THE UNIVERSITY OF MANITOBA

THE EFFECTS OF SELECTION FOR GROWTH RATE AND

OF HETEROSIS ON LONG-TERM REPRODUCTIVE

PERFORMANCE IN MALE MICE

BY

SOPHIE M. BOUCHART

A THESIS SUBMITTED TO THE FACULTY

OF GRADUATE STUDIES IN PARTIAL FULFILLMENT

OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ANIMAL SCIENCE

WINNIPEG, MANITOBA

THE EFFECTS OF SELECTION FOR GROWTH RATE AND OF HETEROSIS

ON LONG-TERM REPRODUCTIVE PERFORMANCE IN MALE MICE

BY

SOPHIE M. BOUCHART

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

© 1987

ACKNOWLEDGEMENTS

I wish to express my gratitude to DR. R.J. Parker and members of my committee for their guidance and encouragement in carrying out this study.

I wish to state my appreciation to many faculty members, graduate students, technicians and summer students for their help and support throughout this endeavor.

Special thanks to my family and close friends for their comments, invaluable support and understanding during my course of study.

ABSTRACT

Male mice of three lines and their line crosses were measured over five mating periods, to observe the effects of selection for growth and of heterosis on long-term reproductive performance. The three pure lines consisted of two selected lines (A and C) and control line (E) differing in body weight at six weeks. Average six week weight of males was 49g for line A, 41g for line C and 26g for line E. Each male was mated to two females at each mating period. Females were from an unrelated line (S). Litter traits were analyzed as overall production (OP), and totals (T) and averages (A) of litters produced at each mating period. The litter traits studied were litter size (LS) and litter weight (LW) at birth (B) and at weaning (W). Testes weight (TESTW) was measured at 196 days of age.

Differences among lines and line crosses were significant ($P<0.05$) for all litter traits except for TLWW and ALSW. Least square means for OPLSB and OPLSW were (SE = 3.07, 3.01) A = 93.50, 88.59, C = 83.28, 77.44, E = 98.73, 92.00, AC = 102.42, 93.97, AE = 99.71, 90.54, CE = 101.31, 93.33. Least square means for OPLWB and OPLWW (g) were (SE = 5.27, 36.44) A = 167.00, 1,193.88, C = 145.88, 995.03, E = 160.10, 1,100.71, AC = 178.03, 1,204.93, AE = 168.68, 1,152.55, CE = 170.10, 1,159.28. Differences among lines and line crosses were significant ($P<0.05$) for age at first mating (MINFERT), number of fertile matings (NFM) and testes weight

(TESTW).   Least square means for MINFERT were (SE = 0.73) A = 46.31, C = 49.82, E = 45.93, AC = 43.78, AE = 44.17, CE = 44.96. Least square means for NFM were (SE = 0.24) A = 9.51, C = 8.31, E = 9.35, AC = 9.67, AE = 9.54, CE = 9.71.

All line crosses displayed heterosis for all litter traits and all other reproductive traits studied. The percent heterosis (H) for OPLSB and OPLSW was AC = 14.05, 10.99, AE = 3.60, 0.24, CE = 10.25, 8.58.   H for OPLWB and OPLWW was AC = 21.62, 111.00, AE = 5.13, 5.26, CE = 17.04, 111.02. H for MINFERT was AC = -4.28, AE = -1.95, CE = -2.89.

Selection for growth rate resulted in a decrease in long-term reproductive performance of males. Male heterosis was found to positively influence long-term reproductive performance.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

In most animal production systems, a great emphasis has been placed upon obtaining animals which reach market weight at a younger age; yet, high reproductive levels, in terms of number of offspring/dam/year produced, remains important to maintain a higher profit level. In livestock production, it is common practice to select for larger animal body size. However, most of this selection has been undertaken without considering its possible effect on reproduction. Selection for postweaning growth rate in laboratory animals has resulted in a decrease in fertility. Through the use of cross-breeding, reduction in fitness can often be overcome.

The laboratory mouse is considered an excellent model for the study of reproduction genetics in livestock species, requiring less time, money and resources. Therefore, mice were used in this experiment.

The objectives of this study were to examine the effect of selection for growth in pure lines on long-term reproductive performance of pure line and line cross males and to examine the effects of heterosis on long-term reproductive performance in males.

LITERATURE REVIEW

1. Correlated responses in reproductive performance of males to selection for increased postweaning growth rate or body weight

Populations under various types of selection exhibit correlated responses (Rahnefeld et al., 1966). The primary connotation of a correlated response is that the trait under selection is genetically correlated to another trait, even though the magnitude of the correlated response is influenced by other parameters (Roberts, 1961; Rahnefeld et al., 1966). It is through selection that breeders improve or change the genetic composition of their herds or flocks (Aaron et al., 1986a). Quantitative characters may be altered through selection of extreme phenotypic values or directional selection (Johnson and Eisen, 1975). In livestock production, growth rate is of economic importance (Aaron et al., 1986b). Numerous studies have demonstrated that efficiency and rate of growth are responsive to selection (Allrich et al., 1981).

There has been concern about the effects on reproductive performance of selection for body weight or postweaning gain (Fowler and Edwards, 1960; Allrich et al., 1981). Eisen (1974) reviewed numerous selection experiments designed to increase growth in mice. These studies generally reported a decline in reproductive fitness (Fowler and Edwards, 1960; Bradford, 1971; Eisen et al., 1973). Johnson and Eisen (1975) suggested that this

response was expected because, for quantitative traits, natural selection ordinarily favors an intermediate expression. Most studies which have observed the correlated response of reproductive traits arising from selection have been mainly concerned with female fertility; 'little work has been aimed towards studying changes in male fertility concommitant with selection for increased body size' (Johnson and Eisen, 1975).

Studies have examined the possible effects of selection for increased postweaning growth upon the age at which animals reach puberty. Falconer (1984) questioned whether puberty was weight-dependent or age-dependent in male mice. In that experiment, Falconer (1984) defined the attainment of puberty by the presence of vaginal plugs. His results showed that puberty in males was almost totally age-dependent; puberty was reached by the males of the various strains at the same age, regardless of their weight. Allrich et al. (1981) and Rios et al. (1986) examined the effect of selecting for growth upon age at first spontaneous mating in male rats. Rios et al. (1986) selected for increased 3-9 week gain and found no difference amongst the different lines in age of males at first spontaneous mating. Similarly, Allrich et al. (1981) observed that selecting for efficiency or rate of lean growth did not influence age at first spontaneous mating. These results seem to indicate that the age of the male may be more substantial in delineating the onset of mating ability than body weight (Allrich et al., 1981). Similarly, Davis et al. (1986)

suggested that selection for increased weaning weight had no effect on age at puberty in ram lambs. Selecting for increased postweaning gain does not seem to influence the age at which males reach puberty.

Testicular growth and development have been studied to determine whether these traits might be affected by selection for increased growth rate. Johnson and Eisen (1975) reported an increase in reproductive organ weight in male mice from lines which had been selected for increased postweaning gain compared to the controls. When these organs (testes, epididymides and seminal vesicle) were expressed per gram of body weight, they were actually smaller in the selected line, which seems to indicate that the growth of these organs was reduced, relative to total weight (Johnson and Eisen, 1975). Rios et al. (1986) similarly reported that once the testes weight of male rats were adjusted by covariance for body weight, no differences remained between the control and the selected lines. Eisen and Johnson (1981) indicated similar findings. Allrich et al. (1981) suggested that selecting for increased efficiency of postweaning lean growth in the male resulted in a decrease in testes weight. It was noted that this decrease did not affect the male's ability to impregnate females; however, since each male was mated to only one female, this might not be valid under a more strenuous mating scheme. The same authors also found that selection for increased rate of postweaning lean growth did not affect testes weight. Schinckel et

al. (1983) indicated that boars selected for rate of lean growth, compared to two other lines, reached the same level of testicular development at a later age (14-20 days later). They proposed that selection for lean growth might have delayed sexual maturity. Hough et al. (1985) studied the effect of selecting bulls for increased yearling weight and reported scrotal circumference remained unchanged. Johnson and Eisen (1975) noted that there was no significant difference in unadjusted sperm count between the line selected for increased postweaning gain and the controls (mice). However, since the selected line had significantly larger testes, it can be deduced that sperm production from the testes of the selected males has decreased in efficiency compared to the control males (Johnson and Eisen, 1975). The above studies indicate that selection for increased weight gain may have had a negative effect upon testicular development.

Numerous studies have looked at the effect of selection for postweaning growth on litter size. However, most experiments which have dealt with litter size have merely looked at the parental effect rather than the male and female effects separately. Litter size is classified as a female trait; however, some studies (discussed later) have shown that the male also plays a role. The correlated response of litter size due to selection for growth will be presented as a parental or line effect.

A positive correlation between litter size and body weight in mice was discerned in experiments reported by Fowler and Edwards (1960), Rahnefeld et al. (1966), Land (1970a), Eisen et al. (1973), Hanrahan and Eisen (1974), Baker and Chapman (1975), Eisen and Johnson (1981), and Fuente and San Primitivo (1982). Conversely, Bradford (1971), Lasalle et al. (1974), Hetzel and Nicholas (1982) (mice) and Kasser et al. (1986) (rats) noted no significant response in litter size resulting from selection for postweaning gain. Wang and Dickerson (1984) found litter size to be unaffected by selection for postweaning rate or for efficiency of protein deposition in rats. Morris and Lineweaver (1972) reported a decrease in litter size due to selection for increased postweaning gain (control averaged 10.8 pups/litter and selected averaged 8.8 pups/litter). McLellan and Frahm (1973) reported that selection of mice for increased hindleg muscle weight resulted in an increase in litter size.

Litter size is a complex trait which depends upon ovulation rate, uterine environment and postnatal maternal care, semen quality and libido (Nagai et al., 1984). Most selection experiments have attempted to explain the correlated response of litter size in terms of maternal influence. It has been proposed that divergent selection for body weight will generally alter litter size in the same direction as body weight through changes in ovulation rate (Fowler and Edwards, 1960; Land, 1970a; Bradford, 1971; Barria and Bradford, 1981; Roberts, 1979; Bayon et al.,

1986). However, Allrich et al. (1981) did not observe an increase in ovulation rate in rats which had been selected for increased body weight. A decrease in embryo survival has been associated with selection for increased body weight (Fowler and Edwards, 1960; Bradford, 1971; Barria and Bradford, 1981; Bayon et al., 1986). Eisen and Johnson (1981) observed a positive correlation between litter size and testes weight. A few reports have demonstrated a positive correlation between testes weight and ovulation rate (Land, 1973; Islam et al., 1976). Selecting for increased testes weight resulted in a correlated increase in ovulation rate; yet litter size did not follow the positive correlation, which indicates an increase in embryo mortality (Islam et al., 1976; Wirth-Dzieciolowska and Martyniuk, 1986).

The effect of selection for increased growth rate on male reproductive efficiency has been examined. Lasalle et al. (1974) reported a decrease in percent fertile matings in lines selected for increased weight gain from 21-42 days of age. Morris and Lineweaver (1972) illustrated similar findings: 86% of the control littered compared to 64% for the selected lines. Baker and Chapman (1975) noted the percent of females that did not conceive was higher for the selected line than the control. Morris and Lineweaver (1972) observed that selection for growth in mice resulted in a significant increase (P<0.01) in the number of days from introduction of the male until plugging, the control being two days sooner compared to the selected line. This finding agrees

with the results of Fowler and Edwards (1960) which indicated that males selected for increased body weight exhibited a lower libido. Morris and Lineweaver (1972) noted that control males produced 15% more plugs than the selected males. Hetzel and Nicholas (1982) reported that selected mice were always slower to mate compared to the control mice. Once again these findings might reflect a decrease in libido arising from selection. However, McLellan and Frahm (1973) found no significant difference in conception rate when selecting for increased hindleg muscle weight.

In his review Roberts (1979) observed that the majority of the literature from laboratory animals seem to agree that large animals become fat. It is suggested that this increase in fat is responsible for the reduced fertility of large body size females through either mechanical obstacles, females not breeding once they become too fat, or from a hormonal imbalance (Bradford, 1971; Roberts, 1979). However, the author is not aware of such reports concerning the male.

Some reports have proposed that animals selected for increased body weight have a reduced reproductive life (Roberts, 1961). Eklund and Bradford (1977) looked at longevity in mice selected for rapid growth. On average, they reported that the selected animals had a life span of only 57% of the control line. Barria and Bradford (1981) observed that fertility will be very rapidly restored once reversed selection is applied.

The effects of selection for increased postweaning growth rate on progeny performance have been considered. None of the studies have indicated birth weight to be affected by selection (Baker and Chapman, 1975 (rats); Hetzel and Nicholas, 1982 (mice); Hough et al., 1985 and Aaron et al., 1986b (cattle)). Hough et al. (1985) also noted no increase in calving difficulties nor in calf mortality. No effects due to selection were found for weaning weight for mice (Hetzel and Nicholas, 1982; Lasalle et al., 1974). However, a significant increase was observed for six week weight (Bradford, 1971; Lasalle et al., 1974; Baker and Chapman, 1975; Hetzel and Nicholas, 1982). McLellan and Frahm (1973) found selection for increased hindleg weight resulted in a significant increase in both average daily gain between 21-42 days and in 42 day weight while weaning weight (21 days) showed slight change.

2. Reproductive performance of crossbred males

The benefits of crossbreeding have been known for many years. Systematic crossing has been used commercially to "capitalize on heterosis and complementarity" which in turn has been shown to be positively correlated with the reproductive potential of the species (Willham and Pollak, 1985). In most species, fitness or the reproductive complex has a low heritability ($h^2 < 0.15$), but the exploitation of non-additive genetic variance is considerable (Willham and Pollak, 1985). Through the use of crossbreeding, both

additive and non-additive genetic components may be exploited by, "the additive through the complementarity of traits giving rise to economic merit, and the non-additive in exhibiting heterosis" (Land et al., 1983). Previous research has shown the impact of heterosis for reproductive efficiency. The benefits of using crossbred females has been extensively demonstrated in all domesticated species as well as for laboratory animals. In contrast, relatively little interest has been shown in evaluating the benefits of using crossbred males for their reproductive performance (Nitter, 1978; Stritzke et al., 1984; Fahmy and Holtmann, 1977; Bradford et al., 1963).

Various reasons for using crossbred sires have been advanced (Rempel et al., 1964; Fahmy and Holtmann, 1977). Crossbred males are commonly more hardy and vigorous than purebreds, which in turn might presumably decrease breeding problems for commercial producers. Using crossbred males would permit an economical system of augmenting the numbers of genetically good sires from a limited number of tested purebred parent stock (Rempel et al. 1964). However, the extent with which crossbred males are used will rely on the level and variability of performance of the crossbred sired progeny compared with purebred sired progeny (Rempel et al., 1964).

Normal efficiency in reproduction is of great economic importance in all domesticated species (Philipsson, 1981). Reproductive rate is determined by the female through uterine

environment, ovulation rate and post-natal care which encompasses lactation; however, it is also influenced by the male directly, through libido and semen quality, and indirectly through its progeny, such as survival rate before weaning (Nagai et al., 1984). Thus, the reproductive rate of females mated to crossbred males will be affected by heterosis due to the male.

Crossbred males have been shown to be superior to purebred males. The crossbred male's superiority might arise from the observed heterosis present in the male's sexual performance, survival rate of fetuses and/or growth rate of the young (Nagai et al., 1984). Researchers have studied testicular and epididymidal characteristics, reproductive efficiency, mating behaviour and progeny performance of crossbred males in various species. At this time, the work undertaken in this field has primarily concentrated on the use of crossbred boars, but data are also available for crossbred rams, bulls, mice and rats.

Testicular and epididymidal characteristics in crossbred males have been investigated (Land, 1973; Wilson et al., 1977; Conlon and Kennedy, 1978; Neely et al., 1980; Fent et al., 1983; Neely and Robison, 1983; Lal and Pant, 1984). Testicular growth may be an indicator of the reproductive performance of males (Schinckel et al., 1983); thus, examining this trait in crossbred males is of significance. In swine, Wilson et al. (1977) and Fent et al. (1983) found the mean testicular weight to be heavier for crossbred

boars than for purebred boars. Similarly, Neely et al. (1980) indicated that crossbred boars tended to have wider, longer testes at all ages examined, and that the excised testes of the crossbred boars were larger than the purebred boars (P<0.01). Land (1973) recognized that testes of crossbred rams grew faster in diameter than those of the parental breeds, thereby showing heterosis in this character.

Crossbred boar testes were noted to contain more sperm than purebred boars (Wilson et al., 1977; Neely et al., 1980; Fent et al., 1983; Neely and Robison, 1983). Neely et al. (1980) obtained heterosis values for length, weight, total sperm, sperm per gram of right testis and combined width of testis of 8.5, 25.4, 33.7, 23.3 and 10.4%, respectively. These estimates tended to decrease once adjusted for body weight to 2.5, 8.1, 14.4, 15.1 and 4.5%, respectively. These results indicate that the increased sperm content and larger testes found in crossbred boars were not associated with an increase in body weight, but rather were in part an increase in activity of spermatogenic elements (Neely et al., 1980). Conlon and Kennedy (1978) reported that crossbred boars showed no heterosis for sperm concentration. However, they found crossbred boars to produce more than twice the semen volume of their purebred parent lines. Thus, the sperm numbers per ejaculate were considerably greater in the crossbred boars. Conlon and Kennedy (1978) also noted that crossbred boars' semen scored highest for total semen score, with the difference from the parent

lines being not very large. Crossbred boars scored highest for sperm morphology but lowest for live-dead rate (Conlon and Kennedy, 1978). Lal and Pant (1984) looked at sperm dimensions in sheep and observed that larger sperm dimensions were found in crossbred rams in comparison to the parental breeds, except in head breadth. Napier (1961) noted a positive correlation of fertility with head length. Combining these results seems to indicate a relationship between fitness (or reproductive complex) and hybrid vigour in sperm dimensions (Lal and Pant, 1984). In their experiment, Lal and Pant (1984) also examined sperm-to-sperm variability and found no evidence of significant differences between spermatozoa from crossbred rams compared to those of purebreds. These reports propose that crossbred males seem to be superior in most testicular and epididymidal characteristics. However, there is still some question as to whether or not the increased testis size and sperm number in crossbred males would be reflected in increased libido, conception rate or litter size (Neely et al., 1980).

Reproductive efficiency of crossbred males has been evaluated against purebred males. Wilson et al. (1977) reported that crossbred boars had a 7.9% higher conception rate than purebred boars. They also indicated that crossbred boars sired more embryos per gilt exposed than purebreds. Embryo survival rate, which is percent embryo of corpora luteum, for litters sired by crossbred boars was found to be 76.77±2.87 compared to 69.86±3.69 for litters sired by purebred boars (Wilson et al., 1977). Fahmy and

Holtmann (1977) noted that purebred boars sired larger litters at birth compared to crossbred boars (P<0.05). Ch'ang and Evans (1986) found male heterosis to have a significant effect on litter size at birth in ewes. In contrast, Wilson et al. (1977) and Lishman et al. (1975) recorded no significant difference in litter characteristics in swine between breed of boar (ie purebred versus crossbred). Crossbred male mice sired larger litters at birth than straightbred male mice (Nagai et al., 1984). The average proportion of multiple births from purebred and crossbred rams was found to be very close (Parker, 1971; Fahmy and Bernard, 1973). Parker (1971) indicated that the number of lambs born per ewe mated was significantly larger for crossbred rams than for purebreds, while Bradford et al. (1963) detected no consistent difference between crossbred and purebred sires in lambing percentage (number of lambs born per ewe mated). Humes et al. (1978) indicated crossbred rams to show a non-significant advantage over purebred rams in terms of prolificacy and fertility. Neville et al. (1985) found no significant difference between purebred and crossbred bulls in terms of proportion of cows exposed that had a calf, had a live calf or weaned a calf. Bradford et al. (1986) reported higher values of NOD (number of days from beginning of the breeding period until calves are born) for purebred sires (P<0.05) than crossbred sires. Progeny survival rate, defined as progeny weaned of all those born, has been reported higher for crossbred males than for purebreds (Bradford et al., 1963 (sheep); Fahmy and Holtmann, 1977 (swine)).

Various workers have explored the effect of male heterosis upon progeny performance. Studies with lambs have demonstrated that purebred-sired lambs are slightly heavier at birth than crossbred-sired lambs (Bidner et al., 1978; Hall and Fogarty, 1986; Stritzke et al. 1984). Parker (1971) found crossbred-sired lamb birth weight not to be significantly different from purebred-sired lambs, while Bradford et al. (1963) reported that crossbred-sired lambs were intermediate to the two parents' breed groups in birth weight. Fahmy and Holtmann (1977) and Lishman et al. (1975) found litters produced by crossbred boars to be similar in birth weight to those produced by purebred boars. Kennedy and Conlon (1978), however, reported a significant breed of boar effect on birth weight. In mice, crossbred males have been shown to produce heavier litters at birth (Nagai et al., 1984).

Some discrepancy seems to arise when looking at the effect of using crossbred males versus purebred males on weaning weight of their progeny. Sidwell et al. (1964) found crossbred sired lambs to excel in average weaning weight. Fahmy and Holtmann (1977) and Olson et al. (1985) both reported crossbred-sired progeny to be lighter at weaning than those produced by purebred sires (swine and cattle, respectively).

Various studies have examined ADG (average daily gain) or growth rate of progeny produced from either purebred or crossbred males. Fahmy and Holtmann (1977) reported that piglets sired by crossbred

boars grew slightly faster, the difference not being significant, than those sired by purebred boars. Similarly, Sidwell et al. (1964) found crossbred-sired lambs to have higher ADG compared to purebred-sired lambs. Hall and Fogarty (1986) indicated no difference between growth traits of purebred and crossbred-sired lambs. Olson et al. (1985) found the growth of crossbred-sired calves to be the same or slower than purebred-sired calves. Bidner et al. (1978) reported similar findings in sheep. Stritzke et al. (1984) found that ADG of purebred-sired lambs was higher than crossbred-sired lambs during the winter and summer lambing season, while the reverse was found for lambs born in the fall. Neville et al. (1985) reported that the mean performance of calves produced from crossbred bulls was not significantly different (P>0.05) from those sired by purebred bulls. Ch'ang and Evans (1982) reported crossbred rams to increase average lamb production per ewe joined by 9%, which they suggested would be due in part to male heterosis.

Many livestock producers presume that crossbred sires will produce more variable progeny than purebred sires (Bidner et al., 1978); however, several studies do not support this opinion. The variance of progeny performance was found to be similar for purebred and crossbred sires (Rempel et al., 1964 and Lishman et al., 1975 (swine); Stritzke et al., 1984 (sheep); Neville et al., 1985 (cattle)). Fahmy and Holtmann (1977) (swine), Bradford et al. (1963) and Bidner et al. (1978) (sheep) reported that progeny of crossbred sires were less variable than those produced by purebred

sires for ADG, litter performance and growth traits, respectively. Nagai et al. (1984) found crossbred male mice to have less variation for their lifetime performance compared to males from purebred lines.

Studies have investigated the possible advantages of crossbred males over purebred males in terms of libido or mating behaviour. Wilson et al. (1977) reported that there was a significant difference ($P<0.001$) in mating behaviour between crossbred and purebred boars. They found none of the crossbred boars to have more than one failure, while 42% of purebred boars had two or more failures. Neely and Robison (1983) indicated that crossbred boars showed more sexual interest ($P<0.05$), more mounts and higher proportions of properly orientated mounts ($P<0.05$). Crossbred boars were more aggressive upon entry into the pen. They also reported that more crossbred boars completed a mating than purebred boars (69 versus 27%). Crossbred boars were quicker to mount as compared to purebred boars (Wilson et al., 1977; Neely and Robison, 1983). Dewsbury (1975) studied the copulatory behaviour of rats and found crossbred males to be more likely to mate than purebred males. Results reported by Wilson et al. (1977), Neely et al. (1980) and Neely and Robison (1983) all seem to illustrate that at a given age, crossbred boars are at a later physiological stage in terms of mating behaviour traits in comparison to purebred boars. Heterosis values were found for scrotal and excised testis measurements as well as for mating behaviour. However, no

consistent association between testicular traits and mating behaviour characteristics were found (Neely and Robison, 1983).

Crossbred males have been shown to exhibit superiority in mating behaviour as well as in semen characteristics, conception and survival rates. However, numerous reports have found progeny performance of crossbred males to be similar to purebred males.

3. Effect of age of the male on reproductive performance

Male fertility is affected by numerous factors such as seminal quantity and quality, sex drive and mating ability. The age-of-male effect and its influence on the performance of the male has been examined in various studies. Most of the experiments undertaken to look at age effect have concentrated on comparing young animals to 'mature' animals; very few have examined the effect of using older animals.

In most species, seminal quality is greatly influenced by the age of the animal (Colas, 1983). Swierstra and Rahnefeld (1967) and Swierstra (1973) concluded that semen quality, percent motile sperm and total motile sperm per ejaculate were poorer in young boars than in mature boars. Pubescent rams are reported to produce poor quality semen (Tiwari and Sahni, 1982). Many studies have demonstrated that a great number of abnormal cells are present in

initial ejaculates (Colas, 1983). Raja and Rao (1983) and Chenoweth et al. (1984) indicated a gradual increase in seminal quality in bulls with advancing age. Skinner and Rowson (1968) and Colas (1983) illustrated similar findings in the ram. This is believed to arise as a result of a decrease in spermatozoal abnormalities (Skinner and Rowson, 1968; Colas, 1983; Raja and Rao, 1983; Chenoweth et al., 1984). Colas (1983) observed that abnormalities consist mostly of head malformation and proximal cytoplasmic droplets which indicate inadequate spermatogenetic activity and insufficient epididymal maturation. Raja and Rao (1983) found a significant decrease in tail abnormalities, a non-significant decrease in head abnormalities, a significant decrease in mid-piece abnormalities and a significant increase in free loose heads with advancing age. A gradual increase in BSE (breeding soundness evaluation) score with advancing age was reported by Chenoweth et al. (1984); however, the scores did not differ significantly.

Raja and Rao (1983) found a significant increase in ejaculate volume with age of bulls. In contrast, Cameron (1985) indicated only a slight effect of age on semen volume in boars. Both reports found age to have a significant effect on sperm concentration, total sperm in the ejaculate and daily sperm output. Tiwari and Sahni (1982) reported a positive correlation between age and sperm production in rams. Krolinski (1979) looked at the effect of age-of-bull on sperm survival time. Three different age groups

were present: 1.5-4, 4-7 and 7+ years. At 46.5°C, survival time was not significantly different among age groups, while at 4°C, groups 4-7 and 7+ were significantly different, where survival time was lower for the older animals.

An age effect on conception rate has been detected. Ch'ang and Evans (1979) working with Dorset Horns reported 1.5 year old rams to have a lower rate of conception in mated ewes than those mated to 2.5 year old rams. However, they did not find the same effect in the Corriedale breed. Makarechian et al. (1983) discerned no differences in conception rate between yearling and two year old bulls. Krolinski (1979) found conception rates to be significantly different between bulls of 1.5-4 years old and bulls of 7+ years, where older bulls had a lower level. Bradford et al. (1986) reported older rams to have higher conception rates than ram lambs (76 versus 65%). However, due to the patterns of variability among rams within age groups, the age-of-ram effect did not seem to be consistent. Singh et al. (1985) concluded that conception rate was significantly affected by age of buck. Vakil et al. (1968) observed an age-of-ram effect on twinning. Yearling rams obtained the highest rank, following which a decrease was noted with increasing age of ram; 4-yr old rams being an exception.

Colas (1983) demonstrated a gradual increase in the potential to fertilize with advancing age. Brioris (1980), as cited in Colas (1983), reported lambing rates of 60.95 versus 62.7% for semen from

ram lambs and adult rams, respectively. Makarechian and Farid (1985) similarly indicated that yearling bulls had slightly lower fertility than older bulls; however the differences were not significant. Singh et al. (1985) reported a significant age-of-buck effect on kidding rate. Finn (1964) was unable to demonstrate an effect of age of sire on litter size in mice.

The possible effect of age upon sex drive has been examined. Chenoweth et al. (1984) reported that, apart from the number of mounts, measures of sex drive did not vary with age of bulls. It is most likely that this difference reflects the 'relative inexperience in mating ability' in the younger bulls (Chenoweth et al., 1984). Makarechian and Farid (1985) found that the use of bulls of mixed ages for breeding would generally result in lower fertility of younger bulls due to the social dominance of the older bulls.

In most animal production systems, males are not kept as breeders to a very old age, partly to reduce generation interval and ameliorate genetic improvement. Thus, very little information on the effect of aging on reproduction in male domestic animals is available. Bishop (1970) reviewed the effect of aging on male reproduction, and presented some information available for bulls. Fertility in bulls is found to be at its peak at 3-4 years of age, after which it declines slowly and steadily. With increasing age, sexual activity and interest decrease, with high individual

variation. Slowness in serving behaviour is apparent in most bulls by 5-6 years of age. Infertility, associated with degenerative changes in the testes and deterioration in the quality of the ejaculate, increases with age. Sexual activity is independent of spermatogenic activity.

4. Male effect on reproductive performance

Reproductive performance is measured in terms of progeny produced. This trait is highly dependent on the female; however, the male is also responsible for some of the variation.

Semen characteristics are very important and have been shown to be quite variable. Fields et al. (1979) reported a breed-effect for semen volume and sperm concentration; Chenoweth et al. (1984) found spermatozoal morphology and BSE (breeding soundness evaluation) to be significantly different (P<0.01) between breeds of cattle. Moore et al. (1986) compared rams from lines selected for high and low ewe prolificacy. Sperm swimming speed was not significantly different while sperm concentration differed between lines at nine months of age. Moore and Whyman (1980) also compared rams from high and low prolificacy flocks, and indicated that the only significant difference between the two groups in terms of semen quality was sperm concentration, which was higher for high prolificacy rams. Testicular volume was found to be lower for the

low prolificacy line compared to the high prolificacy line. Louda et al. (1981) studied young rams from two breeds of similar prolificacy levels and reported little difference in semen production between the two breeds. Land (1970b) and Swierstra and Rahnefeld (1967) noted no breed effect on various semen characteristics. Swierstra and Rahnefeld (1967) and Singleton and Shelby (1972) found a significant difference between boars while Singleton and Shelby (1972) also demonstrated a significant difference between ejaculates within the same boars.

Numerous studies have shown the extent of the male effect on various fertility parameters. Conception rate and calving interval were found to be significantly affected by the male (Syrstad, 1981; Singh et al. 1986). Conversely, Reynolds et al. (1986) observed no significant breed of sire effect on pregnancy rate or calf survival. Young et al. (1976) (swine) reported no large or significant differences between breeds of sire for the number of live embryos or percent embryo survival. Singleton and Shelby (1972) and Courot and Colas (1986) both indicated a male difference in their capacity to fertilize ova and commence normal embryonic development. Courot and Colas (1986) concluded that embryo mortality was directly related to the initial quality of the gametes. Johnson and Omtvedt (1973), Burfening et al. (1977), and Humblot (1986) reported a significant sire effect on embryo survival rate while Humblot and Denis (1986) studied late embryonic mortality and found sire effect to be nonsignificant.

Burfening et al. (1977) evaluated rams selected for low and high fertility. Pregnancy rates tended to be higher in the ewes exposed to rams from the high fertility line compared to the low line. A significant effect was also seen in the number of lambs born per ewe lambing. From this study, it was proposed that selecting rams based on the performance of his dam can affect the reproductive rate in females to which he is exposed. Newton and Betts (1968) found a ram-effect on the number of lambs born per ewe. Swierstra and Dyck (1976) found boar-effect to be significant for impregnation rate. Moore and Whyman (1980) reported a higher fertilization rate for rams from a high prolificacy flock, compared to rams from a low prolificacy flock, when mated with ewes with natural multiple ovulation. However, this difference disappeared when the rams were mated to ewes having single ovulations (or multiple ovulations induced by PMSG). This evidence suggests a direct ram effect on multiple birth rate. Similarly, Vakil et al. (1968) noted a significant effect of type of birth of ram on the number of lambs born per ewe lambing; that is to say, rams born as twins sired more offspring compared to those born as singles. Hancock (1949) conducted a study on the sire effect on monozygotic twinning in cattle. The results indicated a definite sire effect and suggested that sperm from certain bulls may be so constituted as to cause the fertilized ovum to split.

Litter size is of great importance in maximizing production in various species, but more specifically in swine. The size of a

litter arises from the combination of various factors. Determining these factors and their importance would enable producers to manipulate them in order to maximize litter size. Factors which affect litter size, whether genetic or environmental, have been studied extensively. However very little attention has been given to the possible role the sire may have (Finn, 1964). The upper limit to litter size is set by the numbers of eggs ovulated (Hauser et al., 1952; Finn, 1964). Due to failure of fertilization or implantation or intra-uterine death of embryos, this maximum is rarely realized (Finn, 1964). The ovulation rate is a maternal trait; however, the other factors might be influenced by the male (Finn, 1964). Thus, various workers have looked at the possible influence of the male on the size of the litters sired.

Various studies have found a significant sire effect on litter size (Falconer, 1960; Finn, 1964; Schilling et al., 1968 (mice); Minkema, 1967; Kennedy and Moxley, 1978 (swine)), while others have found the sire effect not significant (Hanrahan and Eisen, 1974 (mice)). Schilling et al. (1968) suggested that variation in semen quality or hormonal activity might result in producing differences among sires in litter size. Schilling et al. (1968) also demonstrated that the larger litters were sired by sires which had settled a greater number of females. Falconer (1960) estimated that approximately 10% of the total variation in litter size could be attributed to the male. Minkema (1967) found only 2% (or less) of the total variation in litter size to be attributable to the

sire. Thus, he proposed that selecting boars on litter size might not give a good response. In accordance with findings by Schilling et al. (1968) with mice, Swierstra and Dyck (1976) found a positive correlation (r=0.80, P<0.01) between the impregnation rate of boars and the mean litter size sired. Contrary to Minkema's (1967) conclusion, Schilling et al. (1968) and Swierstra and Dyck (1976) concluded that selecting males on their own performances could effectively increase litter size.

Sire effect on progeny performance has been examined. Numerous studies have reported a significant sire effect on birth weight (Kasser et al., 1986 (rats); Touchberry and Bereskin, 1966; Brown and Galvez, 1969; Burfening et al., 1979; Marlowe et al., 1984; Anthony et al., 1986; Thrift et al., 1986; Pandya et al., 1986; Singh and Parekh, 1986 (cattle)), while others found no sire effect on birth weight (Wilson et al., 1962; Gupta et al., 1983 (swine); Kabuga and Agyemang, 1986; Seifert et al., 1986 (cattle)). Brown and Galvez (1969) indicated that 20% and 9.5% of the total variation in birth weight for Hereford and Angus, respectively, was due to sire effect. Anthony et al. (1986) reported significant sire differences (P<0.01) for dystocia score. Burfening et al. (1979) found the sire to be a significant (P<0.01) source of variation for calving ease in both 2-yr-old and mature dams.

Sire effect was reported for weaning weight (Marlowe et al., 1984; Kabuga and Agyemang, 1986 (cattle); Gupta et al., 1983

(swine)). Brown et al. (1985), Seifert et al. (1986) (cattle), Kasser et al. (1986) (rats), Wilson et al. (1962) (swine) did not, however, find a breed of sire effect on weaning weight. Thrift et al. (1986) conducted two studies to examine the breed-of-sire effect. In one study, the effect of breed-of-sire on weaning weight was significant while in the other no difference was found. Johnson and Omtvedt (1973) reported that the average pig weight per litter at any age was not influenced by the breed of sire.

MATERIALS AND METHODS

1. Experimental animals:

1.a Production of males

Three different lines of mice were used in the experiment. The three pure lines consisted of two selected lines (A and C) and a control line (E). Lines A and C resulted from long-term selection for 57 generations. Line A was selected for increased body weight at six weeks of age. Line C was selected for increased tail length at six weeks of age which also resulted in a correlated increase in body weight. Line E was subjected to no selection pressure. Thus, all three lines available differed in growth rate and in six week body weight. The average six week weight for the males of each of the pure lines were approximately 49g, 41g and 26g for lines A, C and E, respectively.

The three lines were mated in a complete diallel to produce all pure lines and line crosses, including reciprocals. Thus nine different lines and line crosses were present. This procedure was followed for each of the two replicates which were three weeks apart.

The progeny were weaned at three weeks of age. At this time, all females were discarded. From each litter, three males were

selected at random, numbered and retained. The remainder of the males were sacrificed. At four weeks of age, one male out of the three males kept from each litter was randomly selected to become a test male. The other two were sacrificed.

Each test male was weighed at four weeks of age and was mated to two females of approximately six weeks of age from a common unrelated line. All nine lines and line crosses were represented in each replicate by 12 to 14 males. The complete diallel and the number of males in each line and line cross and in each replicate are shown in Figure 1 and Table 1.

1.b Production of females

The females were produced from the Nagai S line[1]. Through random mating, batches of at least 300 females were produced every three weeks. The females were approximately six weeks of age upon first being mated. Two six week-old females were randomly assigned to each male.

The use of females from a common line, unrelated to any of the other three lines, was to ensure that the differences observed in reproductive performance in the males were due to the genotype of the male. In addition, the progeny were not inbred, thus

---

[1]Random mated control line obtained from the laboratory of DR. J. Nagai, Animal Research Centre, Agriculture Canada, Ottawa.

Figure 1. Mating plan used to produce pure line and cross
line males

Complete Diallel

Female Line

		A	C	E
	A	AA	AC	AE
Male	C	CA	CC	CE
Line	E	EA	EC	EE

Table 1. Number of males present in each line and line cross
and in each replicate

Line	Replicate	Number of Males
AA	1	13
	2	13
CC	1	14
	2	13
EE	1	13
	2	13
AC	1	13
	2	13
CA	1	13
	2	12
AE	1	13
	2	13
EA	1	13
	2	13
CE	1	13
	2	13
EC	1	14
	2	13

preventing any inbreeding depression which might create some bias to the results (Horstgen-Schwark et al., 1984). All the females were six week of age in order to avoid any bias due to age or parity.

1.c Maintenance of mice

The mice were kept in an air-conditioned laboratory where the temperature was maintained between 20 and 25°C. The mice had a fixed regime of a 12hr light:12hr dark cycle, and were housed in 29X19X12 cm cages with wood shaving bedding. When not being mated, the test males were housed individually.

All mice were fed Wayne Lab Blox F-6; both food and water were available ad libitum. Lactating females had the antibiotic 'Biosol M' (neomycin sulfate USP) added to the drinking water to prevent enteritis which may arise from hypersecretion.

2. Experimental design

The experiment was divided into two replicates which were three weeks apart; all other variables were held the same. Each replicate comprised of 12 to 14 males from each of the nine lines and line crosses.

Each male was first presented to females at four weeks of age. The males were weighed weekly from the age of four weeks to eight weeks of age, inclusive. Long-term reproductive performance was arbitrarily set at five mating periods. At each mating period each male was randomly mated to two six week old females. Thus, a maximum of ten litters could be sired by each male over its reproductive life. The first mating period lasted for six weeks and each of the four subsequent mating periods lasted for three weeks. Each male was weighed upon first being mated for each of the five mating periods. Since the gestation period of the mouse is 19 days, females in later stages of pregnancy were removed from the males a few days earlier. Following each mating period, the males were removed from the females and were individually housed for three weeks. After the fifth mating period, the males were weighed, sacrificed and their testes removed and weighed immediately.

All females were individually housed and checked daily until 4:30 P.M.. All litters born by that time were weighed and the number of pups born alive in each litter was recorded. Any litter born later than 4:30 P.M. was recorded as having being born on the following day. Litter size and weight were also recorded at 12 days of age and at weaning (21 days of age). At weaning, both the female and her litter were discarded. All females which did not show any signs of pregnancy at the end of their mating period were

kept in a cage, along with 3-4 other females, for up to 19 days, by which time if they still did not litter they were discarded.

3. Measurements

All litter traits measured were considered to be male traits. Since all females used were obtained from a common line, the differences among lines in male performance reflect the male's genotype (Horstgen-Schwark et al.(1984)).

For each male, the traits measured to represent reproductive performance included litter size and litter weight of live young only, which were recorded at birth, 12 days of age and at weaning. The litter traits were examined as: overall production, obtained by summing the respective traits produced by each male throughout its reproductive life; mating period totals, derived for each male by summing traits over all litters produced at each mating period; and mating period averages, formed by dividing the totals of each male by the number of litters it produced at each mating period. Traits measured at 12 days will not be reported or discussed in this thesis; 12 day weights are largely a function of the maternal ability of the dams. Age at first fertile mating, average days from exposure to females to conception, number of fertile matings and testes weight represented other parameters utilized to determine reproductive performance of test males. Age at first

mating was used as an indicator of age at puberty. Age at first fertile mating was calculated by subtracting the gestation period (19 days) and the birth date of the male from the birth date of the first litter it had sired.

Age at 1st fertile mating = (Birth date of 1st litter - Gestation period) - Birth date of male

Days from exposure to female to conception for each litter produced was calculated by subtracting the gestation period and the exposure date from the birth date of the litter.

Days from mating to conception = (Birth date of litter- Gestation period) - Exposure date

Days from exposure to female to conception were then averaged for each mating period. The number of fertile matings represented the number of litters comprised of at least one pup born, dead or alive. Testes weight was recorded at 196 days of age at which time each male was dissected and its testes were weighed.

Various genetic parameters were estimated based on the method described by Alenda et al. (1980). Based on least square means from the nine lines and line crosses, estimates were obtained for average direct line effect, average maternal effect and average individual heterosis values. Heterosis was defined as the deviation of the two line crosses from the mean of the parental lines. This model made several assumptions:

"The population mean was equal to the mean of the purebreds. Deviation from this mean by any breed (line) class was assumed to be due to genetic and (or) maternal effects. The means of the additive, maternal and grand maternal effects were equal to zero. It was assumed that full individual interaction (heterosis= dominance plus additive by additive interaction) was reached in two-breed (line) crosses and that the coefficient for additive interaction deviation from the mean of purebreds is the expected proportion of nonparental two-locus combinations of independently segregating genes of each breed class." (Alenda et al. 1980)

Acronyms for traits are listed below:

OPLS - overall production litter size

OPLSB - overall production litter size at birth

OPLSW - overall production litter size at weaning

OTPLW - overall production litter weight (g)

OPLWB - overall production litter weight at birth (g)

OPLWW - overall production litter weight at weaning (g)

TLS - mating period total litter size (at each mating period)

TLSB - mating period total litter size at birth

TLSW - mating period total litter size at weaning

TLW - mating period total litter weight (at each mating period) (g)

TLWB - mating period total litter weight at birth (g)

TLWW - mating period total litter weight at weaning (g)

ALS - mating period average litter size (for each mating period)

ALSB - mating period average litter size at birth

ALSW - mating period average litter size at weaning

ALW - mating period average litter weight (for each mating period) (g)

ALWB - mating period average litter weight at birth (g)

ALWW - mating period average litter weight at weaning (g)

NFM - number of fertile matings

MDCONCEP - average days from exposure to females to conception (for each mating period) (days)

MINFERT - age at first fertile mating (days)

TESTW - testes weight at 196 days of age (g)

4. Statistical Analysis

Mating period totals and mating period averages of the various litter traits, as well as mean days from exposure to females to conception, were analyzed using general analysis of variance procedures for unbalanced data (GLM) as outlined by SAS (1985). The following general linear model was assumed:

$$Y_{ijk} = u + l_i + r_j + p_k + lr_{ij} + lp_{ik} + rp_{jk} + e_{n(ijk)}$$

where:

Y_{ijk} = the observation of the nth sire within the kth mating period, jth replicate and ith line.

u = overall mean

l_i = the effect of the ith line

r_j = the effect of the jth replicate

p_k = the effect of the kth mating period

lr_{ij} = the effect of the interaction between the ith line and the jth replicate

lp_{ik} = the effect of the interaction between the ith and the kth mating period

rp_{jk} = the effect of the interaction between the jth replicate and the kth mating period

lrp_{ijk} = the effect of the interaction between the ith line, the jth replicate and the kth mating period

$e_{n(ijk)}$ = the error term of the nth sire within the ith line, the jth replicate and the kth mating period

The effects of u, l_i, r_j, p_k and their interactions were assumed to be fixed while $e_{n(ijk)}$ was assumed to be random, normal, and independent with expectations equal to zero.

Overall production of the various litter traits, age at first fertile mating, testes weight and number of fertile matings were analyzed using the general analysis of variance procedures for unbalanced data (GLM) as outlined by SAS (1985). The following general linear model was assumed:

$$Y_{ij} = u + l_i + r_j + lr_{ij} + e_{n(ij)}$$

where:

Y_{ij} = the observation of the nth sire within the jth replicate and ith line

u = overall mean

l_i = the effect of the ith line

r_j = the effect of the jth replicate

lr_{ij} = the effect of the interaction between the ith line and the jth replicate

$e_{n(ij)}$ = the error term of the nth sire within the ith line and the jth replicate

The effects of u, l_i, r_j and their interaction were assumed to be fixed while $e_{n(ij)}$ is assumed to be random, normal, and independent with expectations equal to zero.

For all variables, pairwise comparisons were performed to determine significant differences among the least square means of the various lines and line crosses.

The following pre-determined contrasts were established to test various comparisons:

Contrast 1 : established to compare pure lines to linecrosses.

Contrast 2 : determined any direct line effect.

Contrast 3 : investigated maternal genetic effect on reproductive performance of males.

Contrast 4 : simply compared the two selected lines to the control line.

Contrast 5 : examined the differences between the two selected lines.

Contrast 6 : determined heterosis levels for the line crosses.

Contrast 7 : determined whether the differences between the reciprocals were significant.

RESULTS

1. Traits measuring 'long-term' performance

'Long-term' reproductive performance of males was measured over five mating periods. Since each male was mated to two females at each mating period, a maximum of ten litters could be sired by each male over its allocated reproductive life. Quantitative litter traits were recorded at birth and weaning. The data were analyzed in terms of overall production for each male, as well as, mating period totals and mating period averages of litter traits from the two litters produced at each mating period.

1.1. Overall statistical analysis

General analysis of variance procedures for unbalanced data were used to determine the presence of any significant components of the general linear model in order to describe the various litter traits.

1.1.1. Overall production 'long-term' performance

Overall production, derived by summing the variables for each male over its reproductive life, OPLSB, OPLSW, OPLWB and OPLWW were analyzed using the general linear model (Appendix 1). The line of the male significantly influenced all variables (P<0.01).

Least square means for OPLSB, OPLSW, OPLWB and OPLWW are represented in Appendix 2. In order to simplify the results, the reciprocal crosses have been combined. These least square means are found in Table 2.

1.1.1.i. Litter size

In looking at overall production of pups among the pure lines, at birth or weaning, males from line EE ranked the highest. The two selected lines did not significantly differ from one another (P>0.05). Line EE was significantly different only from line CC (P<0.05). Examining the line crosses, the ranking order was AC>CE>AE, yet none were significantly different (P>0.05) from another. For OPLSB all line crosses were superior to the pure lines; for OPLSW only one pure line was superior to a line cross (EE>AE). The line crosses exhibited a significant difference only from line CC (P<0.05). From these values, a definite decrease in overall pup production is seen for both selected lines as compared to the control line. Heterosis also seems to affect OPLS.

1.1.1.ii. Litter weight

Among the pure lines for OPLWB and OPLWW, AA males produced the heaviest litters, followed by EE males, CC males produced the lightest litters. None of the pure lines were significantly different (P>0.05) from one another for OPLWB. For OPLWW, AA line

Table 2. Least square means and standard errors for 'overall production' litter traits (OPLSB, OPLSW, OPLWB, OPLWW) (reciprocals combined)

Line	OPLSB	OPLSW	OPLWB (g)	OPLWW (g)
AA	93.50^{ab} $(3.08)^1$	88.59^{ab} (3.01)	167.00^{ab} (5.28)	$1,193.88^a$ (36.35)
CC	83.28^b (3.02)	77.44^b (2.94)	145.88^b (5.17)	995.03^b (35.59)
EE	98.73^a (3.07)	92.00^a (3.00)	160.10^{ab} (5.26)	$1,100.71^{ab}$ (36.24)
AC	102.42^a (2.19)	93.97^a (2.17)	178.03^a (3.76)	$1,204.93^a$ (25.88)
AE	99.71^a (2.17)	90.54^a (2.12)	168.68^a (3.72)	$1,152.55^a$ (25.63)
CE	101.31^a (2.15)	93.33^a (2.10)	170.10^a (3.69)	$1,159.28^a$ (25.39)

[1]Standard error

a ,b- means in the same column having different superscripts are significantly different (P<0.05).

was significantly different (P<0.05) from line CC. The ranking order of the line crosses for OPLWB and OPLWW remained the same as for OPLS, AC>CE>AE; the differences were not significant (P>0.05). For OPLWB, all line crosses were superior to the pure lines, yet for OPLWW, AC males overall produced heavier litters than AA or CE males. Males AC were superior for all of the overall production traits.

1.1.2. Totals of two litters produced at each mating period

At each mating period, all litter traits measured were summed for each male. TLSB, TLSW, TLWB and TLWW were analyzed using the general linear model (Appendix 3). Line and mating period effects were significant (P<0.01) for TLSB, TLSW and TLWB. For TLWW, mating period was a significant effect, as well as the interaction between replicate and mating period (P<0.01).

1.1.2.a. Line effect

Least square mean values for TLSB, TLSW, TLWB and TLWW, for pure lines and line crosses, are given in Appendix 4. Table 3 presents the least square means for TLSB, TLSW, TLWB and TLWW with the reciprocals combined.

Table 3. Least square means and standard errors for 'mating period total' litter traits (TLSB, TLSW, TLWB, TLWW) mating period averaged over five mating periods (reciprocals combined)

Line	TLSB	TLSW	TLWB (g)	TLWW (g)
AA	18.83^b $(0.38)^1$	17.72 (0.38)	33.63^b (0.63)	238.77 (4.45)
CC	18.84^b (0.40)	17.69 (0.40)	33.00^b (0.65)	228.01 (4.68)
EE	20.67^a (0.39)	19.29 (0.39)	33.53^b (0.64)	231.05 (4.55)
AC	20.79^a (0.27)	19.08 (0.27)	36.14^a (0.45)	244.86 (3.20)
AE	20.17^{ab} (0.27)	18.38 (0.27)	34.39^{ab} (0.44)	234.06 (3.16)
CE	20.56^a (0.27)	19.03 (0.27)	34.53^{ab} (0.44)	236.43 (3.14)

[1] Standard error

a, b- means in the same column having different superscripts are significantly different (P<0.05).

1.1.2.a.i. Litter size.

Comparing the three pure lines for TLSB and TLSW, the ranking order was EE>CC>AA. For each mating period, at birth or weaning, EE males sired the greatest number of pups compared to AA or CC males. The ranking of the line crosses was AC>CE>AE for both TLSB and TLSW. The only change from birth to weaning for TLS is the reversal of the order between line cross AC and pure line EE where for TLSB AC>EE, while for TLSW EE>AC. Thus, TLS produced by either of the two selected lines was less than that of the control. For both TLSB and TLSW, the line crosses performed better than either of the two selected lines.

1.1.2.a.ii. Litter weight

For TLWB, pure line males ranked AA>EE>CC; however, none of these were significantly different (P>0.05) from another. The ranking order for the line crosses was AC>CE>AE (none of which were significantly different from one another(P>0.05)). For TLWB, all line crosses were superior to the pure lines; yet only line cross AC was significantly different (P<0.05) from the pure lines.

1.1.2.b. Mating period effect

Least square mean values for TLSB, TLSW, TLWB and TLWW, for each mating period, are given in Table 4.

Table 4. Least square means and standard errors for 'mating period total' litter traits (TLSB, TLSW, TLWB,TLWW) mating period averaged over pure lines and line crosses

Mating Period	TLSB	TLSW	TLWB (g)	TLWW (g)
1	21.67^a $(0.28)^1$	19.44^a (0.28)	36.20^a (0.46)	240.20^{ab} (3.33)
2	20.81^{ab} (0.28)	18.76^{ab} (0.28)	35.32^{ab} (0.47)	233.15^{ab} (3.32)
3	19.34^c (0.28)	18.25^b (0.28)	33.79^{bc} (0.47)	227.89^b (3.34)
4	19.87^{bc} (0.29)	18.63^{ab} (0.29)	33.86^{bc} (0.47)	237.54^{ab} (3.38)
5	19.07^c (0.29)	18.09^b (0.29)	33.23^c (0.48)	243.99^a (3.44)

[1]Standard error

a, b, c- means in the same column having different superscripts are significantly different (P<0.05).

1.1.2.b.i. Litter size

TLSB and TLSW for the mating periods ranked 1>2>4>3>5. Litter size produced at each mating period for all males, regardless of their genetic composition, was the greatest for mating period 1, after which it gradually declined. For TLSB, mating period 1 was significantly different from periods 3, 4 and 5, which showed no significant difference ($P > 0.05$) from one another; mating periods 2 and 4 were also similar. Yet for TLSW, mating period 1 was only significant from 3 and 5 while mating periods 2, 3, 4 and 5 showed no significant differences ($P > 0.05$).

1.1.2.b.ii. Litter weight

TLWB followed the same trend exhibited by TLS; the ranking order remained: 1>2>4>3>5. Values for mating period 1 were the highest and were significantly different ($P < 0.05$) from those of periods 3, 4 and 5. Mating periods 2, 3 and 4 were not significantly different ($P > 0.05$). For TLWW, the ranking order was altered and became 5>1>4>2>3. Mating period 5 was significantly different ($P < 0.05$) from period 3 , while mating periods 1, 4, 2 and 3 and mating periods 1, 2, 4 and 5 were not significantly different ($P > 0.05$) from one another. Thus, even though mating period was a significant effect, significant differences were only observed when comparing the extremes in production.

1.1.2.c. Interaction between replicate and mating period

TLWW exhibited a significant interaction between replicate and mating period. Least square mean values are given in Table 5. This interaction signifies that the litters from replicate 1 did not act in the same manner as litters from replicate 2 across the five mating periods for TLWW. For replicate 1, TLWW remained relatively similar for the first three mating periods, decreased slightly for mating period 4, while mating period 5 produced the highest values for TLWW. Yet for replicate 2, TLWW decreased gradually from mating period 1 to 3, after which it increased until mating period 5 where the values were similar to mating period 1.

1.1.3. Averages of two litters produced at each mating period

For each male, all measured litter traits were averaged for each mating period. ALSB, ALSW, ALWB and ALWW were analyzed using the general linear model (Appendix 5). Line and mating period were found to be significant effects ($P<0.02$) for ALSB, ALWB and ALWW. For ALSW, line was not a significant effect while replicate and mating period were ($P<0.03$). ALSB was also significantly affected by replicate ($P<0.02$), while ALWW exhibited a significant interaction between replicate and mating period ($P<0.01$).

Table 5. Least square means and standard errors for 'total'
litter weight at weaning (TLWW)

Replicate	Mating Period	TLWW (g)	
1	1	236.44	(4.63)[1]
1	2	235.88	(4.67)
1	3	236.77	(4.67)
1	4	233.50	(4.75)
1	5	244.46	(4.83)
2	1	243.96	(4.79)
2	2	230.43	(4.73)
2	3	219.01	(4.79)
2	4	241.58	(4.82)
2	5	243.53	(4.89)

[1]Standard error

1.1.3.a. Line effect

Least square mean values for ALSB, ALSW, ALWB and ALWW are shown in Appendix 6. Table 6 illustrates the least square means for ALSB, ALSW, ALWB and ALWW with the reciprocals combined.

1.1.3.a.i. Litter size

Line effect was only significant (P<0.05) for ALSB. First comparing the pure lines; their ranking order was EE>CC>AA. Once again litter production of the control line was superior to the two selected lines; however, this was only a trend, none of the pure lines were significantly different (P<0.05) from one another. The ranking order for the line crosses became AC>AE>CE with none of the differences being significant (P>0.05). AC and AA were the only two lines and line crosses which were significantly different from one another(P<0.05). Line EE was superior to line crosses AE and CE for ALSB. ALSW followed the same trend as ALSB, except for the reversal in the ranking of line crosses AE and CE; for ALSB, AE>CE and for ALSW, CE>AE. However, ALSW was not significantly affected by line (P>0.05).

1.1.3.a.ii. Litter weight

Looking at the pure lines for ALWB and ALWW, males from line AA produced heavier litters, followed by CC and EE males. None of the

Table 6. Least square means and standard errors for 'mating period average' litter traits (ALSB, ALSW, ALWB, ALWW) mating period averaged over five mating periods (reciprocals combined)

Line	ALSB	ALSW	ALWB (g)	ALWW (g)
AA	9.85^b $(0.17)^1$	9.47 (0.15)	17.68^{ab} (0.27)	127.60^{ab} (1.65)
CC	9.91^{ab} (0.18)	9.75 (0.16)	17.54^{ab} (0.29)	125.65^{abc} (1.74)
EE	10.50^{ab} (0.17)	9.99 (0.15)	17.12^b (0.28)	119.58^c (1.69)
AC	10.54^a (0.12)	10.03 (0.11)	18.40^a (0.20)	128.89^a (1.19)
AE	10.35^{ab} (0.12)	9.81 (0.11)	17.71^{ab} (0.19)	124.66^{abc} (1.18)
CE	10.34^{ab} (0.12)	9.88 (0.11)	17.50^b (0.19)	123.04^{bc} (1.17)

[1]Standard error

a, b, c- means in the same column having different superscripts are significantly different (P<0.05).

three pure lines were significantly different from one another for ALSB, while for ALWW, AA is significantly different from EE (P<0.05). The two selected lines produced heavier litters than the control males. The ranking AC>AE>CE was obtained for ALWB and ALWW, where only AC and CE were significantly different from one another (P<0.05). For ALWB, the ranking was AA>CC>CE; however, for ALWW, the ranking became AA>CC>AE>CE. Thus for ALWB, line crosses AC and AE obtained higher values than the selected lines, while for ALWW, only line cross AC maintained its superiority over the pure lines AA and CC.

1.1.3.b. Mating period effect

Mating period was found to have a significant effect for all averaged litter traits. Least square mean values for ALSB, ALSW, ALWB and ALWW are given in Table 7.

1.1.3.b.i. Litter size

For ALSB, the ranking of mating periods was 1>2>4>3>5. Mating period 1 was significantly different from periods 4, 3 and 5. Mating period 2 was not significantly different (P<0.05) from 1 or 4. For ALSW, the ranking was 1>2>3>4>5. Mating period 1 was significantly different (P<0.05) from periods 3, 4 and 5. Mating period 2 was similar to periods 3, 4 and 5. Regardless of the

Table 7. Least square means and standard errors for 'mating period average' litter traits (ALSB, ALSW, ALWB, ALWW) for each mating period

Mating Period	ALSB		ALSW		ALWB (g)		ALWW (g)	
1	11.00^a	(0.13)^1	10.41^a	(0.11)	18.55^a	(0.20)	128.54^a	(1.23)
2	10.55^{ab}	(0.13)	9.96^{ab}	(0.11)	18.11^{ab}	(0.20)	124.00^{ab}	(1.23)
3	9.96^c	(0.13)	9.76^b	(0.11)	17.47^{bc}	(0.20)	121.67^c	(1.24)
4	10.09^{bc}	(0.13)	9.58^b	(0.11)	17.24^c	(0.21)	122.24^b	(1.26)
5	9.91^c	(0.13)	9.55^b	(0.12)	17.29^{bc}	(0.21)	129.16^a	(1.27)

[1]Standard error

a, b, c- means in the same column having different superscripts are significantly different (P<0.05)

line, males produced the largest litters for mating period 1 and the smallest litters for mating period 5.

1.1.3.b.ii. Litter weight

For ALWB, the ranking of mating periods was 1>2>3>5>4 where mating period 1 was significantly different (P<0.05) from periods 3, 4 and 5, which were not significantly different (P>0.05) from one another. Mating period 2 was significantly different from periods 3 and 5 (P<0.05). For ALWW, the ranking order was 5>1>2>4>3, mating periods 1 and 5 were similar and were significantly different from periods 3 and 4 which were not similar (P>0.05). The ranking order for ALWB indicated a decrease in litter weight with time; the same general trend was observed for ALWW with the exception of mating period 5, at which time litters were measured as the heaviest.

1.1.3.c. Replicate effect

Replicate was found to be a significant effect for ALSB and ALSW. Least square means for each replicate are shown for ALSB and ALSW in Table 8. Both at birth and weaning, ALS was greater for replicate 1 than replicate 2. This indicates that the males in replicate 1, regardless of their genetic origin, produced on average larger litters than males in replicate 2.

Table 8. Least square means and standard errors for
         'average' litter size (ALSB, ALSW) averaged over
         pure lines and line crosses

Replicate	ALSB	ALSW (g)
1	10.44 (0.08)[1]	9.97 (0.07)
2	10.17 (0.08)	9.73 (0.07)

[1]Standard error

1.1.3.d. Interaction between replicate and mating period

ALWW showed a significant interaction between replicate and mating period. Least square mean values are presented in Table 9. This interaction signifies that the ALWW did not act the same across the five mating periods when comparing replicate 1 to replicate 2. The greatest difference between replicates 1 and 2 was that ALWW reached its lowest value during mating period 4, while mating period 3 resulted in the lowest value for replicate 2.

1.2. Estimation of genetic effects using contrast analysis

Various contrasts were established to describe how 'line' produced a significant effect by estimating genetic effects. The first contrast (pure versus cross) was performed to determine whether the pure lines, on average, would produce differently from the average of the line crosses. The second contrast was done to determine whether there was a significant line direct effect (Alenda et al., 1980). The third contrast determined whether the male's maternal genetic effect had any effect upon its production (Alenda et al., 1980). The fourth contrast compared selected versus control lines. The fifth contrast examined differences between lines AA and CC. The sixth contrast determined heterosis levels for line crosses. The seventh contrast was performed to

Table 9. Least square means and standard errors for 'average' litter weight at weaning (ALWW)

Replicate	Mating period	ALWW	
1	1	128.01	(1.72)[1]
1	2	124.61	(1.73)
1	3	127.28	(1.73)
1	4	120.34	(1.76)
1	5	130.17	(1.79)
2	1	129.06	(1.78)
2	2	123.40	(1.75)
2	3	116.06	(1.78)
2	4	124.13	(1.79)
2	5	128.14	(1.81)

[1]Standard error

determine whether the differences between reciprocals were significant.

1.2.1. Overall 'long-term' performance

The estimates from the seven contrasts, which derived estimations of genetic and maternal effects, for OPLSB, OPLSW, OPLWB and OPLWW are given in Table 10.

1.2.1.i. Litter size

Pure versus cross was significant for both OPLSB and OPLSW for which the average of the line crosses was higher than the average of the pure lines ($P<0.01$). Lines C and E both showed a significant ($P<0.06$) direct line effect on OPLS. Line C performed below the pure lines average while line E was superior. Maternal genetic effect had no influence on the males' performance for OPLS. Heterosis was present for all line crosses. Only AC's and CE's estimates were significantly different ($P<0.01$) from zero. None of the differences between reciprocals were significantly different ($P<0.05$) from zero. The control line performed significantly better ($P<0.05$) than the selected lines. Line AA significantly exceeded line CC's performance ($P<0.05$).

Table 10. Estimates of genetic and maternal effects and heterosis for 'overall production' litter traits (OPLSB, OPLSW, OPLWB, OPLWW)

Contrast		OPLSB	OPLSW	OPLWB (g)	OPLWW (g)
Pure versus Cross		-9.21****	-6.54**	-14.45****	-75.00**
Direct	A	2.61NS	2.37NS	11.35*	81.98*
Line	C	-9.49**	-8.40**	-12.45*	-97.16*
Effect	E	6.88*	6.03*	1.10NS	15.18NS
Maternal	A	-1.46NS	0.27NS	-3.19NS	21.79NS
Genetic	C	-1.55NS	0.12NS	-1.19NS	5.04NS
Effect	E	0.09NS	0.15NS	-1.99NS	16.75NS
	AC	14.05****	10.99***	21.62****	111.00**
Heterosis	AE	3.60NS	0.24NS	5.13NS	5.26NS
	CE	10.25***	8.58**	17.04**	111.02**
Differences	AC-CA	-0.88NS	-0.40NS	-0.65NS	-8.57NS
Between	AE-EA	-3.81NS	-0.15NS	7.02NS	-35.02NS
Reciprocals	CE-EC	-3.98NS	-0.14NS	-3.03NS	1.51NS
Selected versus control		-10.34**	-8.98*	-3.66NS	-6.25NS
A versus C		10.22*	11.15**	21.11**	198.84****

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

**** $P < 0.0001$

NS- Not significant

60

1.2.1.ii. Litter weight

Differences between pure lines and line crosses were significant (P<0.01) for OPLWB and OPLWW , where the average of the line crosses was higher than the averaged pure lines. A significant (P<0.05) direct line effect was found for lines A and C. Line E was not significantly different (P<0.05) from the pure line mean. Line A was significantly greater from the mean while line C was significantly lower (P<0.05). No maternal genetic effect had a significant (P>0.05) effect on male performance. All line crosses showed some level of heterosis with AC and CE showing a significant level (P<0.01). None of the differences between reciprocals were significantly different (P<0.05). Selected lines did not perform significantly different (P>0.05) from the control lines. Line AA was superior to line CC only for TPLW (P<0.01).

1.2.2. Totals of two litters produced at each mating period

The estimates from seven contrasts for TLSB, TLSW, TLWB and TLWW are found in Table 11.

1.2.2.i. Litter size

Performance of the pure lines was significantly different (P<0.05) from that of the line crosses for TLSB and TLSW with the line crosses being superior to the pure lines. Line E was the only

Table 11. Estimates of genetic and maternal effects and heterosis for 'mating period total' litter traits (TLSB, TLSW, TLWB, TLWW)

Contrast		TLSB	TLSW	TLWB (g)	TLWW (g)
Pure versus Cross		-1.05****	-0.60*	-1.62***	-5.85NS
Direct	A	-0.57NS	-0.64NS	0.40NS	1.87NS
Line	C	-0.50NS	-0.28NS	---NS	-0.76NS
Effect	E	1.07**	0.92*	-0.39NS	-1.11NS
Maternal	A	-0.06NS	0.20NS	-0.23NS	6.40NS
Genetic	C	0.16NS	0.38NS	0.57NS	5.74NS
Effect	E	-0.22NS	-0.18NS	-0.81NS	0.66NS
	AC	1.97****	1.39***	2.84****	11.56*
Heterosis	AE	0.41NS	-0.12NS	0.80NS	-0.80NS
	CE	0.81*	0.54NS	1.28*	6.98NS
Differences	AC-CA	-0.50NS	-0.36NS	-0.69NS	-5.47NS
Between	AE-EA	0.61NS	-0.04NS	1.15NS	-7.34NS
Reciprocals	CE-EC	-0.18NS	0.41NS	0.46NS	6.01NS
Selected versus Control		-1.83****	-1.58***	-0.21NS	2.34NS
A versus C		---NS	0.02NS	0.63NS	10.76NS

   * $P<0.05$

  ** $P<0.01$

 *** $P<0.001$

**** $P<0.0001$

 NS- Not significant

line which exhibited a significant direct line effect on TLS (P<0.05). Maternal genetic effect had no influence on the males' performance (P>0.05). Heterosis was present in all line crosses. For TLSB, AC and CE showed a significant level (P<0.05) of heterosis, while for TLSW only AC showed a significant level (P<0.05) of heterosis. None of the differences between the reciprocals were significantly different from zero (P<0.05). For TLS, the control line was significantly superior (P<0.01) to the selected lines. Lines AA and CC did not perform significantly different from each other for TLS (P>0.05).

1.2.2.ii. Litter weight

Differences between the pure lines and the line crosses were only significant for TLWB (P<0.01), where the line crosses were superior to the pure lines. No direct line effect had a significant influence (P>0.05) on TLW. Maternal genetic effects did not influence the male's performance (P>0.05). All line crosses showed some level of heterosis. For TLWB, line crosses AC and CE demonstrated a significant level of heterosis, while for TLWW only line cross AC had a significant level of heterosis (P<0.05). None of the differences between the reciprocals were significantly different from zero (P>0.05). The selected lines did not differ in performance from the control (P>0.05). Line AA and line CC performed similarly for TLW.

1.2.3. Average of two litters produced at each mating period

The estimates from the seven contrasts as well as their probabilities of differing from zero for ALSB, ALSW, ALWB and ALWW are shown in Table 12.

1.2.3.i. Litter size

Differences between the pure lines and line crosses were significantly different from zero for ALSB (P<0.05) but not for ALSW (P>0.05). For ALSB, the line crosses were superior to the pure lines. None of the lines showed a significant direct line effect for ALS (P>0.05). Maternal genetic effects did not significantly affect the males' performance (P>0.05). Heterosis was present for all line crosses for TLS; however, only line cross AC's value was significantly different from zero (P<0.05). None of the differences between reciprocals were significantly different from zero (P>0.05). The selected lines' production was significantly lower than that of the control for ALS (P<0.05). Lines AA and CC performed similarly to each other (P>0.05).

1.2.3.ii. Litter weight

The pure lines differed significantly from the line crosses for ALWB (P<0.05). Line E showed a direct line effect on ALW (P<0.05). Maternal genetic effect did not influence the males' performance

Table 12.   Estimates of genetic and maternal effects and heterosis for 'mating period average' litter traits (ALSB, ALSW, ALWB, ALWW)

Contrast		ALSB	ALSW	ALWB (g)	ALWW (g)
Pure versus Cross		-0.32**	-0.17NS	-0.42*	-1.25NS
Direct	A	-0.18NS	-0.22NS	0.22NS	2.44NS
Line	C	-0.15NS	0.08NS	0.35NS	2.77NS
Effect	E	0.33NS	0.13NS	-0.58*	-5.21**
Maternal	A	-0.08NS	-0.06NS	0.01NS	1.28NS
Genetic	C	0.04NS	0.11NS	0.39NS	2.13NS
Effect	E	-0.12NS	-0.17NS	-0.39NS	-0.85NS
	AC	0.67***	0.42**	0.80**	2.26NS
Heterosis	AE	0.17NS	0.08NS	0.30NS	1.09NS
	CE	0.13NS	0.01NS	0.18NS	0.44NS
Differences	AC-CA	-0.12NS	-0.04NS	-0.30NS	-1.17NS
Between	AE-EA	0.29NS	0.16NS	0.29NS	-1.39NS
Reciprocals	CE-EC	-0.04NS	0.18NS	0.48NS	3.10NS
Selected versus Control		-0.63**	-0.38*	0.48NS	7.04***
A versus C		-0.06NS	-0.27NS	0.13NS	1.95NS

* $P<0.05$

** $P<0.01$

*** $P<0.001$

**** $P<0.0001$

NS- Not significant

for ALW (P>0.05). All line crosses showed some level of heterosis; however, only line cross AC's heterosis value was significant for ALWB (P<0.05). None of the differences between reciprocals were significantly different from zero for ALW (P>0.05). For ALWB, the selected and the control lines performed similarly, while for ALWW, the selected lines were significantly superior to the control (P<0.05). Lines AA and CC were not significantly different in terms of ALW (P>0.05).

2. Other reproductive parameters

Other parameters, not directly associated to litter traits, have some influence on the males' 'long-term' performance. Age at first fertile mating is of importance; the earlier a male reproduces, the shorter the generation interval becomes. Average days from exposure to females to conception, number of fertile matings and testes weight may be used as indicators of libido or reproductive efficiency.

2.1 Overall statistical analysis

General analysis of variance procedures were used to determine the presence of any significant components of the general linear model in order to describe the 'other' reproductive parameters.

2.1.1. Age at first fertile conception

Age at first fertile conception was analyzed using the general linear model (Appendix 7). Line was found to have a significant effect (P<0.01). The least square mean values for age at first fertile conception (MINFERT) are given in Appendix 8. Table 13 presents the least square means with the reciprocals combined. Among the pure lines, the control line (EE) reached puberty at the earliest age, followed by line AA, CC males were the oldest. Lines AA and EE were significantly different from line CC (P<0.05). None of the line crosses were significantly different from one another, yet all were significantly different from line CC (P<0.05), the ranking order being CE>AE>AC. All line crosses reached puberty earlier than the pure lines.

2.1.2. Mean days to conception

Mean days to conception was analyzed using the general linear model (Appendix 9). Appendix 10 presents the least square mean values for means days to conception (MDCONCEP), while Table 14 gives the values with the reciprocals combined. No tested effects were found to be significant (P<0.05). This indicates that all males were similarly efficient in impregnating their females regardless of their genetic composition. The ranking order for the pure lines was AA>CC>EE. The line crosses ranked AE>AC>CE, where line EE's performance was lower than the line crosses.

Table 13. Least square means and standard errors for age at
first fertile mating (MINFERT) (reciprocals
combined)

Line	MINFERT (days)
AA	46.31^a $(0.73)^1$
CC	49.82^b (0.72)
EE	45.93^a (0.75)
AC	43.78^a (0.52)
AE	44.17^a (0.52)
CE	44.96^a (0.51)

[1]Standard error

a, b- means having different superscripts are significantly
different (P<0.05)

Table 14. Least square means and standard errors for average
days to conception (MDCONCEP) (reciprocals
combined)

Line	MDCONCEP (days)	
AA	3.69	(0.31)[1]
CC	3.09	(0.32)
EE	2.23	(0.31)
AC	2.77	(0.22)
AE	2.92	(0.21)
CE	2.61	(0.21)

[1]Standard error

2.1.3. Number of fertile matings

Number of fertile matings was analyzed using the general linear model (Appendix 11). Line was found to be significant (P<0.01). The least square means for number of fertile matings (NFM) are given in Appendix 12. Table 15 represents the least square means with the reciprocals combined. The pure lines ranked AA>EE>CC, line CC was significantly different from lines AA and EE (P<0.05). Line crosses ranked CE>AC>AE, all performed better than the pure lines but were only significantly different from line CC (P<0.05).

2.1.4. Testes weight

Testes weight was analyzed using the general linear model (Appendix 13). A significant effect was found to arise from line (P<0.01). The least square mean values for testes weight (TESTW) are represented in Appendix 14. Table 16 shows the least square means with the reciprocals combined. The pure lines ranked AA>EE>CC; line AA was significantly different from lines CC and EE (P<0.05). The line crosses ranked AC>AE>CE; all three were significantly different from each other (P<0.05). Line AA was similar to both line crosses AC and AE. Line cross CE and line EE were similar to one another.

Table 15. Least square means and standard errors for number
of fertile matings (NFM) (reciprocals combined)

Line	NFM
AA	9.51^a $(0.24)^1$
CC	8.31^b (0.24)
EE	9.35^a (0.24)
AC	9.67^a (0.17)
AE	9.54^a (0.17)
CE	9.71^a (0.17)

[1]Standard error

a, b- means having different superscripts are significantly different (P<0.05)

Table 16. Least square means and standard errors for testes
weight (TESTW) (reciprocals combined)

Line	TESTW (g)
AA	0.3318^{ab} $(0.0088)^1$
CC	0.1848^{d} (0.0094)
EE	0.2134^{c} (0.0092)
AC	0.3427^{a} (0.0065)
AE	0.3047^{b} (0.0062)
CE	0.2368^{c} (0.0063)

[1] Standard error

a, b, c, d- means having different superscripts are
significantly different (P<0.05)

2.2. Estimation of genetic effects using contrast analysis

Using the same seven contrasts, as for litter traits, the 'other' parameters were analyzed similarly.

2.2.1. Age at first fertile conception

The estimates from the seven contrasts for MINFERT are found in Table 17. The pure lines were significantly older for MINFERT as compared to the line crosses (P<0.01). Lines C and E exhibited a significant direct line effect; line C was older compared to the average, and line E was younger (P<0.01). Maternal genetic effect had a significant influence on the males' performance for lines C and E (P<0.05). Males with line C mothers obtained higher values for MINFERT, while males with line E mothers conceived their first litter at a younger age. All line crosses showed a significant level of heterosis (P<0.01). Only reciprocals from line cross CE exhibited a significant difference from one another, where CE had a higher value then EC (P<0.05). The selected males had significantly different values as compared to the control males (P<0.05), where selected males scored lower than the controls. Line CC was significantly older than line AA at age at first mating (P<0.01).

Table 17. Estimates of genetic and maternal effects and
           heterosis for age at first mating (MINFERT)

Contrast		MINFERT (days)
Pure versus Cross		3.01****
Direct	A	-0.90NS
Line	C	3.46****
Effect	E	-2.55***
Maternal	A	-0.19NS
Genetic	C	1.54*
Effect	E	-1.73*
	AC	-4.28****
Heterosis	AE	-1.95**
	CE	-2.89****
Differences	AC-CA	-0.80NS
Between	AE-EA	1.19NS
Reciprocals	CE-EC	2.27*
Selected versus Control		-2.13*
A versus C		-3.51***

   * P<0.05

  ** P<0.01

 *** P<0.001

**** P<0.0001

  NS- Not significant

2.2.2. Average days to conception

The estimates from the seven contrasts for MDCONCEP are given in Table 18. Differences between line crosses and pure lines were not significant (P>0.05). No direct line effect or any maternal genetic effect had any significant influence upon MDCONCEP (P>0.05). All line crosses showed some level of heterosis, yet only line cross AC's value was significantly different from zero (P<0.05). None of the differences between reciprocals were significantly different from zero (P>0.05). Control males were significantly superior than the selected males (P<0.01). The two selected lines did not differ significantly from one another (P>0.05).

2.2.3. Number of fertile matings

The estimates from the seven contrasts for NFM are given in Table 19. The line crosses produced more fertile matings as compared to the pure lines (P<0.01). Lines A and C demonstrated significant direct line effects where line A produced a greater number of fertile matings while line C produced a lesser number (P<0.05). No maternal genetic effect showed any effect on NFM (P<0.05). Selected and control males were not significantly different from one another (P>0.05). The two selected lines performed differently, where line AA was superior to line CC (P<0.01).

Table 18. Estimates of genetic and maternal effects and
heterosis for average days to conception (MDCONCEP)

Contrast		MDCONCEP (days)
Pure versus Cross		0.24NS
Direct	A	0.51NS
Line	C	0.05NS
Effect	E	-0.56NS
Maternal	A	0.26NS
Genetic	C	-0.05NS
Effect	E	0.31NS
	AC	-0.62*
Heterosis	AE	-0.05NS
	CE	-0.06NS
Differences	AC-CA	-0.23NS
Between	AE-EA	-0.29NS
Reciprocals	CE-EC	-0.32NS
Selected versus Control		-1.16**
A versus C		0.60NS

* $P<0.05$

** $P<0.01$

NS- Not significant

Table 19. Estimates of genetic and maternal effects and
           heterosis for number of fertile matings (NFM)

Contrast		NFM
Pure versus Cross		-0.58***
Direct	A	0.56*
Line	C	-0.91***
Effect	E	0.35NS
Maternal	A	-0.18NS
Genetic	C	-0.27NS
Effect	E	0.10NS
	AC	0.76**
Heterosis	AE	0.11NS
	CE	0.88***
Differences	AC-CA	0.12NS
Between	AE-EA	0.23NS
Reciprocals	CE-EC	-0.42NS
Selected versus Control		-0.44NS
A versus C		1.19***

   * P<0.05

  ** P<0.01

 *** P<0.001

**** P<0.0001

 NS- Not significant

2.2.4. Testes weight

The estimates from the seven contrasts for TESTW are given in Table 20. Differences between the pure lines and the line crosses were significant, where the line crosses had heavier testes weights compared to the pure lines (P<0.01). All three lines showed a significant direct line effect. Line A was superior to the average values, while lines C and E were lower. None of the maternal genetic effects had a significant effect on TESTW. All line crosses exhibited significant levels of heterosis (P<0.01). None of the differences between the reciprocals were significantly different from zero (P<0.01). The selected lines showed significantly higher values than the control (P<0.01). Line AA was superior to line CC (P<0.01).

Table 20. Estimates of genetic and maternal effects and heterosis for testes weight (TESTW)

Contrast		TESTW (g)
Pure versus Cross		-0.0512****
Direct	A	0.0842****
Line	C	-0.0549****
Effect	E	-0.0293**
Maternal	A	0.0051NS
Genetic	C	0.0045NS
Effect	E	0.0006NS
	AC	0.0852****
Heterosis	AE	0.0321***
	CE	0.0378****
Differences	AC-CA	-0.0075NS
Between	AE-EA	-0.0027NS
Reciprocals	CE-EC	0.0015NS
Selected versus Control		0.0449****
A versus C		0.1469****

* P<0.05

** P<0.01

*** P<0.001

**** P<0.0001

NS- Not significant

DISCUSSION

Mating period was found to significantly affect male reproductive performance. For all production traits, litter size and weight, a definite trend was expressed by all males regardless of their genetic make-up. Production was highest during the first mating period, after which, a gradual decline was observed. Throughout the experiment, the environment and the management of the mice were kept constant; thus, neither of these two factors should have influenced performance over the various mating periods. The mating periods, being specific for certain age frames, may be regarded as representing an age effect. From the literature, it has been established that young and less mature males increase their reproductive performance with age and this is maintained for mature males; a decrease is not expected until 'older' animals are used. Initial lower reproductive performance of young animals has been attributed to lower semen quality (Swierstra and Rahnefeld, 1967; Skinner and Rowson, 1968; Swierstra, 1973; Colas, 1983; Raja and Rao, 1983; Chenoweth et al., 1984) and libido (Chenoweth et al., 1984; Makarechian and Farid, 1985). However, in this experiment, the males generated their highest production levels during their first mating period (except for litter weight at weaning). Production decreased after this point. This decline does not reflect the expected lower fertility obtained from 'older' males since the males were not old. During the final mating period, the males were 185-196 days of age. Throughout the

reproductive life of the male mice observed in this experiment, the males were undergoing a maturing process rather than an aging process.

Due to restricted space in the laboratory, the experiment was subdivided into two replicates, three weeks apart. Otherwise, both replicates were treated identically, and no significant replicate effect was expected. ALSB and ALSW were both significantly affected by replicate where males from replicate 1 produced larger ALS as compared to males from replicate 2. The reason for this unexpected effect is not known. TLWW and ALWW exhibited a significant interaction between replicate and mating period.

Production achieved during each mating period was analyzed in two ways: mating period totals, obtained by summing the various production traits within each mating period; and mating period averages, averaging the litter traits measured at each mating period. Since females were randomly assigned to the males, no bias should be present across the lines and line crosses in terms of female fertility; that is, the presence of females of lesser fertility should have been dispersed across the various lines. Thus, any differences arising when comparing the two analyses should reflect differences amongst the males in terms of fertility; female fertility should have no effect. Mating period totals illustrate the male's overall production per mating period, while mating period averages remove the bias as to whether one or both

females produced litters. Overall, the differences in conclusions between averaged versus totalled litter traits were small. However, it would be of interest to create a more challenging mating regimen by providing the males with a much larger number of females. In this experiment, each male was given only two females which might not have been enough of a challenge to expose possible differences in fertility amongst the males.

1. Correlated responses in reproductive performance of males to selection for increased postweaning growth rate or body weight.

Reproductive fitness was determined through litter size and litter weight produced, as well as through other parameters such as age at puberty, average days to conception, number of fertile matings and testes weight. The results presented have demonstrated a reduction in reproductive fitness from selection for increased body weight.

Reduced fertility found in selected animals has been suggested to arise due to an increase in fat (Roberts, 1979). McKay et al. (1985) analyzed the body composition of the three pure lines A, C and E and reported no difference between the selected lines and the control in terms of fatness. Overfatness can thus not be responsible for the reduction in fertility found in this experiment.

Within selected lines, inbreeding depression is often encountered; especially when the effective population size is small. Clearly the three pure lines must have accumulated a considerable level of inbreeding during 57 generations. However, with parent population size the same in all three lines with maximum avoidance of inbreeding and random mating, it could be expected that the level of inbreeding would be similar in all three lines. Thus, the decrease in fertility exhibited by the selected lines cannot be explained with any certainty through inbreeding depression.

Age at puberty was shown to be delayed as a result of selection. This finding is not in agreement with the literature, where it has been reported that age at puberty is unaffected by selection for increased growth (Allrich et al., 1981; Falconer, 1984; Davis et al., 1986; Rios et al., 1986). However, the results might demonstrate slower testicular development as reported by Schinckel et al. (1983); thereby delaying sexual maturity.

Average days to conception, along with number of fertile matings, were used as indicators of reproductive efficiency. Average days to conception was not significantly affected by selection for increased growth rate, indicating no significant changes in efficiency in impregnating females. However, the average of the two selected lines was significantly different from the control. A trend was seen among the pure lines which

demonstrated that MDCONCEP was greater for the selected lines than the control. This trend, while not significant in this study, is in agreement with Morris and Lineweaver (1972) who reported an increase in the number of days from introduction of the male until plugging for selected males as compared to control males. Fowler and Edwards (1960), Morris and Lineweaver (1972) and Hetzel and Nicholas (1982) postulated a correlated decrease in libido resulting from selection which might account for the slight increase in time required by the selected males to impregnate females. The results of this experiment tend to support this finding, even though the differences were not significant. As mentioned earlier, this parameter (MDCONCEP) must be examined carefully considering the limited challenge two females would place on a male.

Looking at the number of fertile matings produced, line AA, selected for increased body weight, was not significantly different from the control line, while line CC, indirectly selected for increased body weight, was significantly different from the other selected line as well as the control. Thus these findings do not illustrate a clear response of this variable due to selection. The production of line AA relative to the control is in agreement with McLellan and Frahm (1973) who reported no significant differences in conception rates. The average of line CC relative to the control line, on the other hand, supports the findings of Lasalle et al. (1974), Morris and Lineweaver (1972) and Baker and Chapman

(1975) who reported a decrease in fertile matings, arising from selection for body weight.

Testes weight was significantly higher for the line selected for increased body weight; however, CC males, selected for tail length, had smaller testes than the control. These results, once again, do not demonstrate a clear response to selection but rather an opposite response depending on which characteristic the animals were selected for. Line AA's response is in agreement with the findings of Johnson and Eisen (1975), while line CC's measurements support the results of Hough et al. (1985). The results of this experiment together with other reports in the literature would suggest that the increase in testis weight is related to an increase in body size. The greater the increase in body size, the larger the testes weight, thus explaining line AA's measurements, while leaving line CC's values unexplained.

When combining the testes weight results with the number of fertile matings and average days to conception, it was noticed that line AA's large difference in terms of testes weight is not seen in the other two traits, which are used to measure reproductive efficiency. Thus, this indirectly supports Johnson and Eisen (1975) who concluded that selection for increased postweaning gain resulted in larger testes with lower efficiency. Selection for increased body weight may result in larger testes, yet sperm count and semen quality remain unchanged (Johnson and Eisen, 1975) thus

explaining why reproductive efficiency is not correspondingly altered.

Selection for increased body weight or tail length resulted in a reduction in litter size at birth and weaning, regardless of whether analyzed as overall production, mating period totals or mating period averages. This finding does not support the majority of reports found in the literature; however it agrees with Morris and Lineweaver's (1972) results. When comparing the two selected lines to one another, line AA was significantly greater than line CC only for overall litter size production. This difference was removed once production was broken down into the five mating periods. This finding indicates that the differences between lines AA and CC were not significant within each mating period but adding overall number of pups resulted in line AA being superior to line CC. Taking this further indicates that at a given time lines AA and CC produced similarly but looking at lifetime production (or in this case long-term production) line AA became superior. This decrease in litter size produced by the selected males may be explained in various ways. Selected males may produce semen of lower quality, thereby producing smaller litters. Selection for increased body weight has been associated with a decrease in embryo survival, thereby resulting in smaller litters (Fowler and Edwards, 1960; Bradford, 1971; Islam et al., 1976; Barria and Bradford, 1981; Bayon et al., 1986; Wirth-Dzieciolowska and Martyniuk, 1986). Lower libido levels of selected males reported by Fowler and

Edwards (1960) may also explain the production of smaller litters (Nagai et al., 1984).

Litter weight at birth was not significantly affected by the line of the sire which produced the litter. This is in total agreement with other reports in the literature, selection does not affect progeny birth weight (Baker and Chapman, 1975; Hetzel and Nicholas, 1982; Hough et al., 1985; Aaron et al., 1986b). Litter weight at birth is a trait which is limited by the uterine environment, males do have some influence but it is the space limiting factor of the female which is the ultimate limiting factor. Hetzel and Nicholas (1982) and Lasalle et al. (1974) reported selection to influence weaning weight. In our experiment, overall production along with mating period totals for weaning weight are in agreement with the literature, yet, for weaning weights averaged per mating period, the selected males sired heavier litters than the control males.

2. Effects of heterosis in crossbred males on long-term reproductive performance.

The effects of heterosis were studied through the use of two contrasts. One contrast compared the average of the line crosses to the average of the pure lines. The second contrast estimated heterosis values for the specific line crosses and determined their

significance.

When comparing the average of the line crosses to the average of the pure lines, the pure lines were found to reach puberty at a significantly older age than the line crosses. From this experiment, the results clearly demonstrate that crossbred males become reproductively active earlier in life. All three heterosis estimates being highly significant, reinforce the finding of superiority of line crosses over pure lines for this trait. The precocity seen in crossbred males may be related to the fact that crossbred males exhibit more rapid testicular development and growth when compared to purebred males, thereby showing heterosis in this character (Land, 1973; Wilson et al., 1977; Neely et al., 1980; Fent et al., 1983).

Average days to conception showed no significant differences between the pure lines and the line crosses. Similarly, only the heterosis value of line cross AC was significant, with its level being close to marginal. Generally, heterosis was not expressed for this variable, the pure lines and line crosses performed similarly, however, pure line males tended to have higher values as compared to line cross males. This trend is in agreement with Bradford et al. (1986) who reported higher values for the number of days to conception for purebred sires compared to crossbred sires. Crossbred males are reported to exhibit definite hybrid vigour in terms of testicular, epididymidal and libido characteristics which

do not seem to be reflected in terms of reproductive efficiency.

In terms of reproductive efficiency, the literature does not consistently show advantages for crossbred males. The number of fertile matings produced in this experiment demonstrated a significant difference between pure line and line cross males, with the line cross males siring the greatest number. Line crosses AC and CE showed a significant level of heterosis, their estimates being positive values indicating heterosis to being beneficial. Thus in both cases, line cross males produced the greatest number of fertile matings, which concurs with the results found by Parker (1971) with sheep. An increase in the number of fertile matings produced may reflect hybrid vigour for conception rates (Wilson et al., 1977). Heterosis in mating behaviour has also been demonstrated (Dewsbury, 1975; Wilson et al., 1977; Neely et al., 1980; Neely and Robison, 1983) which may also influence the number of fertile matings produced.

Line crosses possessed large testes compared to pure lines. All three line crosses showed highly significant heterosis values. Line cross males demonstrated superiority for testes weight over pure line males. These results are in agreement with the literature (Wilson et al., 1977; Neely et al., 1980; Fent et al., 1983).

Fahmy and Holtmann (1977), Nagai et al. (1984) and Ch'ang and

Evans (1986) reported crossbred males to sire larger litters than pure line males. In this experiment, examining the performance of crossbred males in terms of litter size produced generally showed line cross males to be superior to pure line males, except in the case of ALSW where the differences were not significant. For litter size expressed as overall production, as well as mating period totals, highly significant levels of heterosis were obtained for line crosses AC and CE, except for TLSW where only line cross AC was significantly different from zero. For ALS, heterosis for line cross AC was significantly different from zero. Combining both contrast estimates clearly demonstrate line cross males to be superior in terms of litter size produced. Larger litter size may arise from an increase in embryo survival rate found in litters sired by crossbred males (Wilson et al., 1977).

Litters sired by crossbred males produced heavier litters at birth than pure line males regardless of the variable analyzed. This finding agrees with the results of Nagai et al. (1984). Heterosis values for overall production and mating period totals for litter weight at birth were highly significant for line crosses AC and CE. Only line cross CE showed a significant level of heterosis for ALSB. When looking at litter weight at weaning, the comparison between pure lines and line crosses varied depending on whether analyzed as overall production or mating period totals, or mating period averages. Overall production values for litter weaning weights were significantly higher for line cross males

than pure line males, while this was not the case for either totals or averages per mating period. Thus, overall, line cross males produced heaviest litters. However, when their performance was examined per mating period, line cross males' production was similar to that of the pure lines. Line cross AC showed a significant level of heterosis for both OPLWW and TLWW. Line cross CE showed only a significant level of heterosis for TLWW. Advantages of using crossbred males in terms of weaning weight is only significant when looking at long-term production.

As a whole, the benefits of using crossbred males are quite clear. Crossbred males had larger testes, reached puberty at an earlier age, and sired more litters which were not only larger but also heavier. Generally, the males obtained from crossing the two selected lines showed the highest level of heterosis. In the literature it has been suggested that larger heterosis values will be exhibited from crosses between genetically diverse lines as compared to crosses between less diverse lines (Roberts, 1961; Nagai et al., 1980; Falconer, 1981; Nagai and McAllister, 1985). Thus, this might suggest that the different selection schemes used in deriving lines A and C altered the gene frequencies of the alleles in different directions so that lines A and C are more diverse than either line is from the control; thereby giving rise to a greater heterosis value for line cross AC than line crosses AE or CE. Similar findings were reported by Davis (1986) for reproductive performance of the crossbred females in the

laboratory.

3. Estimation of direct genetic and total maternal effects.

Using various contrasts, all variables were analyzed to estimate direct genetic and total maternal effects. These estimates are given as a deviation from the mean of the pure lines. For the litter traits, these effects will be discussed with both birth and weaning data combined, unless otherwise stated. Lines C and E were found to have a significant effect upon the age of the males at which they reached puberty. Line A's effect was not significantly different from the overall line average. Males comprised of line C reached puberty at a later age, while line E's effect caused the males to reach puberty at a younger age. A significant maternal effect was found for both lines C and E. This implies that the MINFERT value of males, whose dams were from either lines C or E, was significantly influenced by the origin of their dam. The maternal genetic effect of line C was above the line average, while for line E, the value was below the line average. Thus, the MINFERT value of males whose dam originated from line C would be increased due to its dam and similarly, the value would be lowered if the dam was from line E. This effect is accentuated when looking at the differences between line crosses CE and EC, where in one case the maternal effect value was positive and in the other case, the maternal effect was negative.

No direct effect or maternal genetic effect were found to influence 'average days to conception'. This suggested that lines A, C and E's effects were not significantly different from their average. Similarly, the origin of the male's dam had no effect upon MDCONCEP. This is also reinforced by the fact that none of the differences between the reciprocals were significant.

Lines A and C were found to exhibit a significant line direct effect on the number of fertile matings produced. Males comprised of line A produced more fertile matings while males comprised of line C produced less fertile matings compared to the line average. None of the maternal genetic effects were significant, implying that the number of fertile matings produced by the males were not affected by their dam's origin. This is supported by the fact that none of the differences between the reciprocals were significant.

There was a significant line direct effect for testes weight. Males from line A had testes heavier than the line average, while males of lines C and E had testes lighter than the line average. No maternal genetic effect or the differences between reciprocals were significant. Thus once again, this variable was not influenced by the origin of the male's dam.

Males comprised of line A had no direct effect upon litter size production, whether looking at overall production, mating period totals or mating period averages. Line A males' production was not

significantly different from the average line value. Line C demonstrated a significant effect upon litter size expressed as 'overall production ' being poorer than the average. However, once the data were analyzed per mating period, line C's production was not significantly different. This suggested that line C's production was similar to the average per mating period, but not for overall production. Line E exhibited a significant effect upon all litter size variables, except OPLSW and ALSW. In all the cases where line E was significant, its production was the highest; however, for two of the weaning variables, OPLSW and ALSW, its values decreased and then became nonsignificant. This might indicate a greater pre-weaning loss for this line relative to the others. No maternal genetic effects were significant for litter size, which indicated that the genetic origin of a male's dam had no influence on its litter size production, be it overall production, mating period totals or mating period averages. This was also reflected in the fact that none of the differences between the reciprocals were significantly different from zero.

Analysis of litter weight for direct line effect gave rise to extremely varied results depending upon whether the variables for overall production, mating period totals or mating period averages were being used. First looking at OPLW. Lines A and C showed a

overall. When the data were analyzed per mating period, both lines A and C's significant effects were lost, indicating that these two lines performed more closely to the mating period average, as compared to overall production. When litter weights were totalled per mating period, none of the lines had a direct effect; all three lines performed closely to the line average. However, once the litter weights were averaged per mating period, line E's direct effect was significantly different from zero. For ALW, line E performed below the line average. For all litter weight variables, maternal genetic effects were not significant. Once again, this implied that the males' litter weight production was not influenced by the genetic source of their dam. The nonsignificance of the differences between the reciprocals reinforced these results.

4. General Discussion

Selection for increased body weight is commonly practiced in the industry. The degree to which this selection is taken is markedly less than that which is carried out with laboratory animals. However, the results obtained from laboratory animals may be extrapolated and used to illustrate the possible animal performance if the selection pressures presently applied continues for many generations.

In general, selection for increased growth rate resulted in a

significant decrease in litter size. Selection did not result in shortening the male reproductive life; however, this experiment only examined long-term performance in contrast to lifetime performance. Extending the males reproductive life might have shown a decrease in performance of selected males.

CONCLUSIONS

Selection for growth resulted in:

- a retardation of onset of puberty.

- a decrease in litter size.

- an increase in litter weaning weight.

Generally, direct selection for growth (line A) and indirect selection (line C) generated similar results with line A demonstrating a greater effect.

Male heterosis resulted in a clear increase in long-term performance. Crossbred males reached puberty earlier, and sired more litters which were not only larger but also heavier.

Crosses between the two selected lines were more productive than crosses between a selected line and the control line.

LITERATURE CITED

Aaron, D.K., Frahm, R.R. and Buchanan, D.S. 1986a. Direct and correlated responses to selection for increased weaning and yearling weight in Angus cattle. I Measurement of selection applied. J. Anim. Sci. 62:54-65.

Aaron, D.K., Frahm, R.R. and Buchanan, D.S. 1986b. Direct and correlated responses to selection for increased weaning and yearling weight in Angus cattle. II Evaluation of response. J. Anim. Sci. 62:66-76.

Alenda, R., Martin, T.G., Lasley, J.F. and Ellersieck, M.R. 1980. Estimation of genetic and maternal effects in crossbred cattle of Angus, Charolais and Hereford parentage. I. birth and weaning weights. J. Anim. Sci. 50:226-234.

Allrich, R.D., Wang, G.T., Dickerson, G.E. and Zimmerman, D.R. 1981. Selection for increased rate or efficiency of lean growth in rats: correlated responses in reproductive performance. J. Anim. Sci. 53:1458-1464.

Almquist, J.O., Branas, R.J. and Barker, K.A. 1976. Postpubertal changes in semen production of Charolais bulls ejaculated at high frequency and the relation between testicular measurements and sperm output. J. Anim. Sci. 42:670-676.

Anthony, R.V., Bellows, R.A., Short, R.E., Staigmiller, R.B., Kaltenbach, C.C. and Dunn, T.G. 1986. Fetal growth of beef calves. II Effect of sire on prenatal development of the calf and related placental characteristics. J. Anim. Sci. 62:1375-1387.

Baker, R.L. and Chapman, A.B. 1975. Correlated responses to selection for postweaning gain in the rat. Genetics 80:191-203.

Barria, N. and Bradford, G.E. 1981. Long-term selection for rapid gain in mice. II Correlated changes in reproduction. J. Anim. Sci. 52:739-747.

Bayon, Y., Fuente, L.F. and San Primitivo, F. 1986. Effects of selecting for litter size and body weight on the components of litter size in mice. Livest. Prod. Sci. 14:195-203.

Bidner, T.D., Humes, P.E., Boulware, R. and Schilling, P.E. 1978. Characterization of ram and ewe breeds. II Growth and carcass traits. J. Anim. Sci. 47:114-123.

Bishop, M.W.H. 1970. Ageing and reproduction in the male. J. Reprod. Fert. Suppl 12:65-87.

Bradford, G.E., Torell, D.T., Spurlock, G.M. and Weir, W.C. 1963. Performance and variability of offspring of crossbred and purebred rams. J. Anim. Sci. 22:617-623.

Bradford, G.E. 1971. Growth and reproduction in mice selected for rapid body weight gain. Genetics 69:499-512.

Bradford, G.E., Quirke, J.F. and Famula, T.R. 1986. Fertility, embryo survival and litter size in lines of Targhee sheep selected for weaning weight or litter size. J. Anim. Sci. 62:895-904.

Brien, F.D. and Hill, W.G. 1986. Reproductive performance over repeated parities of lines of mice selected for appetite, lean growth and fatness. Anim. Prod. 42:397-410.

Brown, C.J. and Galvez, V.M. 1969. Maternal and other effects on birth weight of beef calves. J. Anim. Sci. 28:162-167.

Brown, A.H., Brown, C.J., Johnson, Z., Loe, W.C. and Parham R.W. 1985. Effects of breed of sire and dam on weaning weight of calves. Arkansas Farm Research. 34(6).

Burfening, P.J., Friedrick, R.L. and Van Horn, J.L. 1977. Estimates of early embryonic loss in ewes mated to rams selected for high and low prolificacy. Theriogenology 7:285-291.

Burfening, P.J., Kress, D.D., Friedrich, R.L. and Vaniman, D. 1979. Ranking sires for calving ease. J. Anim. Sci. 48:293-297.

Cameron, R.D.A. 1985. Factors influencing semen characteristics in boars. Aust. Vet. J. 62:293-297.

Ch'ang, T.S. and Evans, R. 1979. Age and breed effect of ram on ewe's reproductive performance. Proc. New Zealand Soc. Anim. Prod. 39:77-86.

Ch'ang, T.S. and Evans, R. 1982. Heterotic basis of breeding policy for lamb production. Proc. 2nd World Congr. Genet. Appl. Livest. Prod., Madrid. 8:796-801.

Ch'ang, T.S. and Evans, R. 1986. Male heterosis effect on lamb production traits of the ewe. Proc. 2nd World Congr. Genet. Appl. Livest. Prod., Lincoln, Nebraska. 9:547-552.

Chenoweth, P.J., Farin, P.W., Mateos, E.R., Rupp, G.P. and Pexton, J.E. 1984. Breeding soundness and sex drive by breed and age in beef bulls used for natural mating. Theriogenology 22:341-349.

Colas, G. 1983. Factors affecting the quality of ram semen. Proc.- Easter School in Agricultural Science, University of Nottingham. 1983. p.453-465.

Conlon, P.D. and Kennedy, B.W. 1978. A comparison of crossbred and purebred boars for semen and reproductive characteristics. Can. J. Anim. Sci. 58:63-70.

Courot, M. and Colas, G. 1986. The role of the male in embryonic mortality (cattle and sheep). In: "Embryonic mortality in farm animals". Sreenan, J.M. and Diskin, M.G. (Ed.) A seminar in the C.E.C. programme of coordination of research on livestock productivity and management. 1986. p. 195-206.

Davis, G. 1986. Effects of selection for growth and of heterosis on lifetime reproductive performance. Phd thesis. University of Manitoba, Winnipeg, Manitoba.

Davis, G.P., Hinch, G.N., Thwaites, C.J. and Kinghorn, B.P. 1986. Attainment of puberty in rams selected on weaning weight. Proc. Aust. Soc. Anim. Prod. 16:175-178.

Dewsbury, D.A. 1975. A diallel cross analysis of genetic determinants of copulatory behavior in rats. J. Comp. Physiol. Psychol. 88:713-722.

Eisen, E.J., Hanrahan, J.P. and Legates, J.E. 1973. Effects of population size and selection intensity on correlated responses to selection for postweaning gain in mice. Genetics 74:157-170.

Eisen, E.J. 1974. A laboratory mouse as a mammalian model for genetics of growth. Proc. 1st World Congress on Genet. Appl. Livestock Prod. 1:467-492.

Eisen, E.J. and Johnson, B.H. 1981. Correlated responses in male reproductive traits in mice selected for litter size and body weight. Genetics 99:513-524.

Eklund, J. and Bradford, G.E. 1977. Longevity and lifetime body weight in mice selected for rapid growth. Nature 265:48-49.

Fahmy, M.H. and Bernard, C.S. 1973. Effects of crossbreeding and certain environmental factors on multiple births, wool production and growth in sheep. Anim. Prod. 16:147-155.

Fahmy, M.H. and Holtmann, W.B. 1977. Evaluation of three- and four-breed cross litters and pigs sired by purebred and crossbred boars. Anim. Prod. 24:261-270.

Falconer, D.S. 1960. The genetics of litter size in mice. J. Cell. Comp. Physiol. 56(Suppl. 1):153-167.

Falconer, D.S. 1981. Introduction to quantitative genetics, 2nd ed. Longman, London.

Falconer, D.S. 1984. Weight and age at puberty in female and male mice of strains selected for large and small body size. Genet. Res. 44:47-72.

Fent, R.W., Wettemann, R.P. and Johnson, R.K. 1983. Breed and heterosis effects on testicular development and endocrine function of puberal boars. J. Anim. Sci. 57:425-432.

Fields, M.J., Burns, W.C. and Warnick, A.C. 1979. Age, season and breed effects on testicular volume and semen traits in young beef bulls. J. Anim. Sci. 48:1299-1304.

Finn, G.A. 1964. Influence of the male on litter size in mice. J. Reprod. Fertil. 7:107-111.

Fowler, R.E. and Edwards, R.G. 1960. The fertility of mice selected for large or small body size. Genet. Res. 1:393-407.

Fuente, L.F. and San Primitivo, F. 1982. Selection for body weight in mice. Proc. 2nd World Congr. Genet. Appl. Livest. Prod., Madrid. 7:82-87.

Gupta, R.N., Dhingra, M.M. and Parmar, S.N.S. 1983. A study on litter weight at birth and weaning in Large White Yorkshire pigs. Indian Vet. J. 60:381-383.

Hall, D.G. and Fogarty, N.M. 1986. Growth of crossbred progeny of Dorset and DorsetxMerino rams. Proc. Aust. Soc. Anim. Prod. 16:413.

Hancock, J. 1949. Studies in monozygotic cattle twins: I Organization of twin collection. New Zealand J. Sci. Technol. 30:257-270.

Hanrahan, J.P. and Eisen, E.J. 1974. Genetic variation in litter size and 12-day weight in mice and their relationships with post-weaning growth. Anim. Prod. 19:13-23.

Hauser, E.R., Dickerson, G.E. and Mayer, D.T. 1952. Reproductive development and performance of inbred and crossbred boars. Missouri Agri. Exp. Sta. Bull. 503.

Hetzel, D.J.S. and Nicholas, F.W. 1982. Direct and correlated responses to selection for post-weaning weight gain on ad libitum or restricted feeding in mice. Theor. Appl. Genet. 63:145-150.

Horstgen-Schwark, G., Eisen, E.J., Saxton, A.M. and Bandy, T.R. 1984. Diallel cross among lines of mice selected for litter size and body weight: growth traits. Z. Tierzuchtg. Zuchtgbiol. 101: 96-111.

Horstgen-Schwark, G., Eisen, E.J., Saxton, A.M. and Bandy, T.R. 1984. Reproductive performance in a diallel cross among lines of mice selected for litter size and body weight. J. Anim. Sci. 58: 846-862.

Hough, J.D., Benyshek, L.L. and Mabry, J.W. 1985. Direct and correlated response to yearling weight selection in Hereford cattle using nationally evaluated sires. J. Anim. Sci. 61:1335-1344.

Humblot, P. 1986. Embryo mortality in cattle. Effects of sire. Anim. Breed. Abst. 54:368.

Humblot, P. and Denis, J.B. 1986. Sire effects on cow fertility and late embryonic mortality in the Montbeliard breed. Liv. Prod. Sci. 14:139-148.

Humes, P.E., Boulware, R. and Schilling, P.E. 1978. Characterization of ram and ewe breeds. I Reproductive traits. J. Anim. Sci. 47: 106-113.

Islam, A.B.M.M., Hill, W.G. and Land, R.B. 1976. Ovulation rate of lines of mice selected for testis weight. Genet. Res. 27:23-32.

Johnson, R.K. and Omtvedt, I.T. 1973. Evaluation of purebreds and two-breed crosses in swine: reproductive performance. J. Anim. Sci. 37:1279-1288.

Johnson, B.H. and Eisen, E.J. 1975. Effects of selection for postweaning gain on testicular function in mice. Can. J. Genet. Cytol. 17:93-104.

Kabuga, J.D. and Agyemang, K. 1986. Performance of Canadian Holstein-Friesian cattle in the humid forest zone of Ghana. II Preweaning performance. Anim. Breed. Abst. 54:6

Kasser, T.G., Mabry, J.W., Benyshek, L.L. and Martin, R.J. 1986. Heterotic and maternal effects in L and S growth strain rats: I Reproductive performance. Growth 50:102-108.

Kennedy, B.W. and Conlon, P.D. 1978. Comparison of crossbred and purebred boars for progeny growth and carcass merit. Anim. Prod. 27:29-34.

Kennedy, B.W. and Moxley, J.E. 1978. Genetic and environmental factors influencing litter size, sex ratio and gestation length in pigs. Anim. Prod. 27:35-42.

Krolinski, J. 1979. The effect of age of bull on sperm survival time and conception rate of cows. Anim. Breed. Abst. 48:17.

Lal, A. and Pant, K.P. 1984. Effect of crossbreeding on the quantitative biometry of ovine spermatozoa. Indian J. Anim. Sci. 54:954-957.

Land, R.B. 1970a. Genetic and phenotypic relationships between ovulation rate and body weight in the mouse. Genet. Res. 15:171-182.

Land, R.B. 1970b. The mating behaviour and semen characteristics of Finnish Landrace and Scottish Blackface rams. Anim. Prod. 12:551- 560.

Land, R.B. 1973. The expression of female sex-limited characters in the male. Nature 241:208-209.

Land, R.B., Atkins, K.D. and Roberts, R.C. 1983. Genetic improvement of reproductive performance. Proc.- Easter School In Agricultural Sci., University of Nottingham 1983:515-535.

Lasalle, T.J., White, J.M. and Vinson, W.E. 1974. Direct and correlated responses to selection for increased postweaning gain in mice. Theor. Appl. Genet. 44:272-277.

Lishman, W.B., Smith, W.C. and Bichard, M. 1975. The comparative performance of purebred and crossbred boars in commercial pig production. Anim. Prod. 21:69-75.

Louda, F., Doney, J.M., Stolc, L., Krizek, J. and Smerha, J. 1981. The development of sexual activity and semen production in ram lambs of two prolific breeds: Romanov and Finnish Landrace. Anim. Prod. 33:143-148.

Makarechian, M., Berg, R.T. and Farid, A. 1983. Effects of mating type and age of bull on reproductive performance. Agri. and Forest. Bull. Alberta Univ. Falc. Ext. p.12-14.

Makarechian, M. and Farid, A. 1985. Effect of system of mating and age of bull on natural service fertility of bulls at pasture. Agri. and Forest. Bull. Alberta Univ. Falc. Ext. p.19-21.

Marlowe, T.J., Notter, D.R., Brown, R.A. and Tolley, E.A. 1984. Sire breed effects in matings with Angus cows: I Fertility, calf survival and performance to 18 months. J. Anim. Sci. 59:11-22.

McKay, R.I., Parker, R.J. and Guenter, W. 1986. Response to selection for body weight or feed efficiency in mice tested on corn, rye and wheat diets. Can. J. Anim. Sci. 66:389-397.

McLellan, C.R.Jr. and Frahm, R.R. 1973. Direct and correlated responses to two-way selection for hindleg muscle system weight in mice. J. Anim. Sci. 36:442-451.

Minkema, D. 1967. Some factors affecting litter size in pigs. Anim. Breed. Abst. 35:652.

Moore, R.W. and Whyman, D. 1980. Fertilizing ability of semen from rams of high- and low-prolificacy flocks. J. Reprod. Fert. 59:311-316.

Moore, R.W., Wilson, M.C., Lynch, P.R. and Miller, C.M. 1986. Total testicle volume, sperm concentration of ejaculate and sperm swimming speed of Romney rams from lines selected for high and low ewe prolificacy. Proc. Aust. Soc. Anim. Prod. 16:422.

Morris, S.M. and Lineweaver, J.A. 1972. Lowered reproductive efficiency in selected mice. J. Anim. Sci. 35:181 (abst).

Nagai, J., Harris, D.L. and McAllister, A.J. 1980. Growth, feed efficiency and lifetime performance of crosses between lines selected for nursing ability and/or adult weight in mice. Theor. Appl. Genet. 58:59-69.

Nagai, J., McAllister, A.J. and Chesnais, J.P. 1984. Male and female contributions to heterosis in lifetime performance of mice. Theor. Appl. Genet. 67:479-484.

Nagai, J. and McAllister, A.J. 1985. Comparison of lifetime performance in mice under crisscross, repeat hybrid male cross and random mating systems. Theor. Appl. Genet. 69:447-455.

Napier, R.A.N. 1961. Fertility in male rabbit. III The estimation of spermatozoan quality by mixed insemination and the inheritance of spermatozoan characters. J. Reprod. Fert. 2:273-289.

Neely, J.D., Johnson, B.H. and Robison, O.W. 1980. Heterosis estimates for measures of reproductive traits in crossbred boars. J. Anim. Sci. 51:1070-1077.

Neely, J.D. and Robison, O.W. 1983. Estimates of heterosis for sexual activity in boars. J. Anim. Sci. 56:1033-1038.

Newton, J.E. and Betts, J.E. 1968. Factors affecting litter size in the Scotch Half-bred ewe. II Superovulation and the synchronization of oestrus. J. Reprod. Fert. 17:485-493.

Neville, W.E., Utley, P.R. and McCormick, W.C. 1985. Comparative performance of straightbred and crossbred (F1) sires. J. Anim. Sci. 60:632-643.

Nitter, G. 1978. Breed utilization for meat production in sheep. Anim. Breed. Abst. 46:131-143.

Olson, T.A., van Dijk, A., Koger, M., Hargrove. D.D. and Franke, D.E. 1985. Additive and heterosis effects on preweaning traits, maternal ability and reproduction from crossing of the Angus and Brown Swiss breeds in Florida. J. Anim. Sci. 61:1121-1131

Pandya, D.K., Johar, K.S. and Singh, A. 1986. A note on birth weight of Jersey calves. Anim. Breed. Abst. 54:98.

Parker, C.F. 1971. Crossbred (F1) rams for improving rate and percentage of lambing in Columbia and Targhee rams. J.Anim. Sci. 33:203-204.

Philipsson, J. 1981. Genetic aspects of female fertility in Dairy cattle. Livest. Prod. Sci. 8:307-319.

Rahnefeld, G.W., Comstock, R.E., Singh, M. and NaPuket, S.R. 1966. Genetic correlation between growth rate and litter size in mice. Genetics 54:1423-1429.

Rahnefeld, G.W. and Swierstra, E.E. 1970. Influence of the sire on litter size in swine. Can. J. Anim. Sci. 50:671-675.

Raja, C.K.S.V. and Rao, A.R. 1983. The semen characteristics of Brown Swiss cross-bred bulls in relation to age. Indian Vet. J. 60:451-454.

Rempel, W.E., Comstock, R.E. and Enfield, F.D. 1964. Comparison of performance of crossbred pigs sired by purebred and crossbred boars. J. Anim. Sci. 23:87-89.

Reynolds, W.L., Bellows, R.A., Urick, J.J. and Knapp, B.W. 1986. Crossing beef x beef and beef x Brown Swiss: pregnancy rate, calf survival, weaning age and rate. J. Anim. Sci. 63:8-16.

Rios, J.G., Nielsen, M.K., Dickerson, G.E. and De Shazer, J.A. 1986. Selection for postweaning gain in rats: II Correlated response in reproductive performance. J. Anim. Sci. 63:46-53.

Roberts, R.C. 1961. The lifetime growth and reproduction of selected strains on mice. Heredity 16:369-381.

Roberts, R.C. 1979. Side effects of selection for growth in laboratory animals. Livest. Prod. Sci. 6:93-104.

SAS. 1985. SAS User's guide. Statistical Analysis System Institute, Inc., Cary, NC.

Schilling, P., North, W. and Bogart, R. 1968. The effect of sire on litter size in mice. J. Hered. 59:351-352.

Schinckel, A., Johnson, R.K., Pumfrey, R.A. and Zimmerman, D.R. 1983. Testicular growth in boars of different genetic lines and its relationship to reproductive performance. J. Anim. Sci. 56:1065-1076.

Seifert, G.W., Hetzel, D.J.S., Ronchietto, P. and Hofmeyr, J.H. 1986. A preliminary note on a comparison of Belmont Red and Bonsmara cattle in the Republic of South Africa. Anim. Breed. Abst. 54:6.

Sidwell, G.M., Everson, D.O. and Terrill, C.E. 1964. Lamb weights in some pure breeds and crosses. J. Anim. Sci. 23:105-110.

Singh, D.K., Singh, R., Singh, L.B., Singh, C.S.P. and Mishra, H.R. 1985. Effect of age and breed of bucks on reproductive traits of Black Bengal does. Indian J. Anim. Sci. 55:207-210.

Singh, A. and Parekh, H.K.B. 1986. Non-genetic and genetic factors affecting birth weight and linear body measurements in JerseyxGir F2 cross-calves at birth. Anim. Breed. Abst. 54:758.

Singh, A., Taylor, C.M. and Singh, B.N. 1986. Factors affecting some reproduction and production traits in Malvi cattle. Anim. Breed. Abst. 54:1025.

Singleton, W.L. and Shelby. D.R. 1972. Variation among boars in semen characteristics and fertility. J. Anim. Sci. 34:762-766.

Skinner, J.D. and Rowson, L.E.A. 1968. Puberty in Suffolk and cross-bred rams. J. Reprod. Fert. 16:479-488.

Stritzke, D.J., Whiteman, J.V. and McNew, R.W. 1984. Transmitted effect of purebred versus crossbred rams on rate and variability of lamb growth. J. Anim. Sci. 58:1138-1143.

Swierstra, E.E. and Rahnefeld, G.W. 1967. Semen and testis characteristics in young Yorkshire and Lacombe boars. J. Anim. Sci. 26:149-157.

Swierstra, E.E. 1973. Influence of breed, age, and ejaculation frequency on boar semen composition. Can. J. Anim. Sci. 53:43-53.

Swierstra, E.E. and Dyck, G.W. 1976. Influence of the boar and ejaculation frequency on pregnancy rate and embryonic survival in swine. J. Anim. Sci. 42:455-460.

Syrstad, O. 1981. Selection for fertility on the basis of A.I. data. Livest. Prod. Sci. 8:247-252.

Thrift, F.A., Franke, D.E. and Aaron, D.K. 1986. Preweaning breed-of-sire comparisons involving the Senepol breed of cattle. J. Anim. Sci. 62:1247-1254.

Tiwari, S.B. and Sahni, K.L. 1982. Semen production in relation to age, body weight and testes dimension in cross-bred rams (Rambouillet x Malpura) under semi-arid condition. Indian Vet. J. 59:995-997.

Touchberry, R.W. and Bereskin, B. 1966. Crossbreeding Dairy Cattle. II Weights and body measurements of Purebred Holstein and Guernsey females and their reciprocal crossbreds. J. Dairy Sci. 49:647-658.

Vakil, D.V., Botkin, M.P. and Roehrkasse, G.P. 1968. Influence of hereditary and environmental factors on winning in Sheep. J. Heredity 59:256-259.

Wang, C.T. and Dickerson, G.E. 1984. Selection for rate and for efficiency of lean growth in rats: responses to selection and relaxation of selection. J. Anim. Sci. 58:831-845.

Willham, R.L. and Pollak, E. 1985. Symposium: heterosis and crossbreeding. Theory of heterosis. J. Dairy Sci. 68:2411-2417.

Wilson, S.P., Whatley, J.A., Whiteman, J.V. and Morrison, R.D. 1962. Influence of sire and line of breeding on sow productivity. J. Anim. Sci. 21:119-122.

Wilson, E.R., Johnson, R.K. and Wettemann, R.P. 1977. Reproductive and testicular characteristics of purebred and crossbred boars. J. Anim. Sci. 44:939-947.

Wirth-Dzieciolowska, E. and Martyniuk, E. 1986. Indirect effects of selection for testis weight in mice in female reproduction performance. Proc. 3rd World Congr. Genet. Appl. Livest. Prod., Lincoln, Nebraska. 11:254-257.

Young, L.D., Johnson, R.K. and Omtvedt, I.T. 1976. Reproductive performance of swine bred to produce purebred and two-bred cross litters. J. Anim. Sci. 42(5):1133-1149.

Appendix 1. Analysis of variance for 'overall production' litter traits (OPLSB, OPLSW, OPLWB, OPLWW)

Source	df	OPLSB	OPLSW	OPLWB	OPLWW
		MS	MS	MS	MS
Line (L)	8	1,064.21****	723.97**	2,610.03***	116,831.12**
Replicate (R)	1	54.65NS	82.43NS	216.29NS	2,723.23NS
LxR	8	216.08NS	185.98NS	560.20NS	28,127.06NS
Error	217	246.69	236.86	725.54	34,674.79

* $P<0.05$

** $P<0.01$

*** $P<0.001$

**** $P<0.0001$

NS- Not significant

Appendix 2. Least square means for 'overall production' litter traits (OPLSB, OPLSSW, OPLWB, OPLWW) for each pure line and line cross

Line	OPLSB	OPLSW	OPLWB (g)	OPLWW (g)
AA	93.50^{ab} $(3.08)^{1}$	88.59^{ab} (3.01)	167.00^{ab} (5.28)	$1,193.88^{a}$ (36.35)
CC	83.28^{b} (3.02)	77.44^{b} (2.95)	145.88^{b} (5.17)	995.03^{b} (35.86)
EE	98.73^{a} (3.08)	92.00^{a} (3.02)	160.10^{ab} (5.28)	$1,100.71^{ab}$ (36.52)
AC	102.00^{a} (3.08)	93.81^{a} (3.02)	177.73^{a} (5.28)	$1,201.18^{a}$ (36.52)
CA	102.88^{a} (3.14)	94.21^{a} (3.08)	178.38^{a} (5.39)	$1,209.74^{a}$ (37.27)
AE	101.61^{a} (3.08)	90.46^{ab} (3.02)	172.19^{a} (5.28)	$1,135.04^{a}$ (36.52)
EA	97.81^{a} (3.08)	90.62^{ab} (3.02)	165.17^{ab} (5.28)	$1,170.06^{a}$ (36.52)
EC	103.25^{a} (3.02)	93.38^{a} (2.96)	171.55^{a} (5.19)	$1,158.13^{a}$ (35.86)
CE	99.27^{a} (3.08)	93.23^{a} (3.02)	168.52^{ab} (5.28)	$1,159.64^{a}$ (36.52)

[1] Standard error

a, b- means in the same column having different superscripts are significantly different (P<0.05)

Appendix 3. Analysis of variance for 'mating period total' litter traits (TLSB, TLSW, TLWB, TLWW)

		TLSB	TLSW	TLWB	TLWW
Source	df	MS	MS	MS	MS
Line (L)	8	81.11****	49.14**	161.52**	4,934.53NS
Replicate (R)	1	34.55NS	18.76NS	3.65NS	826.07NS
LxR	8	23.34NS	15.18NS	48.92NS	2,807.86NS
Mating Period (M)	4	265.38****	63.01**	346.18***	8,803.23**
LxM	32	10.38NS	15.06NS	37.16NS	3,004.08NS
RxM	4	16.41NS	15.04NS	50.80NS	6,477.21*
LxRxM	32	14.53NS	15.14NS	45.60NS	2,309.09NS
Error	1051	18.59	18.73	50.31	2,567.36

* P<0.05

** P<0.01

*** P<0.001

**** P<0.0001

NS- Not significant

Appendix 4. Least square means and standard errors for 'mating period total' litter traits (TLSB, TLSW, TLWB, TLWW) for each pure line and line cross

Line	TLSB		TLSW		TLWB (g)		TLWW (g)	
AA	18.84^c	$(0.38)^1$	17.72	(0.38)	33.63^b	(0.63)	238.78	(4.46)
CC	18.84^c	(0.40)	17.69	(0.40)	33.00^b	(0.65)	228.01	(4.69)
EE	20.67^a	(0.39)	19.29	(0.39)	33.53^b	(0.64)	231.05	(4.55)
AC	20.55^{ab}	(0.38)	18.91	(0.38)	35.81^{ab}	(0.62)	242.22	(4.46)
CA	21.05^a	(0.39)	19.27	(0.39)	36.50^a	(0.64)	247.69	(4.59)
AE	20.47^{abc}	(0.38)	18.35	(0.38)	34.95^{ab}	(0.63)	230.44	(4.48)
EA	19.85^{abc}	(0.38)	18.40	(0.38)	33.80^{ab}	(0.63)	237.78	(4.48)
EC	20.65^{ab}	(0.37)	18.83	(0.37)	34.31^{ab}	(0.61)	233.51	(4.38)
CE	20.47^{abc}	(0.38)	19.24	(0.38)	34.77^{ab}	(0.63)	239.52	(4.52)

[1] Standard error

a, b, c- means in the same column having different superscripts are significantly different (P<0.05)

Appendix 5. Analysis of variance for 'mating period average' litter traits (ALSB, ALSW, ALWB, ALWW)

		ALSB	ALSW	ALWB	ALWW
Source	df	MS	MS	MS	MS
Line (L)	8	8.95*	4.29NS	25.40**	1,273.08***
Replicate (R)	1	20.89*	15.99*	11.62NS	1,049.81NS
LxR	8	4.24NS	3.91NS	9.68NS	286.66NS
Mating Period (M)	4	49.70****	28.14****	75.69****	2,783.20****
LxM	32	1.97NS	1.19NS	7.16NS	314.67NS
RxM	4	3.90NS	3.30NS	10.04NS	1,830.46***
LxRxM	32	3.35NS	2.19NS	10.38NS	419.30NS
Error	1051	3.85	3.00	9.67	353.35

* $P<0.05$

** $P<0.01$

*** $P<0.001$

**** $P<0.0001$

NS- Not significant

Appendix 6. Least square means and standard errors for 'mating period average' litter traits (ALSB, ALSW, ALWB, ALWW) for each pure line and line cross

Line	ALSB		ALSW		ALWB (g)		ALWW (g)	
AA	9.85	$(0.17)^1$	9.47	(0.15)	17.68^{ab}	(0.27)	127.61^{ab}	(1.65)
CC	9.91	(0.18)	9.75	(0.16)	17.54^{ab}	(0.29)	125.65^{abc}	(1.74)
EE	10.50	(0.18)	9.99	(0.15)	17.13^{b}	(0.28)	119.59^{c}	(1.69)
AC	10.49	(0.17)	10.01	(0.15)	18.26^{ab}	(0.27)	128.30^{ab}	(1.66)
CA	10.60	(0.18)	10.05	(0.16)	18.56^{a}	(0.28)	129.47^{a}	(1.70)
AE	10.49	(0.17)	9.89	(0.15)	17.85^{ab}	(0.27)	123.99^{abc}	(1.66)
EA	10.20	(0.17)	9.73	(0.15)	17.56^{ab}	(0.28)	125.38^{abc}	(1.66)
EC	10.36	(0.17)	9.79	(0.15)	17.27^{b}	(0.27)	121.51^{bc}	(1.63)
CE	10.32	(0.17)	9.97	(0.15)	17.76^{ab}	(0.28)	124.61^{abc}	(1.68)

[1]Standard error

a, b, c- means in the same column having different superscripts are significantly different (P<0.05)

Appendix 7. Analysis of variance for age at first mating
              (MINFERT)

Source	df	MINFERT MS
Line (L)	8	108.95****
Replicate (R)	1	3.71NS
L x R	8	11.74NS
Error	216	13.85

**** P<0.0001

  NS- Not significant

Appendix 8. Least square means and standard errors for age at first mating (MINFERT)

Line	MINFERT (days)
AA	46.31^a $(0.73)^1$
CC	49.82^b (0.72)
EE	45.93^a (0.74)
AC	43.38^a (0.73)
CA	44.19^a (0.74)
AE	44.77^a (0.73)
EA	43.58^a (0.73)
CE	46.11^a (0.73)
EC	43.84^a (0.72)

[1] Standard error

a, b- means having different superscripts are significantly different (P<0.05)

Appendix 9. Analysis of variance for mean days to
conception (MDCONCEP)

		MDCONCEP
Source	df	MS
Line (L)	8	17.78NS
Replicate (R)	1	1.91NS
L x R	8	4.97NS
Mating Period (M)	3	19.45NS
L x M	24	6.78NS
R x M	3	19.43NS
L x R x M	24	8.28NS
Error	835	9.63

NS- Not significant (P>0.05)

Appendix 10. Least square means and standard errors for
average days to conception (MDCONCEP)

Line	MDCONCEP (days)	
AA	3.69	$(0.31)^1$
CC	3.09	(0.32)
EE	2.23	(0.31)
AC	2.66	(0.30)
CA	2.89	(0.31)
AE	2.77	(0.30)
EA	3.06	(0.31)
CE	2.44	(0.31)
EC	2.76	(0.30)

[1]Standard error

Appendix 11. Analysis of variance for number of fertile
matings (NFM)

Source	df	NFM MS
Line (L)	8	5.63***
Replicate (R)	1	2.61NS
L x R	8	1.21NS
Error	217	1.56

*** P<0.001

NS- Not significant

Appendix 12. Least square means and standard errors for number of fertile matings (NFM)

Line	NFM
AA	9.51^a $(0.25)^1$
CC	8.31^b (0.24)
EE	9.35^{ab} (0.24)
AC	9.73^a (0.24)
CA	9.61^a (0.25)
AE	9.65^a (0.24)
EA	9.42^a (0.24)
CE	9.50^a (0.24)
EC	9.92^a (0.24)

[1] Standard error

a, b- means having diiferent superscripts are significantly different (P<0.05)

Appendix 13. Analysis of variance for testes weight (TESTW)

Source	df	TESTW MS
Line (L)	8	0.0878****
Replicate (R)	1	0.0032NS
L x R	8	0.0030NS
Error	223	0.0020

**** P<0.0001

NS- Not significant

Appendix 14. Least square means and standard errors for
testes weight (TESTW)

Line	TESTW (g)
AA	0.3318^{ab} $(0.0087)^{1}$
CC	0.1848^{d} (0.0093)
EE	0.2134^{cd} (0.0091)
AC	0.3397^{ab} (0.0089)
CA	0.3472^{a} (0.0093)
AE	0.3033^{b} (0.0087)
EA	0.3060^{b} (0.0087)
CE	0.2376^{c} (0.0091)
EC	0.2361^{c} (0.0086)

[1]Standard error

a, b, c, d- means having different superscripts are significantly different (P<0.05)