140
TRT x REP	199.33	2	99.67		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	65.73	66.94	- 1.22
Standard Deviation	3.83	8.28	4.46
N	3	3	3

INDEPENDENT	T = 0.231	DF = 4	Probability = 0.829
PAIRED	T = 0.473	DF = 2	Probability = 0.683

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	264.28	1	264.28	0.224	0.683
TRT x REP	2362.78	2	1181.39		

Table J2 : Experiment FS1 - Conditional Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	78.15	58.19	20.96
Standard Deviation	3.88	3.13	1.11
N	3	3	3

INDEPENDENT	T = 7.293	DF = 4	Probability = 0.002
PAIRED	T = 32.784	DF = 2	Probability = 0.001

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	56659.35	1	56659.35	1070.315	0.001
TRT x REP	105.87	2	52.94		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	68.39	65.91	2.48
Standard Deviation	7.74	8.65	1.42
N	3	3	3

INDEPENDENT	T = 0.371	DF = 4	Probability = 0.730
PAIRED	T = 3.038	DF = 2	Probability = 0.093

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	411.65	1	411.65	9.229	0.093
TRT x REP	89.21	2	44.60		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	67.83	67.17	0.67
Standard Deviation	3.53	8.17	4.66
N	3	3	3

INDEPENDENT	T = 0.130	DF = 4	Probability = 0.903
PAIRED	T = 0.249	DF = 2	Probability = 0.827

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	78.71	1	78.71	0.062	0.827
TRT x REP	2553.23	2	1276.62		



Table J3 : Experiment FS1 - Female Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	35.27	67.36	-32.09
Standard Deviation	3.37	12.11	15.45
N	3	3	3

INDEPENDENT	T = 4.422	DF = 4	Probability = 0.011
PAIRED	T = 3.597	DF = 2	Probability = 0.069

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	146687.55	1	146687.55	13.021	0.069
TRT x REP	22531.30	2	11265.65		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	47.71	46.93	0.77
Standard Deviation	6.09	2.82	3.68
N	3	3	3

INDEPENDENT	T = 0.199	DF = 4	Probability = 0.852
PAIRED	T = 0.363	DF = 2	Probability = 0.751

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	42.94	1	42.94	0.132	0.751
TRT x REP	650.02	2	325.01		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	51.57	47.32	4.25
Standard Deviation	4.81	4.38	5.40
N	3	3	3

INDEPENDENT	T = 1.133	DF = 4	Probability = 0.320
PAIRED	T = 1.365	DF = 2	Probability = 0.306

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3462.69	1	3462.69	1.866	0.305
TRT x REP	3711.57	2	1855.78		

Table J4 : Experiment FS1 - Male Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	24.15	51.67	-27.52
Standard Deviation	2.91	9.31	10.12
N	3	3	3

INDEPENDENT	T = 4.889	DF = 4	Probability = 0.008
PAIRED	T = 4.710	DF = 2	Probability = 0.042

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	108826.40	1	108826.40	22.153	0.042
TRT x REP	9824.90	2	4912.45		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	36.07	37.70	- 1.63
Standard Deviation	4.26	3.34	1.27
N	3	3	3

INDEPENDENT	T = 0.522	DF = 4	Probability = 0.629
PAIRED	T = 2.233	DF = 2	Probability = 0.155

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	191.43	1	191.43	4.988	0.155
TRT x REP	76.75	2	38.38		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	37.94	36.88	1.06
Standard Deviation	4.72	3.77	1.21
N	3	3	3

INDEPENDENT	T = 0.303	DF = 4	Probability = 0.777
PAIRED	T = 1.507	DF = 2	Probability = 0.271

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	213.56	1	213.56	2.273	0.271
TRT x REP	187.92	2	93.96		

Table J5 : Experiment FS1 - Female Longevity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	35.94	53.81	-17.86
Standard Deviation	1.96	8.56	9.99
N	3	3	3

INDEPENDENT	T = 3.524	DF = 4	Probability = 0.024
PAIRED	T = 3.098	DF = 2	Probability = 0.090

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	46900.14	1	46900.14	9.641	0.090
TRT x REP	9729.32	2	4864.66		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	44.98	45.34	- 0.36
Standard Deviation	3.85	7.13	3.81
N	3	3	3

INDEPENDENT	T = 0.076	DF = 4	Probability = 0.943
PAIRED	T = 0.163	DF = 2	Probability = 0.886

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	25.07	1	25.07	0.027	0.885
TRT x REP	1884.21	2	942.10		

Table J6 : Experiment FS1 - Male Longevity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	34.43	53.92	-19.50
Standard Deviation	3.87	3.64	3.89
N	3	3	3

INDEPENDENT	T = 6.356	DF = 4	Probability = 0.013
PAIRED	T = 8.681	DF = 2	Probability = 0.003

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	55860.41	1	55860.41	74.913	0.013
TRT x REP	1491.34	2	745.67		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	44.23	43.45	0.78
Standard Deviation	3.33	2.58	0.86
N	3	3	3

INDEPENDENT	T = 0.321	DF = 4	Probability = 0.764
PAIRED	T = 1.571	DF = 2	Probability = 0.257

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	118.31	1	118.31	2.457	0.258
TRT x REP	96.30	2	48.15		

Table J7 : Experiment FS2 - Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	92.65	72.64	20.01
Standard Deviation	9.92	9.27	1.91
N	3	3	3

INDEPENDENT	T = 2.553	DF = 4	Probability = 0.063
PAIRED	T = 18.180	DF = 2	Probability = 0.003

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	54442.05	1	54442.05	332.695	0.003
TRT x REP	327.29	2	163.64		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	85.23	88.23	- 3.00
Standard Deviation	11.48	5.15	7.53
N	3	3	3

INDEPENDENT	T = 0.413	DF = 4	Probability = 0.701
PAIRED	T = 0.690	DF = 2	Probability = 0.562

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	612.26	1	612.26	0.487	0.558
TRT x REP	2515.05	2	1257.53		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	82.23	86.69	- 4.46
Standard Deviation	9.97	8.10	4.48
N	3	3	3

INDEPENDENT	T = 0.602	DF = 4	Probability = 0.580
PAIRED	T = 1.725	DF = 2	Probability = 0.227

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3621.77	1	3621.77	2.934	0.229
TRT x REP	2469.14	2	1234.57		

Table J8 : Experiment FS2 - Conditional Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	96.08	73.34	22.74
Standard Deviation	7.17	8.61	3.74
N	3	3	3

INDEPENDENT	T = 3.517	DF = 4	Probability = 0.025
PAIRED	T = 10.539	DF = 2	Probability = 0.009

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	68442.01	1	68442.01	116.404	0.008
TRT x REP	1175.94	2	587.97		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	86.98	89.55	- 2.57
Standard Deviation	10.43	6.10	4.93
N	3	3	3

INDEPENDENT	T = 0.368	DF = 4	Probability = 0.731
PAIRED	T = 0.903	DF = 2	Probability = 0.462

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	612.26	1	612.26	0.487	0.558
TRT x REP	2515.05	2	1257.53		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	84.02	88.29	- 4.27
Standard Deviation	8.31	8.16	3.87
N	3	3	3

INDEPENDENT	T = 0.634	DF = 4	Probability = 0.560
PAIRED	T = 1.908	DF = 2	Probability = 0.197

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3241.84	1	3241.84	3.671	0.195
TRT x REP	1766.04	2	883.02		

Table J9 : Experiment FS2 - Female Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	31.97	39.46	- 7.49
Standard Deviation	15.09	6.73	19.67
N	3	3	3

INDEPENDENT	T = 0.785	DF = 4	Probability = 0.476
PAIRED	T = 0.660	DF = 2	Probability = 0.577

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	7751.17	1	7751.17	0.421	0.583
TRT x REP	36858.01	2	18429.01		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	30.62	31.27	- 0.65
Standard Deviation	3.53	5.58	2.05
N	3	3	3

INDEPENDENT	T = 0.170	DF = 4	Probability = 0.874
PAIRED	T = 0.546	DF = 2	Probability = 0.640

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	29.77	1	29.77	0.310	0.634
TRT x REP	192.00	2	96.00		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	36.33	30.93	5.39
Standard Deviation	6.35	4.56	5.97
N	3	3	3

INDEPENDENT	T = 1.194	DF = 4	Probability = 0.298
PAIRED	T = 1.563	DF = 2	Probability = 0.258

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	5484.05	1	5484.05	2.371	0.264
TRT x REP	4626.56	2	2313.28		

Table J10 : Experiment FS2 - Male Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	23.94	32.81	- 8.87
Standard Deviation	12.67	7.78	19.67
N	3	3	3

INDEPENDENT	T = 1.033	DF = 4	Probability = 0.360
PAIRED	T = 0.781	DF = 2	Probability = 0.516

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	10888.87	1	10888.87	0.590	0.523
TRT x REP	36883.05	2	18441.53		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	20.72	26.19	- 5.47
Standard Deviation	3.73	4.76	1.69
N	3	3	3

INDEPENDENT	T = 1.569	DF = 4	Probability = 0.192
PAIRED	T = 5.607	DF = 2	Probability = 0.030

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	32.45	1	2132.45	30.394	0.031
TRT x REP	140.32	2	70.16		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	29.03	23.52	5.51
Standard Deviation	3.85	4.16	5.36
N	3	3	3

INDEPENDENT	T = 1.682	DF = 4	Probability = 0.168
PAIRED	T = 1.778	DF = 2	Probability = 0.217

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	5723.20	1	5723.20	3.062	0.222
TRT x REP	3737.63	2	1868.82		



Table J11 : Experiment FS3 - Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	106.66	80.56	26.09
Standard Deviation	8.88	2.66	6.70
N	3	3	3

INDEPENDENT	T = 4.877	DF = 4	Probability = 0.008
PAIRED	T = 6.748	DF = 2	Probability = 0.021

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	80111.85	1	80111.85	50.056	0.019
TRT x REP	3200.88	2	1600.44		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	101.22	101.01	0.20
Standard Deviation	6.40	7.79	3.91
N	3	3	3

INDEPENDENT	T = 0.035	DF = 4	Probability = 0.974
PAIRED	T = 0.090	DF = 2	Probability = 0.936

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3.47	1	3.47	0.008	0.935
TRT x REP	830.23	2	415.12		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	91.55	101.09	- 9.55
Standard Deviation	7.01	6.86	7.93
N	3	3	3

INDEPENDENT	T = 1.687	DF = 4	Probability = 0.167
PAIRED	T = 2.084	DF = 2	Probability = 0.173

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	18283.45	1	18283.45	4.494	0.168
TRT x REP	8136.50	2	4068.25		

Table J12 : Experiment FS3 - Conditional Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	109.90	83.90	26.01
Standard Deviation	4.57	3.31	2.95
N	3	3	3

INDEPENDENT	T = 7.990	DF = 4	Probability = 0.001
PAIRED	T = 15.271	DF = 2	Probability = 0.004

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	76370.69	1	76370.69	259.250	0.004
TRT x REP	589.17	2	294.58		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	103.03	101.01	2.02
Standard Deviation	6.55	7.79	3.78
N	3	3	3

INDEPENDENT	T = 0.343	DF = 4	Probability = 0.749
PAIRED	T = 0.926	DF = 2	Probability = 0.452

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	337.80	1	337.80	0.882	0.447
TRT x REP	766.14	2	383.07		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	94.72	101.99	- 7.27
Standard Deviation	5.89	6.95	5.90
N	3	3	3

INDEPENDENT	T = 1.382	DF = 4	Probability = 0.239
PAIRED	T = 2.135	DF = 2	Probability = 0.166

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	10391.99	1	10391.99	4.709	0.162
TRT x REP	4413.48	2	2206.74		

Table J13 : Experiment FS3 - Female Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	25.52	47.30	-21.78
Standard Deviation	2.19	10.67	10.42
N	3	3	3

INDEPENDENT	T = 3.465	DF = 4	Probability = 0.026
PAIRED	T = 3.619	DF = 2	Probability = 0.069

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	55523.63	1	55523.63	11.549	0.077
TRT x REP	9517.33	2	4807.67		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	34.00	35.64	- 1.65
Standard Deviation	8.38	7.20	1.89
N	3	3	3

INDEPENDENT	T = 0.809	DF = 4	Probability = 0.809
PAIRED	T = 1.507	DF = 2	Probability = 0.271

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	232.78	1	232.78	2.210	0.275
TRT x REP	210.67	2	105.33		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	38.34	34.82	3.52
Standard Deviation	7.22	7.75	4.47
N	3	3	3

INDEPENDENT	T = 0.576	DF = 4	Probability = 0.595
PAIRED	T = 1.365	DF = 2	Probability = 0.306

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2489.96	1	2489.96	1.991	0.294
TRT x REP	2501.05	2	1250.53		

Table J14 : Experiment FS3 - Male Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	18.45	39.28	-20.83
Standard Deviation	1.51	9.33	9.26
N	3	3	3

INDEPENDENT	T = 3.817	DF = 4	Probability = 0.019
PAIRED	T = 3.897	DF = 2	Probability = 0.060

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	50618.77	1	50618.77	13.215	0.068
TRT x REP	7660.65	2	3830.33		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	24.47	30.03	- 5.56
Standard Deviation	5.04	4.66	1.58
N	3	3	3

INDEPENDENT	T = 1.403	DF = 4	Probability = 0.233
PAIRED	T = 6.086	DF = 2	Probability = 0.026

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2647.40	1	2647.40	38.278	0.025
TRT x REP	138.33	2	69.16		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	30.71	27.21	3.50
Standard Deviation	6.34	4.78	3.53
N	3	3	3

INDEPENDENT	T = 0.763	DF = 4	Probability = 0.488
PAIRED	T = 1.718	DF = 2	Probability = 0.228

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2454.57	1	2454.57	2.940	0.279
TRT x REP	1669.59	2	834.80		

Table J15 : Experiment FS3 - Female Longevity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	32.10	49.59	-17.50
Standard Deviation	5.72	4.71	8.01
N	3	3	3

INDEPENDENT	T = 4.089	DF = 4	Probability = 0.015
PAIRED	T = 3.784	DF = 2	Probability = 0.063

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	45126.23	1	45126.23	14.275	0.063
TRT x REP	6322.50	2	3161.25		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	40.70	47.55	- 6.85
Standard Deviation	3.45	5.08	3.08
N	3	3	3

INDEPENDENT	T = 1.930	DF = 4	Probability = 0.126
PAIRED	T = 3.851	DF = 2	Probability = 0.061

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	9239.14	1	9239.14	14.831	0.061
TRT x REP	1240.95	2	622.98		

Table J16 : Experiment FS3 - Male Longevity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	26.60	47.47	-20.87
Standard Deviation	2.28	0.76	1.53
N	3	3	3

INDEPENDENT	T = 15.076	DF = 4	Probability = 0.000
PAIRED	T = 23.593	DF = 2	Probability = 0.002

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	64421.54	1	64421.54	556.627	0.002
TRT x REP	231.47	2	115.74		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	36.89	42.83	- 4.94
Standard Deviation	1.56	3.52	1.99
N	3	3	3

INDEPENDENT	T = 2.218	DF = 4	Probability = 0.091
PAIRED	T = 4.294	DF = 2	Probability = 0.050

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	4772.91	1	4772.91	18.289	0.051
TRT x REP	521.94	2	260.97		

Table J17 : Experiment FS4 - Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	88.36	72.12	16.24
Standard Deviation	7.53	4.66	2.94
N	3	3	3

INDEPENDENT	T = 3.177	DF = 4	Probability = 0.034
PAIRED	T = 9.552	DF = 2	Probability = 0.011

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	36031.79	1	36031.79	90.662	0.011
TRT x REP	794.86	2	397.43		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	76.17	76.75	- 0.58
Standard Deviation	11.77	5.90	5.88
N	3	3	3

INDEPENDENT	T = 0.076	DF = 4	Probability = 0.943
PAIRED	T = 0.170	DF = 2	Probability = 0.881

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	22.39	1	22.39	0.029	0.879
TRT x REP	1518.10	2	759.05		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	80.72	76.45	4.26
Standard Deviation	5.33	8.67	3.51
N	3	3	3

INDEPENDENT	T = 0.725	DF = 4	Probability = 0.508
PAIRED	T = 2.104	DF = 2	Probability = 0.170

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3305.70	1	3305.80	4.388	0.171
TRT x REP	1506.65	2	753.32		

Table J18 : Experiment FS4 - Conditional Fecundity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	90.16	72.87	17.30
Standard Deviation	7.74	5.34	2.40
N	3	3	3

INDEPENDENT	T = 3.186	DF = 4	Probability = 0.033
PAIRED	T = 12.475	DF = 2	Probability = 0.006

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	40316.05	1	40316.05	150.587	0.007
TRT x REP	535.45	2	267.73		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	77.27	77.37	- 0.09
Standard Deviation	10.59	6.94	3.83
N	3	3	3

INDEPENDENT	T = 0.013	DF = 4	Probability = 0.991
PAIRED	T = 0.041	DF = 2	Probability = 0.971

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	0.56	1	0.56	0.002	0.971
TRT x REP	647.82	2	323.91		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	82.01	77.31	4.70
Standard Deviation	5.75	8.66	2.96
N	3	3	3

INDEPENDENT	T = 0.783	DF = 4	Probability = 0.478
PAIRED	T = 2.747	DF = 2	Probability = 0.111

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3958.94	1	3958.94	7.537	0.111
TRT x REP	1050.53	2	525.26		



Table J19 : Experiment FS4 - Female Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	38.72	65.70	-26.98
Standard Deviation	6.82	10.30	7.19
N	3	3	3

INDEPENDENT	T = 3.784	DF = 4	Probability = 0.019
PAIRED	T = 6.500	DF = 2	Probability = 0.023

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	100390.32	1	100390.32	45.412	0.021
TRT x REP	4421.27	2	2210.64		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	51.44	55.40	- 3.96
Standard Deviation	4.36	8.08	3.92
N	3	3	3

INDEPENDENT	T = 0.746	DF = 4	Probability = 0.497
PAIRED	T = 1.748	DF = 2	Probability = 0.223

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1100.23	1	1100.23	3.075	0.222
TRT x REP	715.68	2	357.84		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	51.26	53.42	- 2.17
Standard Deviation	7.64	6.19	4.09
N	3	3	3

INDEPENDENT	T = 0.382	DF = 4	Probability = 0.722
PAIRED	T = 0.916	DF = 2	Probability = 0.456

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	880.24	1	880.24	0.859	0.452
TRT x REP	2049.35	2	1024.68		

Table J20 : Experiment FS4 - Male Starvation

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	25.01	48.70	-23.69
Standard Deviation	3.74	7.53	4.07
N	3	3	3

INDEPENDENT	T = 10.087	DF = 4	Probability = 0.008
PAIRED	T = 4.881	DF = 2	Probability = 0.010

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	77399.29	1	77399.29	106.338	0.009
TRT x REP	1455.72	2	727.86		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	34.21	39.17	- 4.96
Standard Deviation	5.51	7.94	4.10
N	3	3	3

INDEPENDENT	T = 0.889	DF = 4	Probability = 0.424
PAIRED	T = 2.096	DF = 2	Probability = 0.171

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	1728.96	1	1728.96	4.353	0.172
TRT x REP	794.46	2	397.23		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	35.89	36.77	- 0.88
Standard Deviation	5.39	6.47	1.91
N	3	3	3

INDEPENDENT	T = 0.181	DF = 4	Probability = 0.865
PAIRED	T = 0.797	DF = 2	Probability = 0.509

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	145.07	1	145.07	0.626	0.512
TRT x REP	463.72	2	231.86		

Table J21 : Experiment FS4 - Female Longevity

FF SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	33.90	50.94	-17.04
Standard Deviation	1.69	3.04	2.65
N	3	3	3

INDEPENDENT	T = 8.488	DF = 4	Probability = 0.001
PAIRED	T = 11.146	DF = 2	Probability = 0.008

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	33738.74	1	33738.74	123.455	0.008
TRT x REP	546.60	2	273.30		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	44.33	42.24	2.08
Standard Deviation	1.54	3.60	2.06
N	3	3	3

INDEPENDENT	T = 0.922	DF = 4	Probability = 0.409
PAIRED	T = 1.751	DF = 2	Probability = 0.222

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	253.21	1	253.21	3.043	0.223
TRT x REP	166.65	2	83.33		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	42.45	43.29	- 0.84
Standard Deviation	2.12	2.57	0.47
N	3	3	3

INDEPENDENT	T = 0.435	DF = 4	Probability = 0.686
PAIRED	T = 3.083	DF = 2	Probability = 0.091

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	108.99	1	108.99	9.429	0.092
TRT x REP	23.12	2	11.56		

Table J22 : Experiment FS4 - Male Longevity

FF - SS DIFFERENCESMethod 1 - t-test

	FF Lines	SS Lines	DIF
Mean	32.15	52.89	-20.73
Standard Deviation	4.70	1.91	6.24
N	3	3	3

INDEPENDENT	T = 7.076	DF = 4	Probability = 0.002
PAIRED	T = 5.758	DF = 2	Probability = 0.029

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	50500.68	1	50500.68	33.326	0.029
TRT x REP	3030.68	2	1515.34		

MATERNAL EFFECTSMethod 1 - t-test

	FS Lines	SF Lines	DIF
Mean	41.21	42.64	-1.44
Standard Deviation	5.05	7.07	2.02
N	3	3	3

INDEPENDENT	T = -0.286	DF = 4	Probability = 0.789
PAIRED	T = -1.232	DF = 2	Probability = 0.343

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	116.40	1	116.40	1.489	0.347
TRT x REP	156.32	2	78.16		

DOMINANCE EFFECTSMethod 1 - t-test

	Parental Lines	Crossed Lines	DIF
Mean	42.45	41.90	0.54
Standard Deviation	1.72	6.01	4.66
N	3	3	3

INDEPENDENT	T = 0.151	DF = 4	Probability = 0.888
PAIRED	T = 0.202	DF = 2	Probability = 0.859

Method 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	45.05	1	45.05	0.040	0.360
TRT x REP	2241.28	2	1120.64		

Table J23 : Experiment FS5 - Fecundity

FF - SS DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	19277.25	1	19277.25	27.378	0.000
ERROR	108434.76	154	704.12		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	135.20	1	135.20	0.196	0.659
ERROR	53876.75	78	690.73		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	966.44	1	966.44	1.244	0.266
ERROR	181723.95	234	776.60		

Table J24 : Experiment FS5 - Conditional Fecundity

FF - SS DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	20144.85	1	20144.85	51.046	0.000
ERROR	59195.97	150	394.64		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	605.59	1	605.59	1.154	0.286
ERROR	40412.72	77	524.84		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	423.30	1	423.30	0.805	0.370
ERROR	120359.12	229	525.59		

Table J25 : Experiment FS5 - Female Starvation

FF - SS DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	15229.51	1	15229.51	114.388	0.000
ERROR	21035.94	158	133.14		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	35.11	1	35.11	0.478	0.491
ERROR	5729.38	78	73.45		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	2371.85	1	2371.85	13.431	0.000
ERROR	42029.93	238	176.60		

Table J26 : Experiment FS5 - Male Starvation

FF - SS DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	10080.63	1	10080.63	108.682	0.000
ERROR	14654.98	158	92.75		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	470.45	1	470.45	4.754	0.032
ERROR	7718.30	78	98.95		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	93.63	1	93.63	0.677	0.411
ERROR	32924.35	238	138.34		



Table J27 : Experiment FS5 - Female Longevity

FF - SS DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	3904.69	1	3904.69	17.981	0.000
ERROR	34312.41	158	217.17		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	14.45	1	14.45	0.085	0.772
ERROR	13287.35	78	170.35		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	32.03	1	32.03	0.148	0.701
ERROR	51518.90	238	216.47		

Table J28 : Experiment FS5 - Male Longevity

FF - SS DIFFERENCESMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	11759.66	1	11759.66	55.388	0.000
ERROR	33545.53	158	212.31		

MATERNAL EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	115.20	1	115.20	0.737	0.393
ERROR	12192.35	78	156.31		

DOMINANCE EFFECTSMethod 2 - ANOVA

SOURCE	SS	DF	MS	F	P
TRT	20.42	1	20.42	0.084	0.772
ERROR	57612.74	238	242.07		

## APPENDIX K

### Summary Statistics of F and S Gene Number Estimates

Table K1 : Experiment GFS1 - Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	82.49 (173.5) 90	57.72 (376.0) 90	76.28 (167.5) 89	71.09 (205.6) 89
2	74.27 (214.1) 88	51.67 (241.7) 88	60.51 (89.78) 89	60.66 (161.3) 88
3	74.33 (343.2) 88	53.99 (260.8) 89	64.04 (138.6) 90	61.93 (153.5) 89
Mean Std Error N	77.03 (2.73) 3	54.46 (1.76) 3	66.94 (4.78) 3	64.56 (3.29) 3

Table K2 : Experiment GFS1 - Conditional Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	82.49 (173.5) 90	60.38 (232.4) 86	76.28 (167.5) 89	71.88 (152.5) 88
2	75.02 (166.5) 87	54.13 (118.5) 84	60.51 (89.78) 89	60.66 (161.3) 88
3	76.94 (153.0) 85	57.05 (107.2) 84	64.71 (100.1) 89	61.93 (153.5) 89
Mean	78.15	57.19	67.17	64.82
Std Error	(2.24)	(1.81)	(4.72)	(3.55)
N	3	3	3	3

Table K3 : Experiment GFS1 - Female Starvation

Mean Survival Time (hours) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	32.02 (74.72) 90	80.00 (249.7) 96	47.14 (127.4) 96	50.94 (142.6) 96
2	35.04 (72.16) 96	66.23 (173.0) 96	51.78 (157.9) 96	52.71 (154.6) 96
3	38.75 (149.9) 96	55.86 (186.1) 96	43.04 (121.7) 96	45.66 (177.1) 96
Mean	35.27	67.36	47.32	49.77
Std Error	(1.95)	(6.99)	(2.52)	(2.12)
N	3	3	3	3

Table K4 : Experiment GFS1 - Male Starvation

Mean Survival Time (hours) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	21.06 (38.85) 96	57.17 (145.1) 96	38.58 (91.46) 96	40.63 (148.2) 96
2	26.84 (64.96) 95	56.91 (194.3) 96	39.51 (79.23) 96	39.33 (120.6) 96
3	24.56 (87.73) 96	40.93 (95.86) 96	32.56 (55.47) 96	35.12 (139.1) 96
Mean Std Error N	24.15 (1.68) 3	51.67 (5.37) 3	36.88 (2.18) 3	38.36 (1.66) 3

Table K5 : Experiment GFS1 - Female Longevity

Replicate	Mean Longevity (days)			
	(variance)			
	Number of Individuals			
	FF	SS	FS1	FS2
1	33.86 (186.0) 95	62.80 (265.9) 99	49.96 (289.1) 100	47.17 (183.0) 100
2	36.22 (110.7) 99	45.76 (269.4) 98	37.12 (137.6) 97	39.62 (174.0) 100
3	37.75 (202.2) 98	52.87 (269.0) 99	48.93 (238.7) 97	45.59 (228.3) 100
Mean	35.94	53.81	45.34	44.13
Std Error	(1.13)	(4.97)	(4.12)	(2.30)
N	3	3	3	3



Table K6 : Experiment GFS1 - Male Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	38.53 (177.1) 95	57.20 (338.6) 99	46.42 (197.1) 98	48.53 (178.6) 100
2	33.93 (127.4) 97	50.01 (353.6) 99	42.13 (264.3) 97	43.99 (257.4) 99
3	30.83 (78.77) 100	54.56 (319.7) 98	41.79 (187.1) 95	41.43 (235.5) 97
Mean	34.43	53.92	44.45	44.65
Std Error	(2.24)	(2.10)	(1.49)	(2.08)
N	3	3	3	3

Table K7 : Experiment GFS2 - Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	96.51 (1550.7) 49	78.14 (646.9) 100	101.7 (384.5) 104	89.84 (470.2) 141
2	85.83 (656.3) 93	69.13 (352.2) 100	70.93 (346.2) 120	77.56 (529.6) 118
3	113.0 (505.2) 96	83.40 (936.0) 97	107.6 (552.1) 115	104.5 (396.7) 131
Mean	93.45	76.89	93.41	90.64
Std Error	(7.903)	(4.167)	(11.38)	(7.791)
N	3	3	3	3

Table K8 : Experiment GFS2 - Conditional Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	105.1 (769.6) 45	82.23 (342.9) 95	102.7 (286.0) 103	91.14 (358.4) 139
2	89.69 (336.2) 89	71.21 (216.5) 97	73.34 (182.3) 116	80.27 (329.3) 114
3	114.2 (378.1) 95	87.71 (623.6) 92	108.6 (453.5) 114	105.3 (316.1) 130
Mean	103.0	80.39	94.86	92.24
Std Error	(7.146)	(4.849)	(10.90)	(7.248)
N	3	3	3	3

Table K9 : Experiment GFS2 - Female Starvation

Mean Survival Time (hours) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	23.30 (19.79) 52	50.76 (145.8) 80	31.26 (36.35) 106	31.90 (110.5) 148
2	31.14 (48.89) 100	53.91 (278.1) 100	36.12 (83.42) 120	38.41 (152.3) 120
3	25.58 (64.22) 100	35.33 (50.52) 100	29.48 (58.55) 120	29.37 (62.48) 159
Mean	26.68	46.67	32.29	33.23
Std Error	(2.327)	(5.741)	(1.982)	(2.692)
N	3	3	3	3

Table K10 : Experiment GFS2 - Male Starvation

Mean Survival Time (hours)  
(Variance)  
Number of Individuals

Replicate	FF	SS	FS1	FS2
1	16.79 (11.69) 52	41.16 (127.8) 80	24.73 (82.83) 106	24.73 (57.82) 147
2	21.07 (55.48) 100	47.25 (160.4) 100	31.69 (68.32) 120	32.06 (119.2) 120
3	18.83 (50.73) 100	29.15 (51.03) 100	24.18 (42.81) 120	25.48 (58.30) 160
Mean	18.90	39.19	26.87	27.42
Std Error	(1.238)	(5.318)	(2.418)	(2.328)
N	3	3	3	3

Table 1 : Experiment GFS2 - Female Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	27.82 (186.0) 100	54.28 (334.4) 96	51.12 (320.0) 100	48.04 (313.6) 100
2	29.88 (175.1) 99	44.85 (390.0) 95	41.73 (285.5) 96	43.53 (209.6) 95
3	38.59 (249.3) 100	49.64 (344.1) 100	49.80 (217.4) 100	41.24 (274.3) 96
Mean	32.10	49.59	47.55	44.27
Std Error	(3.30)	(2.72)	(2.93)	(2.00)
N	3	3	3	3

Table K12 : Experiment GFS2 -- Male Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	29.22 (102.3) 100	48.34 (431.7) 98	45.89 (238.8) 100	44.82 (329.4) 100
2	25.12 (83.30) 100	47.08 (397.4) 95	39.92 (293.4) 97	42.19 (295.2) 94
3	25.46 (171.9) 100	46.98 (240.6) 99	39.67 (194.5) 96	35.33 (162.3) 90
Mean Std Error N	26.60 (1.31) 3	47.47 (0.44) 3	41.83 (2.03) 3	40.78 (2.83) 3

Table K13 : Experiment GFS3 - Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	97.04 (646.8) 94	78.00 (271.4) 93	86.23 (461.4) 87	79.23 (357.1) 187
2	83.71 (403.3) 93	69.31 (220.9) 96	69.69 (359.2) 89	66.02 (217.2) 183
3	93.85 (487.5) 92	64.72 (248.7) 94	73.44 (184.6) 95	64.00 (351.7) 183
Mean	88.20	70.68	76.45	69.75
Std Error	(4.421)	(3.893)	(5.008)	(4.775)
N	3	3	3	3



Table K14 • Experiment GFS3 - Conditional Fecundity

Mean 24 Hour Fecundity (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	99.10 (460.3) 92	78.85 (206.2) 92	87.23 (378.4) 86	80.07 (293.7) 185
2	85.53 (256.9) 91	69.98 (180.2) 95	71.26 (255.2) 87	66.69 (179.1) 181
3	85.71 (487.5) 92	65.39 (209.6) 93	73.44 (184.6) 95	65.78 (244.9) 178
Mean	90.11	71.41	77.31	70.84
Std Error	(4.493)	(3.951)	(4.999)	(4.621)
N	3	3	3	3

Table K15 : Experiment GFS3 - Female Starvation

Mean Survival Time (hours) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	33.53 (105.3) 96	67.52 (373.5) 96	49.25 (212.2) 90	48.96 (304.3) 186
2	45.84 (146.7) 96	75.95 (376.0) 92	60.53 (289.0) 96	63.13 (315.8) 192
3	36.18 (81.18) 96	54.56 (163.6) 92	50.49 (120.6) 96	50.68 (165.1) 186
Mean Std Error N	38.52 (3.742) 3	66.01 (6.222) 3	53.42 (3.573) 3	54.26 (4.465) 3

Table K16 : Experiment GFS3 - Male Starvation

Mean Survival Time (hours)  
(Variance)  
Number of Individuals

Replicate	FF	SS	FS1	FS2
1	23.02 (40.85) 95	46.46 (322.5) 96	34.55 (184.0) 90	35.34 (166.8) 186
2	30.00 (66.74) 96	56.70 (219.0) 93	44.06 (179.9) 96	42.82 (180.3) 192
3	22.68 (37.96) 96	41.50 (104.0) 93	31.71 (65.68) 96	33.03 (98.45) 186
Mean	25.24	48.22	36.77	37.07
Std Error	(2.385)	(4.477)	(3.736)	(2.955)
N	3	3	3	3

Table K17 : Experiment GFS3 - Female Longevity

	Mean Longevity (days) (Variance) Number of Individuals			
Replicate	FF	SS	FS1	FS2
1	35.62 (149.5) 78	51.03 (290.8) 76	44.38 (252.1) 78	45.88 (181.7) 155
2	32.25 (79.98) 77	47.86 (249.7) 77	40.35 (214.4) 80	37.31 (172.9) 159
3	33.84 (162.9) 77	53.94 (228.7) 80	45.13 (230.9) 76	41.03 (244.7) 154
Mean	33.90	50.94	43.29	41.41
Std Error	(0.97)	(1.76)	(1.48)	(2.48)
N	3	3	3	3

Table K18 : Experiment GFS3 - Male Longevity

Mean Longevity (days) (Variance) Number of Individuals				
Replicate	FF	SS	FS1	FS2
1	37.48 (126.3) 79	51.59 (205.9) 76	47.04 (210.5) 75	52.12 (197.1) 153
2	28.58 (121.3) 79	55.08 (266.6) 78	43.37 (292.1) 73	43.74 (247.3) 155
3	30.39 (155.8) 79	51.99 (245.6) 79	35.30 (149.0) 78	37.26 (187.6) 156
Mean	32.15	52.89	42.56	44.37
Std Error	(2.72)	(1.10)	(2.85)	(4.30)
N	3	3	3	3

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