INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

Phenotypic and genetic changes in growth and reproductive success in *Tribolium castaneum* across four different environments

by

Seyrani Koncagül

A dissertation submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Animal Breeding and Genetics

Program of Study Committee:
Philip J. Berger, Major Professor
Edward Pollak
Rohan Fernando
Doyle E. Wilson
Kendall R. Lamkey

Iowa State University

Ames, Iowa

2001

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

Graduate College
Iowa State University

This is to certify that the doctoral dissertation of

Seyrani Koncagul

has met the dissertation requirements of Iowa State University

Signature was redacted for privacy.

Major Professor

Signature was redacted for privacy.

For the Major Program

TABLES OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Results are presented that describes a selection experiment showing the fundamental changes in growth and fitness associated with a shift towards higher growth rates in four environments. The experiment uses *Tribolium castaneum* to model a selection and mating scheme frequently occurring in commercial populations of livestock where there is an exchange of elite male germplasm to enhance performance in other populations under different environmental conditions. Objectives were to estimate direct response to selection for increased pupa weight in four environments and correlated response in family size. Estimates of genetic parameters are reported for the base population, combining all data across all lines and 23 generations of selection, and within each line.

Sufficient protein in the diet rather than a deficiency of protein was identified as a major contributing factor influencing phenotypic, genetic, and environmental changes across generations. Relative humidity created only minor changes in mean pupa weight between lines on the same diet. Animal models that failed to properly account for males used across environments seriously underestimated the additive genetic variance in the population. The optimum environment, 80% relative humidity (RH) and 5% yeast-fortified whole wheat flour diet, and the poorest environment, 67% RH and a diet of flour alone, set maximum and minimum limits on estimates of phenotypic and additive genetic variance. A large ratio of additive genetic variance to phenotypic variance in some environments than others was clear evidence of genotype by environment interaction.

The experiment draws attention to the fact that undesirable correlated responses in reproductive success are frequently associated with selection for growth. Correlated

responses in reproductive success can no longer be ignored, or left unmeasured in populations under intense selection for growth.

CHAPTER 1. GENERAL INTRODUCTION

INTRODUCTION

Techniques and procedures for genetic enhancement of performance of beef and dairy cattle, pigs and poultry have changed dramatically in the last decade. Milk production per cow or growth rate of beef cattle and pigs increased steadily due to a combination of improved management, better nutrition, and intense genetic selection. Concurrently, techniques for genetic evaluation of livestock and poultry have changed. The quantity and quality of data has improved. Animal models have been adopted with alarming speed. Large computers and more efficient computing algorithms make genetic parameter estimation possible for large populations and different environmental settings.

This dissertation focuses on the analysis of a selection experiment that was designed to describe the fundamental changes in growth and fitness associated with a shift towards higher growth rates. The dissertation describes an experiment that models the selection and mating schemes frequently occurring in livestock. Elite males are allowed to be used across environmental settings. Environmental condition of some countries can even represent extremely different settings for food, temperature and humidity. Yet, there is common belief among breeders of livestock that animals at any level of genetic potential for growth and fitness can be freely moved across environments without any loss in their ability to express their genetic potential to its full extent. Due to artificial insemination and other advanced reproductive techniques, it is easier and more cost effective to exchange male germplasm across environments. Female animals, however, remain under constant environmental

conditions although some selection for increased growth rate can continue within each environment.

Migration

Migration of new animals from other populations introduces new sets of genes into the population and causes changes in breeding values and additive genetic variance to be different than their expectations under random mating, without selection, and without migration. Most selection studies have been conducted by using a closed population, and seldom permit animals from other populations to be introduced in any generation. However, in the real world, countries have been using semen from different countries to breed their cows every generation for years. Pedigree information can be incomplete because sires that come into the population at the t^{th} generation do not have any genetic tie to animals from previous generations. Effectively, this is like having animals within the population originating from different base populations. At this point it is unclear how unrelated sires from different base populations can affect the process of genetic parameter estimation within a particular country by using an animal model.

Today the animal model has become a conventional and preferable method by almost all quantitative geneticists because it has properties that are consistent with quantitative genetic theory. When the data within environment or country are analyzed alone, an animal model without any modifications to account for migration of parents recognizes the migrated parents, with unknown ancestors and without any records, as base population animals with expected breeding value of zero. In reality, however, sires introduced into the population at

some point in time through migration may have superior genetic potential than can be expected if they are all from the same population.

Sires without any records and without any previous pedigree information can be assigned to groups, and these groups can be included as a fixed effect in the model. Some researchers have developed theoretical arguments, supported analytically by simulation, showing how groups can be used to account for genetic merit of sires with unknown ancestors (QUASS and POLLAK 1981; WESTELL and VAN VLECK 1987; WESTELL et al. 1988; WIGGANS et al. 1988). Others have carried the investigation further to say that if the migration rate entails larger than 5% of the population then the need for group effects in the model increases (KENNEDY 1981).

The effect of migration on estimates of breeding values and additive genetic variance has not been reported in detail for biological populations. It is still necessary to have empirical evidence to justify the existing theory in terms of additive genetic variance and genetic parameter estimation. In this dissertation, empirical evidence is provided showing how migration or exchange of male germplasm among environments or countries can affect estimates of additive genetic variance and the genetic parameters. Analyses show how migration can be modeled when the data within environment (or within country) are analyzed as if each country is an independent source of data for genetic evaluation of breeding animals.

Genotype by Environment Interaction

The presence of genotype by environment interactions creates additional points of interest for testing and evaluation of breeding animals. Quantitative geneticists would like to

know if animals should be tested in the same environment where they will be used for breeding or in a relatively different environment, and whether it should be a poorer environment or a better environment than where they will be living or producing offspring. Some researchers have suggested that animals should be selected under the environmental conditions where the animals can fully express the trait of interest (HAMMOND 1947; FRIARS et al. 1971; MARKS 1980), while others believe an adverse environment should be preferred (FALCONER 1960). Others have suggested that selection must be performed where the animals continue their lives (YAMADA and BELL 1969; GEARHEART and GOODWILL 1990). It is apparent that there is no consensus among researchers about the proper environmental setting for selection and genetic evaluation of breeding stock.

Moreover, in terms of correlated response, genotype by environment interaction can also cause a divergence among populations. LYNCH and WALSH (1997, page 647) stated that " If the characters under investigation are sensitive to genotype x environment interaction, then a change in environment may induce a real shift in genetic correlation so that one is no longer estimating the correlation of interest".

The design of this experiment also made it possible to study genotype by environment interaction and its effect on growth and reproductive success by allowing the best sires to have offspring in different environments.

Correlated Response

Associated with selection for one trait there can be a correlated response in other traits due to genetic correlations among them. Sometimes the correlated response may be undesirable. For example, a negative genetic correlation between growth and reproductive

success is undesirable. Direction and magnitude of changes in correlated traits depend on the genetic and environmental correlations between traits under direct and indirect selection. Estimates of the genetic correlations among traits can also be very different across environments. Researchers have conducted studies to investigate the effect of selection on growth and reproductive success, and examined the genetic correlation between them. Some have reported a positive relationship between these two types of traits under various environments and selection regimes (FOWLER and EDWARDS 1960; RAHNEFELD et al. 1966; LAND 1970; HANRAHAN and EISEN 1974; MORRIS 1975; EISEN 1978; DURRANT et al. 1980; RIOS et al. 1986; CAMPO and de la BLANCE 1988). Others have reported a negative relationship (WILSON et al. 1971; LEGAULT 1971; GARNETT and RAHNEFELD 1976; BERGER 1977; BERGER and LIN 1992). Moreover, LYNCH and WALSH (1997, page 647) stated that "Clearly, more work is needed on the degree to which genetic correlations (and covariances) respond to environmental changes".

This dissertation introduces new understanding for the behavior of genetic correlations in respect to environmental changes in a selection experiment with constant flow of germplasm among environments. It brings to light how seriously sires, with unknown ancestors, introduced into the population can affect estimates of genetic variances and genetic correlations between growth and reproductive success.

Tribolium castaneum

The selection experiment described in this dissertation was conducted to study the direct response to selection for increased pupa weight and the correlated response of reproduvtive success under different environmental conditions determined by relative

humidity and diet. Four subpopulations were created by randomly dividing insects from an unselected base population of *Tribolium castaneum* into four subsets. The main reasons for choosing this insect to do the selection experiment were that many other researchers have used them, and that the results and findings will be applicable to larger breeding populations of livestock. *Tribolium castaneum* are easy to handle. They can be maintained with a small amount of resources for a long time. And long-term selection can be applied due to their short life cycle.

Mass selection for increased pupa weight was employed for 23 generations. Every generation the best sires from each line were permitted to migrate among environments, which could define the different climate zones or regions in the United States, or different countries in the world. Design of the experiment made it possible to investigate the importance of accounting for genetic merit of sires that migrated among subpopulations when the subpopulations were analyzed separately. It was possible to examine genotype by environment interaction and its effect on growth and reproductive success. Also, in this experiment, it was possible to estimate the correlated response in reproductive success with a shift towards heavier pupa weight, and to investigate the behavior of the genetic correlation between these two traits under different environmental settings with a constant exchange of male germplasm among subpopulations.

Data created by this experiment were unique for the hypothesis being examined. Specific controlled environmental conditions are uncommon in field data. Balanced subsets of the same sires are rarely used across all environmental settings.

OBJECTIVES

The objectives of the present study are three-fold. First is to estimate the change in mean breeding value and environmental values of the population for pupa weight in lines of *Tribolium castaneum* selected for increased pupa weight. This is accomplished by obtaining estimates of variance components and parameters for the whole population by combining data across all four lines. Existence of a possible genotype by environment interaction will be investigated.

Second is to estimate variance components and genetic parameters for pupa weight within each subpopulation by two different mathematical models. One model ignores the fact that the genetic merit of migrated sires from different subpopulations may be different than the mean level of merit for sires within a line even though they are from the same generation. The second model allows sires from outside the population to have different levels of genetic merit across generations. The effects of variation in environment on estimates of genetic parameters will be discussed in detail. Also, proper environmental settings for selection will be investigated.

Lastly, the correlated response of reproductive success to selection for pupa weight will be examined. The process by which environmental differences affect the correlated response will be described. Results will be presented showing how the genetic correlation between pupa weight and reproductive success of female insects changes under different environmental settings with a constant flow of male germplasm among environments.

ORGANIZATION OF DISSERTATION

The dissertation is organized as five chapters. The first chapter gives a general introduction and review of literature for the next four chapters. The next three chapters are manuscripts of papers to be submitted to *Journal of Animal Breeding and Genetics*. The second chapter gives a detailed description of a particular long-term selection experiment. Estimates of response to selection for increased pupa weight within each environment are given. Parameter estimates for pupa weight are reported for all data across four environments. The third chapter provides a comparison of variance components and parameter estimates in four different environments for pupa weight from models with and without adjustment for different levels of genetic merit of sires created by a constant exchange of male germplasm among environments. Chapter four describes the correlated response in reproductive success of female insects to selection for increased pupa weight. This chapter explains the genetic and environmental relationship between pupa weight and reproductive success in different environments. Chapter five provides a general summary of conclusions based on the results of the previous chapters.

LITERATURE REVIEW

Grouping of Unknown or Migrated Parents

In a selection experiment, all animals in the present generation have a relationship tie to previous generations, because they were selected from previous generations. In the real world, however, farmers in different regions frequently use semen of sires from populations in other environments. Even countries have been importing semen from other countries. In this situation, sires introduced into the population through artificial insemination (A.I.) (or

migration) at some point in time have no genetic relationship to the animals in the previous generations within an environment or a country. If all records for all animals for a particular trait and a breed in the world were available for analysis, then the genetic relationship matrix among all animals in the data being analyzed would be complete. However, if the data within a country or an environment are analyzed alone, then the relationship matrix among animals in the data is not quite complete. When this happens, there must be an additional factor in the model used to analyze the data to account for the unknown or missing information.

Parents not having a genetic tie to previous generations can be defined as unknown parents, which can be assigned to a fixed genetic group effect in the model to account for genetic trend (QUASS and POLLAK 1981; WESTELL et al. 1988). It is not necessary to include the genetic group effects in the model if all relationships among animals are included in the analysis (POLLAK and QUAAS 1983). It is not always possible, however, to know all genetic relationships among all animals in the data. Genetic groups in the model can complete relationships among animals (WIGGANS et al. 1988). Moreover, there may still be a need for grouping, even if all the relationships are included in the model, to account for selection on information not included in the model (TONG et al. 1980). Grouping of unknown parents can provide a more precise way of evaluating the data generated by selection (WESTELL and VAN VLECK 1987). KENNEDY (1981) reported that the necessity for grouping of unknown parents increases when migration from other environments or populations to the population of interest is larger than 5%.

Many different strategies can be used for assigning unknown parents to groups. Unknown parents can be numbered according to their birthday, location that they came from,

generation number when they came into the population. ROBINSON (1986) and WESTELL et al. (1988) gave a list of steps useful for defining the strategy for grouping for unknown parents. In practice, there is no exact way to define groups for unknown parents.

Genotype by Environment Interaction

A large number of researchers have studied the effect of environment and genotype on particular traits using livestock and laboratory animals for years. An overview of traits and environmental treatments appearing in genotype by environment interaction studies for *Tribolium castaneum*, beef cattle, and dairy cattle is given in Table 1.

VAN VLECK (1963) reported that genotypic and phenotypic variance increased according to environment, and that the proportion of genotypic variance in the total variance was larger in the good levels of environment. He estimated parameters from the deviation of daughters' records adjusted to herd-mate average. The study used 45,876 first lactation records and 39,216 second lactation records in dairy cattle. The quantitative traits were milk and fat yield. Heritability estimates for milk yield in the first and second lactations were .28 and .29; .28 and .26; .25 and .21; .19 and .19 from the better environment to the poorer environment, respectively. Heritability estimates for fat production in the first and second lactations were .25 and .28; .25 and .25; .25 and .21; .20 and .21 from the better environment to the poorer environment, respectively. He concluded that different estimates of parameters in different levels of environment were another form of genotype by environment interaction.

MAO and BURNSIDE (1969) examined the effect of genotype by environment interaction on milk yield in Canadian herds. They found a significant ($P < .01$) sire by

Table 1. Overview of traits and environmental treatments appearing in genotype by environment interaction studies for *Tribolium castaneum*, beef cattle, and dairy cattle.

Reference	Trait	Enviroment
Tribolium		
**Hardin et al, 1967	14th day larva weight	Wet: 70% RH, and Dry: 40% RH, 32° C 12 environments: Combinations of 3 levels of Soybean (44% protein), yeast, vitamin premix, corn oil.
**Yamada and Bell, 1969	13th day larva weight	Diet1: 10% Dried yeast plus 5% corn oil Diet2: Contained neither (flour alone)
**Orozco and Bell, 1974	Egg laying(24 h)	Temp: 28, 33, and 38° C
**Benyi and Gall, 1978	13th day larva weight Age at pupation Pupa weight	Nutrition: **Poor**: 12.08% moisture, 0.48% ash, 14.08%crude protein, 1%fat, and 3.936 gross energy **Good**: 11.62% moisture, 1.08%ash, 18.29% crude protein, 1.25% fat, and 4.081% gross energy
**Benyi and Gall, 1981	Egg laying(24 h)	Nutrition: Diet1: 100% flour Diet2: 10% yeast plus 90% flour
**Paterson et al, 1983	13th day larva weight	Parental age: Age1: 3 to 11 days old Age2: 33 to 41 days old, abd Age3: 68 to 76 days old
**Wade, 1990	Lineage	Environment1: 29 C and 70% RH Environment2: 27 C and 22% RH
**Orozco, 1976	Egg laying (24 h)	Temperature: 28, 33, and 38 C

Table 1 Cont'

Dairy cattle

**Robertson et al., 1960	Milk yield	V(g) in high vs low producing herds
**Van Vleck, 1963	Milk yield	V(g) in high vs low producing herds
**Thomas et al., 1968	Milk yield	Sire x Herd
**Mao and Burnside, 1969	Milk yield	Sire Proof for Milk Yield x Herd Sire x level of grain feeding
Stanton et al., 1991	Milk yield	Management x Sex
Carabano et al. 1990	305-d Mature equivalent First Lactation Record Fat yield Fat percentage	Ca, NY, WI Ca, NY, WI Ca, NY, WI Ca, NY, WI Ca, NY, WI

Beef cattle

**Woodward and Clark, 1950	Birth weight Preweaning gain Post weaning gain Feedlot efficiency	Location: Miles City and Harve, Montana (Hereford bulls progeny test)
**Cartwright, 1955	Weight gain (bulls, heifers, steers)	92 yearling cattle, weighed every 28 days, from November to middle of May (rate of gain test in the feetlot). June 1st to September 30 (pasture), Texas

Table 1 Cont'

**Urick et al., 1957	Post weaning growth (genetic correlation among gains during 3 successive post weaning growth period)	First winter, summer, second winter (growing-fattening ratio)
**Rollins et al., 1964	Weight Gain (bulls, heifers, steers)	92 yearling cattle, weighed every 28 days, from November to middle of May (rate of gain test in the feetlot). June 1st to September 30 (pasture), California
**Morris et. al., 1993	Reproductive trait: (Weight of calf weaned Per cow)	161 bulls from 11 breeds mated with Angus cows and Hereford cows (3 locations in New Zealand)
Brown and Gacula, 1962	Post weaning gain	Sire x management in a herd (Arkansas)
Tess et al., 1979	Weaning weight	Three regions of United States.
**Notter et al., 1992	Weaning weight	Sire x Herd

**Genotype by environment interaction exists.

environment interaction when herds were fed different amounts of grain during the summer season. The variance due to interaction was 17.4% of the total variance in their study.

YAMADA and BELL (1969) investigated genotype by environment interaction in the context of selection for high or low 13-day larva weight in *Tribolium castaneum* with two replicates for sixteen generations under two levels of nutrition; 100% whole wheat flour, 85% whole wheat flour with 10% dried brewer's yeast and 5% corn oil. The temperature and humidity were constant at 33 °C and 70% relative humidity. They reported that 13-day larva weight in the poor level of environment was half as large as the weight in the good level of environment; mean larva weights were 227.2(10^{-2}) mg. in replicate 1 and 220.3(10^{-2}) mg. in replicate 2 in the good diet, and 115.7(10^{-2}) mg. in replicate 1 and 116.9(10^{-2}) mg. in replicate 2 in the poor diet. Heritability (h^2) estimates in the good diet were .30 ± .06 and .44 ± .06 in replicates 1 and 2, respectively; .35 ± .06 and .51 ± .06 in replicates1 and 2 of the poor diet, respectively. Genetic correlations between 13-day larva weights in these two levels of environment were .82 ± .04 and .78 ± .04 for replications 1 and 2, respectively. They indicated that dominance and maternal effects increased estimates of the genetic parameters because they calculated them from full-sib covariance components.

OROZCO and BELL (1974) investigated the effect of temperature on egg laying in *Tribolium castaneum* for twenty generations. Changes in temperature were used to create different levels of stress (33°C as an optimal, 38°C as a mild stress and 28°C as a severe stress). They calculated the heritability of egg laying from full-sib correlation and dam-daughter regression and found that heritability estimates from full-sib correlation were higher (.36 at 33°C, .30 at 38°C and .25 at 28°C) than those based on dam-daughter regression.

They also found that when severity of environment increased, additive genetic variance decreased (56.74 at 33°C, 50.51 at 38°C and 20.56 at 28°C).

HAWK et al. (1974) examined the effect of genotype and environment on fertility. They used two different populations (*black* and *pearl*) of *Tribolium castaneum* and a factorial combination of two levels of two environmental factors, temperature (28°C and 33°C) and lighting (lightness and darkness) for assessing the number of eggs laid and hatchability, and found a significant genotype-by-environment interaction for number of egg; *black* produced more eggs than *pearl* in continuous light regardless of temperature, *pearl* produced more eggs than *black* in continuous dark, but only at 33°C. Darkness had a positive effect on the number of eggs laid.

OROZCO (1976) investigated the correlated and direct response to selection and genotype by environment interaction in three environments, which were 28 °C, 33 °C and 38 °C defined as cold, optimum and hot environment, respectively. The quantitative trait was the number of eggs laid by a virgin female from the seventh to eleventh day after adult emergence carried out over 35 generations of selection in *Tribolium castaneum*. They reported that all lines reached a plateau for response after the twentieth generation. The best direct response to selection was obtained at 33 °C, and the lines at hot environment (38 °C) gave better response than the lines at cold environment (28 °C). Adaptation of lines from a hot environment was good when moved to a cold environment, while the lines from a cold environment adapted poorly to any change in environment, even to the same environment. They concluded that the smaller genotypic correlation between performances in different environments was the result of a large genotype by environment interaction.

BENYI and GALL (1978) investigated the effect of genotype by environment interaction on growth and development in *Tribolium castaneum* in four combinations of two levels of two environmental factors; nutrition and temperature. The quantitative traits were 13-day larva weight, age at pupation and pupa weight of daughters. They reported significant genotype by environment interaction, i.e., heavier larva weight and faster development in the offspring raised with a steady diet than in the offspring raised with a poor diet, and heavier pupa weight was observed in the offspring with a poor diet. The poor diet extended the developmental time and decreased body weight.

RICH et al. (1979) examined the differences in gene frequency at the autosomal black 'b' locus in four populations of *Tribolium*. Each population contained 10, 20, 50, or 100 insects per generation. Also, there were three replicates of each population. All populations were kept at 33 °C and 70% relative humidity and fed a diet of 95% whole-wheat flour with 5% dried brewer's yeast. They reported that genetic drift was smaller in the large populations than in the small populations. They concluded that some forces other than random drift influenced change in gene frequencies.

BENYI and GALL (1981) found significant genotype by nutrition interaction on reproductive performance in *Tribolium* from an experiment in which three different lines were used; two of which had been developed for small and large 21-day pupa weight and the third one was a cross between the two lines. They fed the populations with four combinations of two levels of nutrition before and after pupation, and reported that while a poor diet decreased the adult weight before pupation and decreased the number of eggs after pupation, a good diet increased the number of eggs and shortened the time to reach sexual maturity after pupation.

CARABANO et al. (1990) investigated the interaction between genotype and environment using Holstein data obtained from three states: California, New York and Wisconsin. Traits of interest were milk and fat yield. They found that the genetic correlation between milk yield in any pair of states was greater than .90; the correlation for fat yield was also .90. They concluded that there was no significant genotype by environment interaction, and that the ranking of bulls according to performance of their daughters in different environments was not changed significantly.

STANTON et al. (1991) used Holstein cows in the United States, Mexico, Puerto Rico and Colombia to examine the interaction between genotype and environment. They grouped the United Stated as the first environment (US) and the other three countries as a second environment (LA). They found that the genetic correlation between the same trait (milk yield) in different environments, LA and US was .91, this estimate was .78 between US and Colombia, and 0.90 between US and Mexico. They suggested that in their study the differences between the ranking of bulls in LA and US were not significantly different.

Researchers have also conducted several experiments to determine the best possible environment to apply selection methods for particular traits. Table 2 summarizes environmental settings that have been reported in the literature to obtain optimum response to selection. HAMMOND (1947); FRIARS et al. (1971) and MARKS (1980) reported that animals should be selected in the environmental conditions that make them express their full potential for a trait of interest. FALCONER (1960) concluded that selection in an adverse environment should be preferred if selected animals are intended to be used in various environments. On the other hand, YAMADA and BELL (1969) and GEARHEART and GOODWILL (1990) recommended that animals should be selected in the environment in which they are to live.

Table 2. Environmental settings reported in the literature to give optimum response to selection.

References	Trait	Experiment and suggested selection environment.
Falconer, 1960	Weight at 3 wks and 6 wks	Mice, High plane of nutrition: 56.8% Carbohydrate, 18.5% Protein, 4.5% fat, 12.9% water, 7.3% ash Low plane of nutrition: above diet diluted with 50% indigestible fiber in the form of ground oat husks. **Selection environment**: "if good performance under a variety of conditions is desired, then selection should be made under the conditions least favorable to the desired expression of the character"
Friars et. al., 1971	Larval weight Offspring number	Tribolium castaneum, Wet: 28°C and 75 % RH Dry: 28°C and 50% RH **Selection environment**: Optimum environment for selection regardless of environment in which the selected animals are to be living.
Gearheart and Goodwill, 1990	High and Low first day pupa weight	Tribolium castaneum (Purdue black foundation stock) Wet: 80% RH, Dry: 40% RH, and Alternating, with 31°C and 95% whole wheat flour and 5% dried yeast for all populations. **Selection environment**: "Individuals should be selected in the environment in which they are to perform."
Hammond, 1947	Survey paper	Survey paper **Selection environment**: "Character must be best selected under environmental conditions which favor its full expression"
Marks, 1980	High 3-week & 4-week Body weight	Quail, 28% protein and 20% protein **Selection environment**: Optimum environment for selection regardless of environment in which the selected animals are to be living.
Yamada and Bell, 1969	13th day larva weight	Tribolium castaneum, Diet1: 10% Dried yeast plus 5% corn oil Diet2: Contained neither (flour alone) All populations at 33°C and 70% RH **Selection Environment**: The environment where the selected animals are to perform.

Correlated Response

Selection for one character can cause a correlated response on another character. Reproductive success, such as, litter size, fertility, sterility, ovulation rate, etc. as a correlated trait to measurements of growth continues to interest scientists. Magnitude and direction of correlated response depends on genetic and environmental correlations between the selected and unselected characters, and the genetic part is due to pleiotropy (FALCONER and MACKAY 1996).

Table 3 summarizes several studies that have reported the relationship between growth and reproductive traits across many species when there was selection for a growth trait. In a review paper on laboratory animals, ROBERTS (1979) stated that there is a negative correlation between growth and reproductive traits, but it is partly due to physiological problems associated with fattening animals. WILSON et al. (1971) performed a long term selection experiment for large or small body weight in mice. They reported genetic correlations by pooling information in 10-generation intervals; -0.21, -0.46, -0.46, -0.47, -0.36, -0.33, -0.47, and -0.37, for the first, second, ..., and eighth interval, respectively for selection for large body weight, and –0.05, -0.35, -0.47, -0.38, -0.31, -0.26, -0.37, and –0.27, for the first, second, ..., and eight interval, respectively for selection for small body size. BERGER (1977) applied mass selection for large pupa weight for 16 generations in *Tribolium castaneum*. He reported a negative correlation of –0.43 between pupa weight and family size, which was defined as the number of pupa produced by a female insect. SOLIMAN (1972) investigated the correlated response of productivity to natural selection using *Tribolium* at constant environmental conditions of 33°C with 70% RH and a diet of 95% wheat flour with 5% dried yeast. He found a significant effect of developmental time

Table 3. Overview of correlated traits appearing in studies for different species.

Reference	Species	Correlated trait (Reproductive trait)	Primary trait (Growth trait)	Relationship
Fowler and Edwards, 1960	Mice	Egg number (E)	Small body weight (W)	$b_{P(E.on.W)}$=0.49 ± 0.14
Rahnefeld et. al., 1966	Mice	Litter size	Post weaning gain	r_g= 0.89
Land, 1970	Mouse	Ovulation rate	Body weight	r_g=0.40, r_p = 0.40
Bradford, 1971	Mice	Litter size (LS)	Body weight	No significant response in LS
Wilson et. al., 1971	Mice	Litter size at birth	Body weight at 60d	-0.21 <= r_g <= -0.47
		Litter size at 60d	Body weight at 60d	-0.05 <= r_g <= -0.47 in 10 generations interval for 84 generations of selection
Legault, 1971	Pigs	Litter size	Average daily gain	r_g = -0.08
Hanrahan and Eisen, 1974	Mice	Litter size	Post-weaning gain	r_g = 0.58
Morris, 1975	Pigs	Litter size at birth and 3 weeks	Daily gain	r_g = 0.06 in L. White breed r_g = 0.44 in Landrace breed
Garnett and Rafnefeld, 1976	Swine	Litter size (LS)	Post-weaning ADG	No response in LS
		Gestation length (GL)	Post-weaning ADG	Negative response in GL
Berger, 1977	*Tribolium*	No of pupae 19 d	Pupa weight	r_g = -0.43
Eisen, 1978	Mice	Litter size	Body weight	r_g = 0.52
Roberts, 1979**	Mouse	Fertility	Body weight	Negative correlation
Durrant et. al., 1980	Mice	Litter size (LS)	Body weight	Positive response in LS
Rios et. al., 1986	Mice	No of fetus (NF)	Post-weaning gain	Positive response in NF
Campo and de la Blance, 1988	*Tribolium*	No of pupae 21 d	Pupa weight	r_p = 0.17, r_g = 0.13
Berger and Lin, 1992	*Tribolium*	No of pupae 19 d	Pupa weight	r_g = -0.35
Bonczek et. al., 1992	Jersey cattle	Interval from calving to first breeding	Milk yield	Unfavorable positive

**Review paper on laboratory animals.

(pupation time and adult emergence time) on the productivity (number of pupa and number of larvae at 13-day). The longer pupation time and longer adult emergence time decreased the total number of larvae at 13-day and the total number of pupa.

BONCZEK et al. (1992) found that reproductive ability was adversely affected by selection on milk yield in Jersey cattle. They found that interval from calving to first breeding is larger in high milk cows than low milk cows; a positive correlation is unfavorable in this case.

Some studies have reported positive correlations between a reproductive trait and body weight. MORRIS (1975) analyzed data from Large White and Landrace pig herds in Great Britain. He reported a genetic correlation of 0.06 between daily gain and litter size. RIOS et al. (1986) reported a positive correlation between litter size and female body weight from a selection experiment in rats, selected for large and small 3 to 9 week weight gain for 34 generations. RAHNEFELD et al. (1966) reported a positive correlation of 0.89 between post weaning growth and litter size following 30 generations of selection in mice. EISEN (1978) applied 12 generations of individual selection in four lines of mice for increased litter size, increased 6-week body weight, increased litter size and decreased 6-week body weight, and decreased litter size and increased 6-week body weight. He reported realized genetic correlations between litter size and 6-week body weight of 0.52 ± 0.10 and 0.52 ± 0.13. FOWLER and EDWARDS (1960) investigated the effect of selection for large or small body size on fertility in two strains of mice; strain N and strain C. They reported that the regression coefficient of egg number on body size was 0.49 ± 0.14 in strain C selected for small body size. LAND (1970) examined genetic relationships between ovulation rate and body size in the mouse (strain Q). Phenotypic and genetic correlation between ovulation rate and body

weight were estimated to be 0.40 and 0.40, respectively. HANRAHAN and EISEN (1974) examined genetic variation in litter size and 12-day weight in mice and their relationship with post weaning growth. They reported a genetic correlation of 0.58 between litter size and post weaning gain.

However, others, i.e., CAMPO and DE LA BLANCE (1988) in *Tribolium castaneum*, and GARNETT and RAHNEFELD (1976) and BRADFORD (1971) in pigs have reported no significant correlation between these two types of traits.

REFERENCES

BENYI, K.; GALL, G. A. E., 1978: Genotype -environment interaction effects on growth and development in *Tribolium castaneum*. The J. Heredity. **69**: 71-76.

BENYI, K.; GALL, G. A. E., 1981: Genotype-environment interaction effects on reproductive performance in *Tribolium castaneum*. Theor. Appl. Genet. **59**: 123-128.

BERGER, P. J., 1977: Multiple-trait selection experiments: Current status, problem areas and experimental approaches. *In*: Int. Conf. Quant. Genet. pp. 191-204. Iowa State Univ. Press, Ames.

BERGER, P. J.; LIN, E. C., 1992: Comparison between estimates of genetic parameters from univariate and multivariate animal models. NCR-21 Quantitative Genetic Annual Meeting. Clemson University, Clemson, SC. Mimeo. pp: 6.

BONCZEK, R. R.; RICHARDSON D. O.; MOORE, E. D.; MILLER, R. H.; OWEN, J. R.;

BELL, B. R., 1992: Correlated responses in reproduction accompanying selection for milk yield in Jersey. J. Dairy Sci. **75**: 1154-1160.

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

BROWN, C. J.; GACULA, M., 1962: Genotype environment interaction in post-weaning gain of beef cattle. J. Anim. Sci. **21**: 924-926.

CAMPO, J. L.; DE LA BLANCE, A. S., 1988: Experimental comparison of selection methods to improve a non-linear trait in *Tribolium*. Theor. Appl. Genet. **75**: 569-574.

CARABANO, M. J.; WADE, K. M.; VAN VLECK, L. D., 1990: Genotype by environment interaction for milk and fat production across regions of the United States. J. Dairy Sci. **73**: 173-180.

CARTWRIGHT, T. C., 1955: Response of beef cattle to high amblent temperatures. J. Anim. Sci. **14**: 350-362.

DURRANT, B. S.; EISEN, E. J.; ULBERG, L. C., 1980: Ovulation Rate, embryo survival and ovarian sensitivity to gonadotrophins in mice selected for litter size and body weight. J. Reprod. Fert. **59**: 329-339.

EISEN, E. J., 1978: Single-trait and antagonistic index selection for litter size and body weight in mice. Genetics. **88**: 781-811.

FALCONER, D. S., 1960: Selection of mice for growth on high low planes of nutrition. Gen. Res. **1**: 91-113.

FALCONER, D. S.; MACKAY, T. F. C., 1996: Introduction to quantitative genetics. (4th Ed.). Logman. Malaysia.

FOWLER, R. E.; EDWARDS, R. G., 1960: The fertility of mice selected for large or small body

size. Genet. Res. Camb. 1: 393-407.

FRIARS, G. W.; NAYAK, B. N.; JUL, P. Y.; RAKTOE, B. L., 1971: An investigation of genotype x environment interaction in relation to selection experiment in *Tribolium castaneum*. Can. J. Genet. Cytol. 13: 144-154.

GARNETT, I.; RAHNEFELD, G. W., 1976: Mass selection for post-weaning growth in swine. V. Correlated response of reproductive traits and pre-weaning growth. Can. J. Anim. Sci. 56: 791-801.

GEARHEART, W. W.; GOODWILL, R. E., 1990: Divergent selection for pupal weight *of Tribolium castaneum* in optimum and adverse environments. J. Anim. Breed. Genet. 107: 249-253.

HAMMOND, J., 1947: Animal breeding in relation to nutrition and environmental conditions. Biol. Rev. 22: 195-213.

HANRAHAN, J. P.; 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.

HARDIN, R. T.; ROGLER, J. C.; BELL, A. E., 1967: Genetic and environmental interaction in growth of *Tribolium castaneum*. Can. J. Zool. 45: 139-144.

HAWK, J. A.; COLAIANNE, J. J.; BELL, A. E., 1974: Genetic, photic and temperature effects on the fecundity of *Tribolium*. Ecology. 55: 910-912.

KENNEDY, B.W. 1981: Bias and mean square error from ignoring genetic groups in mixed model sire evaluation. J. Dairy Sci. 64: 689-697.

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

LEGAULT, C., 1971: Relationship between fattening and carcass performance and litter performance in pigs. Ann. Genet. Sel. Anim. **3**: 153-160.

LYNCH, M.; WALSH B., 1997: Genetics and Analysis of Quantitative Traits. pp. 644-647. Sinauer Associates, Inc. Sunderland, Massachusetts.

MAO, I.L.; BURNSIDE E. B., 1969: Sire by herd environment interaction for milk production. J. Dairy Sci. **52**(7): 1055-1062.

MARKS, H. L., 1980: Feed efficiency of selected and nonselected Japanese Quail lines. Poultry Science. **59**: 6-10.

MORRIS, C. A., 1975: Genetic relationships of reproduction with growth and with carcass traits in British pigs. Anim. Prod. **20**(1): 31-44.

MORRIS, C. .A.; BAKER, R. L.; HICKEY, S. M.; JOHNSON, D. L.; CULLEN, N. G.; WILSON, J. A., 1993: Evidence of genotype by environment interaction for reproductive and maternal traits in beef cattle. Anim. Prod. **56**: 69-83.

NOTTER, D.R.; TIER, B.; MEYER, K., 1992: Sire x Herd interactions for weaning weight in beef cattle. J. Anim. Sci. **70**: 2359-2365.

OROZCO, F., 1976: A dynamic study of genotype-environment interaction with egg laying of *Tribolium castaneum*. Heredity. **37**(2): 157-171.

OROZCO, F.; BELL, A. E., 1974: A genetic study of egg laying of *Tribolium* in optimal and stress environments. Can. J. Genet. Cytol. **16**: 49-60.

PATTERSON, D. L.; FRIARS, G. W.; MCMILLAN, I., 1983: Effects of parental age and sampling method on response to index selection in *Tribolium castaneum*. Can. J. Genet. Cytol. **25**: 47-52.

POLLAK, E. J.; QUAAS, R. L., 1983: Definition of group effects in sire evaluation models. J.

Dairy Sci. **66**: 1503-1509.

QUAAS, R.L.; POLLAK, E. J., 1981: Modified equations for sire models with groups. J. Dairy Sci. **64**: 1868-1872.

RAHNEFELD, G. W.; COMSTOCK, R. E.; SINGH, M.; NAPUKET, S. R., 1966: Genetic correlation between growth rate and litter size in mice. Genetics. **54**: 1423-1429.

RICH, S.S.; BELL, A. E.; WILSON, S. P., 1979: Genetic drift in small populations of *Tribolium*. Evolution. **33**(2): 579-584.

RIOS, J. G.; NIELSEN, M. K.; DICKERSON, G. E., 1986: Selection for postweaning gain in rats: II. Correlated response in reproductive performance. J. Anim Sci. **63**: 46-53.

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

ROBERTSON, A.; O'CONNOR, L. K.; EDWARDS, J., 1960: Progeny testing dairy bulls at different management levels. Anim. Prod. **2**: 141-152.

ROBINSON, G. K., 1986: Group effects and computing strategies for models for estimating breeding values. J. Dairy Sci. **69**: 3106-3111.

ROLLINS, W. C.; CARROLL, F. D.; ITTNER, N. R., 1964: Comparison of the performance of ¾ Hereford- ¼ Brahman calves with Hereford calves in a variable climate. J. Agric. Sci. **62**: 83-88 in ABA 32:311.

SOLIMAN, M.H., 1972: Correlated response to natural selection in laboratory populations of *Tribolium castaneum*. Can. J. Genet. Cytol. **14**: 971-978.

STANTON, T. L.; BLAKE, R. W.; QUASS, R. L.; VAN VLECK, L. D.; CARABANO, M. J., 1991: Genotype by environment interaction for Holstein milk yield in Colombia, Mexico,

and Puerto Rico. J. Dairy Sci. **74**: 1700-1714.

TESS, M. W.; KRESS, D. D.; BURFENING, P. J.; FRIEDRICH, R. L., 1979: Sire by environment interactions in Simmental-sired cows. J. Anim. Sci. **49**(4): 964-971.

THOMAS, J. N.; BRANTON, C.; FARTHING, B. R., 1968: Genotype-environment interaction for productive traits in dairy cattle. J. Dairy Sci. **51**: 958 (abstr.)

TONG, A. K. W.; KENNEDY, B. W.; MOXLEY, J. E., 1980: Potential error in sire evaluation from regional genetic differences. J. Dairy Sci. **63**: 627-633.

URICK, J.; FLOWER, A. E.; WILSON, F. S.; SHELBY, C. E., 1957: A genetic study in steer progeny groups during successive growth periods. J. Anim. Sci. **16**: 217-223.

VAN VLECK, L.D., 1963: Genotype and environment in sire evaluation. J. Dairy Sci. **46**: 983-987.

WADE, M.J., 1990: Genotype-environment interaction for climate and competition in a natural population of flour beetles, *Tribolium castaneum*. Evolution. **44**(8): 2004-2011.

WESTELL, R.A.; VAN VLECK, L. D., 1987: Simultaneous genetic evaluation of sires and cows for a large population of dairy cattle. J. Dairy Sci. **70**: 1006-1017.

WESTELL, R.A.; QUAAS, R. L.; VAN VLECK, L. D., 1988: Genetics group in an animal model. J. Dairy Sci. **71**: 1310-1318.

WIGGANS, G.R.; MISZTAL, I.; VAN VLECK, L. D., 1988: Animal model evaluation of Ayrshire milk yield with all lactations, herd-sire interaction, and group based on unknown parents. J. Dairy Sci. **71**: 1319-1329.

WILSON, S. P.; GOODALE, H. D.; KYLE, W. H.; GODFREY, E. F., 1971: Long term selection for body weight in mice. The J. Heredity. **62**: 228-234.

WOODWARD, R. R.; CLARK, R. T., 1950: The repeatability of performance of several Hereford sires as measured by progeny records. J. Anim. Sci. 9: 588-592.

YAMADA, Y.; BELL, A. E., 1969: Selection for larval growth and in *Tribolium* under two levels of nutrition. Genet. Res. Camb. 13: 175-195.

Department of Animal Science, Iowa State University, Ames, Iowa, USA

CHAPTER 2. RESPONSE TO SELECTION FOR INCREASED PUPA WEIGHT IN TRIBOLIUM CASTANEUM IN FOUR ENVIRONMENTS[1]

A paper to be submitted to Journal of Animal Breeding and Genetics

By S. KONCAGUL and P. J. BERGER

Summary

Selection for a single quantitative trait, increased pupa weight in *Tribolium castaneum*, was applied over 23 generations to enhance growth and development in four different environments. This research describes a selection and mating scheme frequently occurring in commercial populations of livestock where there is an exchange of elite germplasm to enhance performance in other populations. Main objectives of the present study were to estimate the response to selection for increased pupa weight under different environmental settings, to estimate variance components and parameters across environments for the whole experiment, and to determine if there is a genotype by environment interaction on pupa weight.

Diet and relative humidity were combined in a two by two factorial design to create environmental diversity among four resource populations (lines), 67% and 80% relative humidity (RH), low protein (100% whole wheat flour) and high protein (95% whole wheat flour plus 5% dried yeast.) Every generation, fifteen males and fifty-four females with

---

[1]Journal Paper Number J- of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project number 3538, and supported by Hatch Act and State of Iowa funds.

highest pupa weight were selected within each line to produce the next generation. The best-ranked male from each line was mated to three females in every line. Other elite males were mated to elite females within their lines.

The data were analyzed by using a derivative-free restricted maximum likelihood (MTDFREML) procedure with a univariate animal model for estimating response to selection and parameters.

Sufficient protein in the diet rather than a deficiency of protein was a major contributing influence to phenotypic, genetic, and environmental changes across generations. Relative humidity created only minor changes in mean pupa weight between lines on a similar diet.

Additive genetic variance remained relatively constant throughout the experiment. Total phenotypic variance increased across generations. Changes in phenotypic variance were attributed to changes in common environmental variance and error variance throughout the duration of the experiment. After 23 generations of selection, heritability (h^2) of pupa weight was less than the estimate in the base population, 0.21 ± 0.02, and 0.36 ± 0.02, respectively. There was no evidence of any genotype by environment interaction.

Key words: animal model, genotype by environment interaction, pupa weight, response, selection, *Tribolium castaneum*.

Introduction

The development of genetic resource populations can be expensive. Furthermore, an extensive commitment of time and resources is required to reach the desired level of performance for national needs in food production. This study seeks to model the selection

and mating scheme frequently occurring in commercial populations of livestock where there is an exchange of elite germplasm to enhance the rate of performance in other populations. For example, through artificial insemination, semen of elite males from one resource population can be exported to other targeted populations, and used for mating to females born and raised under different environmental conditions.

Environment and genotype have measurable effects on growth and development. Pupa weight, as a measurement for growth, has frequently been emphasized in *Tribolium castaneum*. Variability in response to selection for pupa weight has been reported by a number of researchers from different selection programs. ENFIELD et al. (1966) conducted an experiment to investigate response to selection for increased pupa weight by applying within family selection. KRESS et al. (1971) applied mass selection for increased pupa weight. MEYER and ENFIELD (1975) performed two-way selection at three selection intensities for 21 d. pupa weights. KATZI and ENFIELD (1977) compared three different selection systems: mass selection, cycles of three generations within line selection followed by a one generation of selection among lines, and cycles of seven generations of selection within line followed by a one generation of selection among lines. BERGER (1977) and LIN (1997) compared responses from four lines, created by mass selection for pupa weight, mass selection for family size, index selection, and control line. MINVIELLE and GALL (1980) compared natural selection and opposing artificial selection models for pupa weight.

Researchers have also conducted experiments by using *Tribolium castaneum* to investigate the effect of environmental differences on growth traits, such as, pupa weight, larva weight, adult weight, development time. HARDIN et al. (1967) reported a significant genotype by environment interaction for 14 d. larva weights. YAMADA and BELL (1969)

reported that a high protein diet increased larval weight compared with a low protein diet. Heavier larvae and faster development were achieved for the offspring on a high protein diet. BENYI and GALL (1981) found that a high protein supplemented diet increased adult weight. In comparison, BENYI and GALL (1978) reported that a low protein diet extended the development time and decreased pupa weight. They also reported a significant line by environment interaction for pupa weight. VIA and CORNER (1995) reported a significant genotype by environment interaction for pupa weight.

The nature and cause for different responses for pupa weight on different diets has not been clearly explained in the literature. Moreover, selection experiments were designed in such a way that migration among selection lines was not permitted. There is still a need to investigate how pupa weight behaves on different diets when there is a constant exchange of elite germplasm among selection lines.

The objectives of this paper are to estimate response to selection for pupa weight in four different environmental settings, to estimate the variance components and parameters for the base population and for the data combined over all lines, and to determine if a genotype by environment interaction exists. Modern statistical techniques are used to analyze the data from a population under selection for 23 generations for heavier pupa weight. Family size was also recorded as an interesting correlated trait indicative of correlated responses in reproductive success. These correlated responses to selection will be discussed in more detail in a subsequent chapter.

Materials and methods

Experimental design

An overview of the design of the experiment is given in Fig. 1. Table 1 supplements Fig. 1 by giving a description of family structure and selection intensity in each generation. The base population was developed by randomly sampling adult males and females from a large random mating population. Historically, this population traces back to the Purdue '+' Foundation wild-type population originally supplied by Purdue University's Population Genetics Institute in 1966. This heterogeneous population had reproduced without selection since 1954 (BELL and BURRIS 1973).

To obtain enough *Tribolium castaneum* of the same age, randomly chosen male-female pairs were held in cardboard-capped 20 ml glass bottles containing 0.4 gm of 5% yeast-enriched whole wheat flour, which had been sifted through a 35 mesh sieve to remove the bran. Yeast was used as a nutritional supplement to provide extra protein (40 to 60% by weight), ash (6 to 9% by weight) and some residual carbohydrates as a source of energy.

Every pupa pair was held at 32.2°C in a 24 h dark cycle in Percival growth chambers. After 19 days, pupae were paired and bred again; after two generations of random mating, 650 pairs were available to be used as a base population for this selection study.

Insects in the base population were randomly assigned to four environments (lines): line 1 (L1), 67% relative humidity (RH) and 5% yeast-enriched whole wheat flour diet; line 2 (L2), 67% RH with flour alone; line 3 (L3), 80% RH and 5% yeast-enriched whole wheat flour diet; and line 4 (L4), 80% RH with flour alone.

	Line 1		Line 2		Line 3		Line 4	
Family	Sire	Dam	Sire	Dam	Sire	Dam	Sire	Dam
	within line mating							
1	$L1^*_1$	x $3L1_f$	$L2_1$	x $3L2_f$	$L3_1$	x $3L3_f$	$L4_1$	x $3L4_f$
2	$L1_2$	x $3L1_f$	$L2_2$	x $3L2_f$	$L3_2$	x $3L3_f$	$L4_2$	x $3L4_f$
	.		.		.		.	
	.		.		.		.	
	.		.		.		.	
14	$L1_{14}$	x $3L1_f$	$L2_{14}$	x $3L2_f$	$L3_{14}$	x $3L3_f$	$L4_{14}$	x $3L4_f$
	across line mating							
15	$L1_{15}$	x $3L1_f$	$L1_{15}$	x $3L2_f$	$L1_{15}$	x $3L3_f$	$L1_{15}$	x $3L4_f$
16	$L2_{15}$	x $3L1_f$	$L2_{15}$	x $3L2_f$	$L2_{15}$	x $3L3_f$	$L2_{15}$	x $3L4_f$
17	$L3_{15}$	x $3L1_f$	$L3_{15}$	x $3L2_f$	$L3_{15}$	x $3L3_f$	$L3_{15}$	x $3L4_f$
18	$L4_{15}$	x $3L1_f$	$L4_{15}$	x $3L2_f$	$L4_{15}$	x $3L3_f$	$L4_{15}$	x $3L4_f$
Environmental Conditions	Low Humidity -high protein		Low Humidity -low protein		High Humidity -high protein		High Humidity -low protein	

* the numbers in the sires' and dams' column stand for lines of birth for sires and dams.

Fig. 1. Mating design within and between lines selected for pupa weight.

Table 1. Population size and structure.

Item	Number per line-generation		
	Males	Females	Total
Pupa (N)	162	162	324
Pupa per full-sib family weighed at 19-day (N)	3	3	6
Full-sib family (N)	....	....	54
Selected (N)	15	54	....
Fraction selected (%)	9.26	33.33	....
Intensity (i)	1.7953	1.0903	....
Effective population size (Ne)	....	....	47
Actual inbreeding per generation (%)	....	....	3.5
Expected inbreeding per generation (%)	....	....	1.06

Traits measured

Pupa weight (PWT) and family size (FST) at 19 d., or number of offspring per family, were measured and recorded every generation. Pupa weight, considered to be a growth trait, was measured on both males and females. Family size was considered to be a trait of the female insects producing families and was recorded only on female insects. Family size was determined by counting the number of larvae, pupae and adult offspring on the 19th day after mating. Weights were taken after removing flour media from the contents of each glass bottle containing a full-sib family by using a vacuum pump and a number 35 mesh sieve. Characteristics of traits for the base population are given in Table 2.

Table 2. Performance of insects in base population

Trait		N	Mean	S.D.	Min.	Max.
Pupa weight (μg)	Males	647	2,802.52	209.87	2,041.00	3,470.00
	Females	648	2,908.97	244.75	1,712.00	3,616.00
Family size at 19-day						
	Total (N)	198	25.88	7.06	2	38
	Larvae (N)	115	8.95	7.53	1	29
	Pupae (N)	198	20.57	8.78	1	37
Females with larvae (%)		58	33.3	25.65	2.7	96.7

198 females have offspring
115 of 198 females = 58% have both pupae and larvae

Selection and matings

Selection was conducted by choosing the highest-ranking males or females based on pupa weight adjusted for environmental effects within generation. Expressing every pupa weight as a deviation from each generation-line-set-sex mean made these adjustments.

Every generation, 15 males and 54 females having the highest pupa weights were selected as parents of the next generation within each line. Each one of the 15 males mated with three females within their line. The best-ranked male from each line was also mated with three females in each one of the other three lines. This mating scheme provided a comparison among sires with progeny in different targeted environments (i.e., comparison of best male in each generation with the best males from other reference lines). Females always remained in the same line as their female ancestors. Matings were made at an age of 33 d. Matings were distributed equally across three consecutive days to distribute the work. Each male was mated with one female on each day within a generation. Each mating day was subsequently referred to as a set that contained a total of eighteen full-sib families. And,

each line contained three sets. Thus, there were 54 full-sib families in total within a line. Three males and three females were sampled at random from each family as pupae at 19 d., and their records were used in the analyses.

Matings among full- and half-sibs were avoided to minimize inbreeding. Computer software was specifically designed to randomize the assignment of selected males to females and to distribute the males across lines. This mating and selection design was repeated for 23 generations. Fitness gradually declined in all lines after generation six to the point where there were insufficient offspring in all families to maintain selection after generation 23.

Statistical analysis

A Multi-Trait Derivative-Free Restricted Maximum Likelihood (MTDFREML) procedure with an animal model was used to obtain estimates of variance components and parameters for PWT (BOLDMAN et al. 1995). Sampling variances and standard error of parameter estimates were obtained by using the "average information" procedure described by DODENHOFF et al. (1998). Absence of a control population was an intentional part of the experimental design. This enabled more resources to be allocated to each of the four environmental treatments.

Variance components and parameters were estimated for the data in the base population as well as for the data combined over all lines. Combined data also included the base population data. In this way, the additive genetic relationship matrix was complete, and all data on which the selection was based were included in the analysis. The Restricted Maximum Likelihood (REML) procedure can be used to account for bias due to selection if the base population consists of unselected, noninbred individuals, and phenotypic records for

all selected and unselected individuals are included in the analysis (SORENSEN and KENNEDY 1984; MEYER and THOMPSON 1984; GIANOLA and FERNANDO 1986; GIANOLA et. al. 1988; FERNANDO and GIANOLA 1990; MEYER 1991). Selection can cause a reduction in estimates of additive genetic variance due to gametic phase disequilibria (BULMER 1971). However, use of the complete additive genetic relationship matrix adjusts for the effect of gametic phase disequilibria by accounting for the flow of genes from one generation to others (SORENSEN and KENNEDY 1984; SORENSON and KENNEDY, 1986; VAN DER WERF and DE BOER, 1990).

The model for estimating variance components and parameters was:

$$pwt_{ijkl} = gls_i + sex_k + anim_l + pe_{ij} + e_{ijkl}$$

where, pwt_{ijkl} is the pupa weight of the l^{th} insect of the k^{th} sex in the ij^{th} family in the i^{th} generation-line-set combination, gls_i is a fixed effect of the i^{th} generation-line-set combination, sex_k is a fixed effect of the k^{th} sex, $anim_{ijkl}$ is a direct random genetic effect of the $ijkl^{th}$ animal, pe_{ij} is an uncorrelated random effect of the ij^{th} family, or common environment, and e_{ijkl} is the random residual.

In matrix notation;

$$\mathbf{y} = \mathbf{X_1 b_1} + \mathbf{X_2 b_2} + \mathbf{Z_1 u_1} + \mathbf{Z_2 u_2} + \mathbf{e}$$

Expectations and variances of random effects in the equation were:

$$\mathbf{E(y) = X_1 b_1 + X_2 b_2,\ E(u) = E(e) = 0}$$

$$\mathbf{V(u_1) = A\sigma^2_{u1} \quad V(u_2) = Ipe\sigma^2_{u2} \quad V(e) = Ie\sigma^2_e}$$

$$\mathbf{Cov(u_1, u_2) = Cov(u_i, e) = 0}$$

where, **A** is the additive genetic relationship matrix among animals in the data; **Ipe** is an identity matrix with order equal to the number of families; and **Ie** is the identity matrix with order equal to the number of observations.

Preliminary analyses were used to determine if there was a significant sire by line (i.e. environment) interaction. First, the data were analyzed by using the method proposed by FALCONER (1952), where the same character is measured in two different environments and treated as two different traits. The genetic correlation between PWT in two different environments was then used as an indication of sire by line interaction. Because the estimate of genetic correlation was one we conclude that there was no interaction. Second, by incorporating a sire by line interaction effect directly in the model. The proportion of total variance due to sire by line interaction was less than 2%. Therefore, we concluded that sire by line interaction was an unnecessary extension of the model.

Rate of change (phenotypic trend) in mean PWT per generation for each line was calculated as the regression of mean phenotypic value on generation number. Environmental and genetic changes (environmental and genetic trends) per generation for each line were calculated by using estimates of fixed effects and the mean of predicted breeding values from MTDFREML. Environmental trend in each line was calculated from the generation-line-set solutions, adjusted for the effect of sex, regressed on generation number. Genetic trend in each line was calculated as the regression of mean breeding value per generation on generation number.

Results and discussion

Response to selection

Phenotypic means for each of the four lines across generations are given in Fig. 2. Apart from some variability in the first two generations of L2 and L4, changes in the means were relatively consistent across generations for all lines. Regression coefficients for the average phenotypic, genetic, and environmental changes per generation are given in Table 3. Selection increased the mean phenotypic values for PWT in all lines regardless of differences in environments. The rates of changes were larger in L1 and L3 on the high protein diet than those in L2 and L4 on the low protein diet. Trends were similar for lines on the same diet, but were significantly different ($P < .001$) between lines on different diets. Although parallel increases were observed in all lines from generation 4 to 16, it appears that the fluctuations in the first four generations of L2 and L4 might have caused the differences among the rates of changes. Insects on diets with extra protein supplements were consistently heavier than the insects on diet without extra protein. RH created only minor differences in mean PWT between lines on a similar diet. There was no indication of any interaction between diet and RH.

Mean phenotypic performance was effectively increased above the effects of environment over 23 generations due to selection. As a factor used to modify or create different target environments, diet (i.e., high versus low protein) had a larger effect on growth and development than two levels of humidity (i.e., 67 and 80% RH)

PWT has been extensively studied as a quantitative trait; therefore, there is a wealth of information in the literature to use for comparing responses to selection under different experimental settings. The design of this experiment provides a comparison for the type of

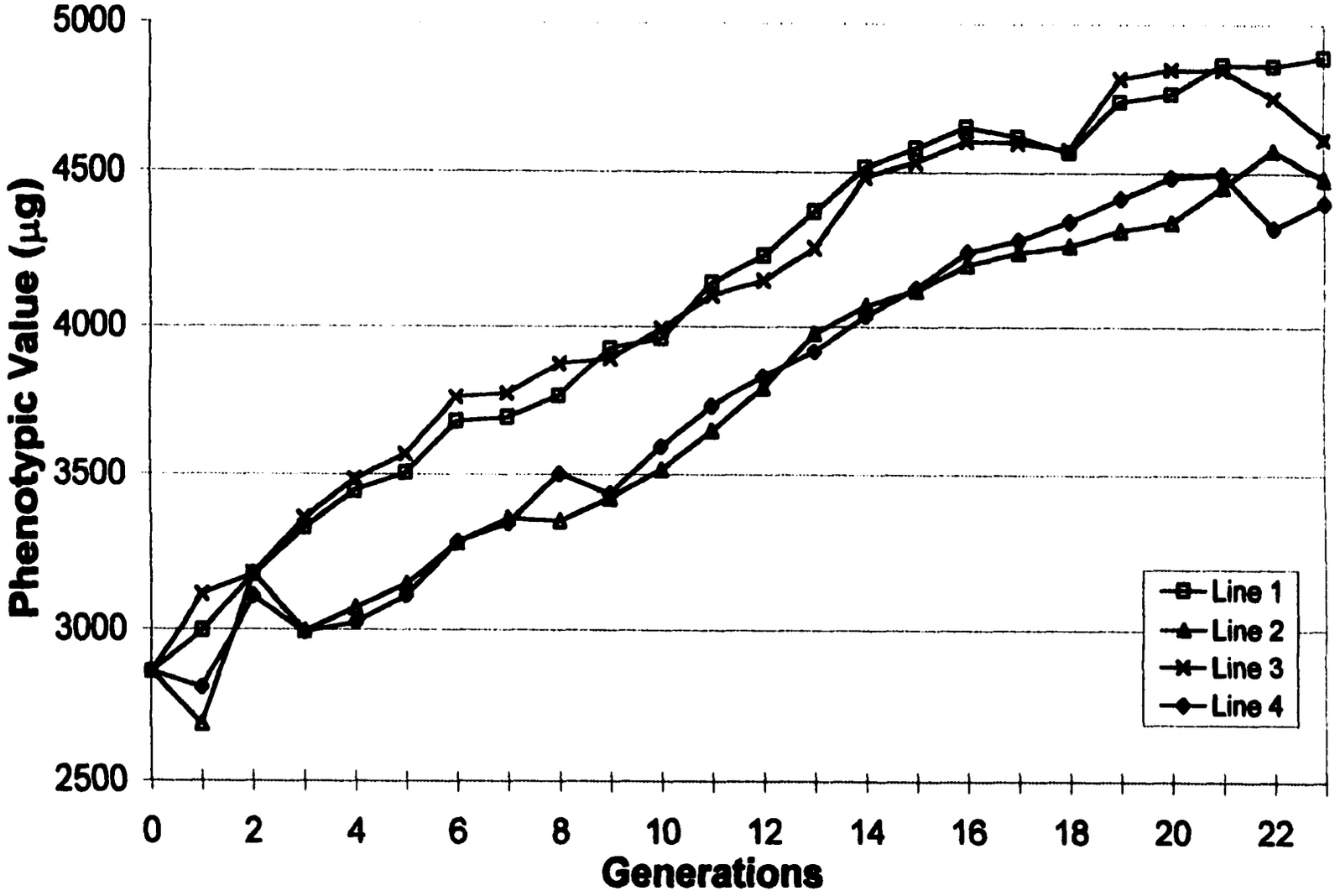

Fig. 2. Phenotypic trends for pupa weight (µg) in four lines under different environmental conditions: L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein, L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein.

Table 3. Response to selection for pupa weight (μg).

	ΔP/gen.[1]	ΔE/gen.[2]	ΔG/gen.[3]
Line 1	96.1 ± 2.8[a]	38.7 ± 2.9[a]	57.2 ± 0.4[a]
Line 2	70.5 ± 2.8[b]	16.6 ± 2.9[b]	54.0 ± 0.4[c]
Line 3	94.0 ± 2.8[a]	35.8 ± 2.9[a]	58.0 ± 0.4[a]
Line 4	71.3 ± 2.8[b]	15.8 ± 3.1[b]	55.1 ± 0.4[d]
Overall	82.6 ± 2.7	26.1 ± 3.0	56.2 ± 0.5

[1]ΔP/gen.= average change in phenotypic mean by generation
[2]ΔE/gen.= average change in environmental mean by generation
[3]ΔG/gen.= average change in mean breeding value by generation
[a,b] Different superscripts show that the regression coefficients are significantly different (P<0.01)
[c,d] (P<0.05)

responses that might be expected in ongoing research with field data in livestock. Some of the variability in responses between experiments reported in the literature can be explained by the type of selection -- e.g., phenotypic responses of 60.3 and 61.8 μg per generation for within family selection (ENFIELD et al., 1966) compared with the larger responses of 70.5 to 96.1 μg per generation for mass selection across four lines in this experiment. MEYER and ENFIELD (1975) reported responses of 70, 50, and 28 μg per generation for 10, 30, and 50% selection percentages, respectively. KATZI and ENFIELD (1977) reported responses of 9.8 to 22.7 μg per generation. Elsewhere, the highest estimates reported were 175 μg (BELL 1969), 55 μg (KRESS et al. 1971), 137 μg (BELL and MOORE 1972), 93 μg (MINVIELLE and GALL 1980).

The results in L3 are directly comparable with results reported by BERGER (1977) and LIN (1997). They both applied selection for increased PWT for 16 generations in one of the four lines in their experiment. Their selection intensity, population size and the level of diet are identical to those in L3 in our experiment, except that the relative humidity in their lines

was about 10% lower. They reported responses of 136 and 135 μg per generation, respectively.

The lines appeared to be approaching a response plateau in the last four generations. BELL and MOORE (1972) reported a response plateau between generation 15 and 21 in both two replicates in their experiment, but continued selection resulted in significant responses on later generations.

Evidence showing that there were changes in PWT attributable to environment is given in Fig. 3. That there was an environmental trend was unexpected due to the controlled environmental conditions maintained for the duration of the experiment. An increasing effect due to environment occurred despite an effort to maintain a constant diet and the use of environmental chambers to control temperature and humidity for growth and development.

Environmental trends were highest in L1 and L3, and lowest in L2 and L4 (Table 3). Differences between environmental trends were significant ($P < .01$) between lines on high and low protein diets across both levels of RH. This is only an approximate test of significance because successive observations are not independent. RH produced small but insignificant changes in environmental effects for the two levels of RH on the same diet. These results also show that nutritional ingredients of the diet have a larger nongenetic effect on growth than RH.

The average of predicted breeding values from the animal model are plotted against generation numbers in Fig. 4. Larger genetic changes ($P < 0.05$) per generation were achieved on the high protein diet than on the low protein diet (Table 3). Preliminary analyses failed to show a significant sire by environment interaction. Thus, the genetic effect of sires used across target environments was interpreted to be the same as the genetic effect of sires

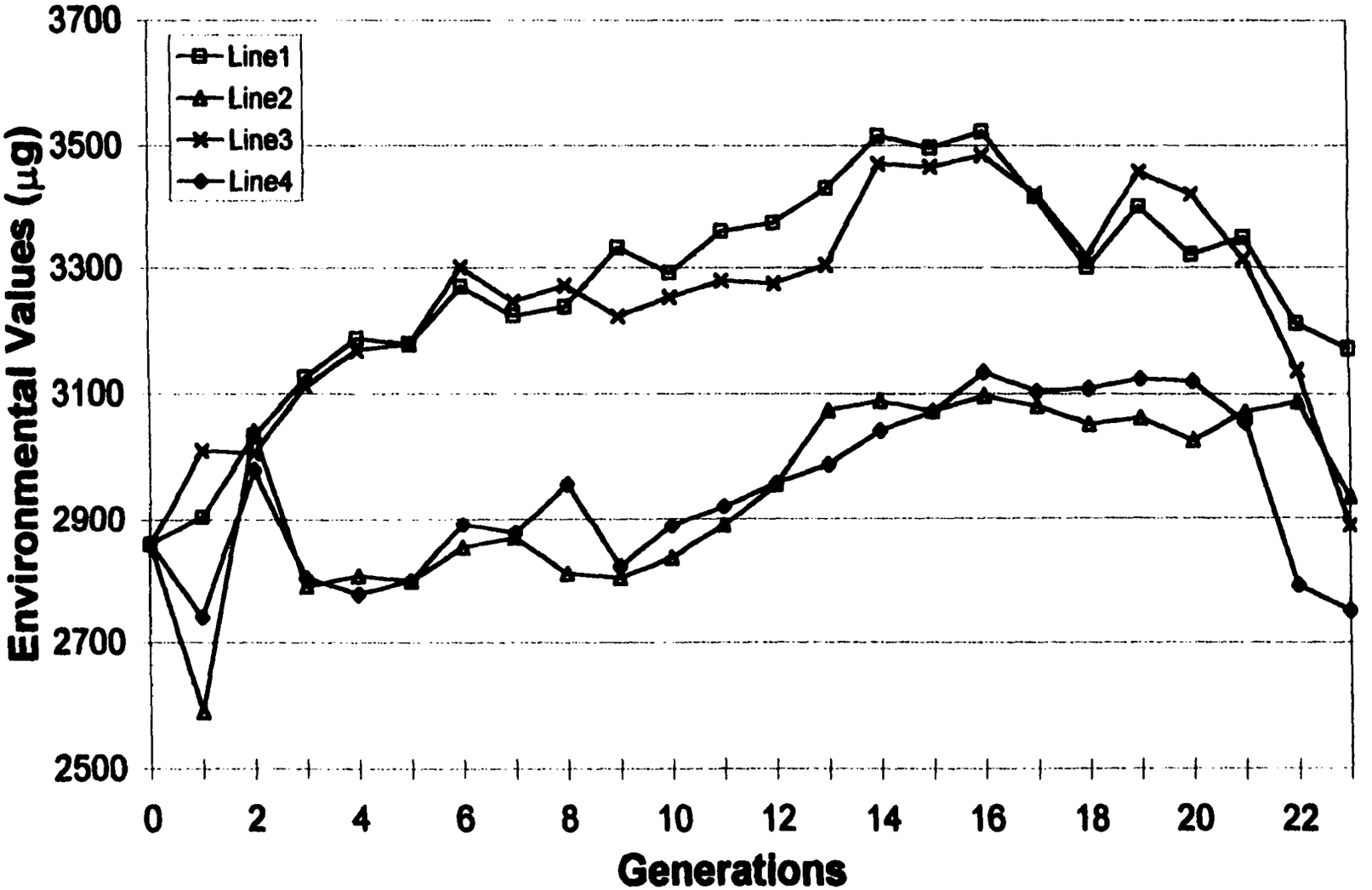

Fig. 3. Environmental trends for pupa weight (µg) in four lines under different environmental conditions: L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein, L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein.

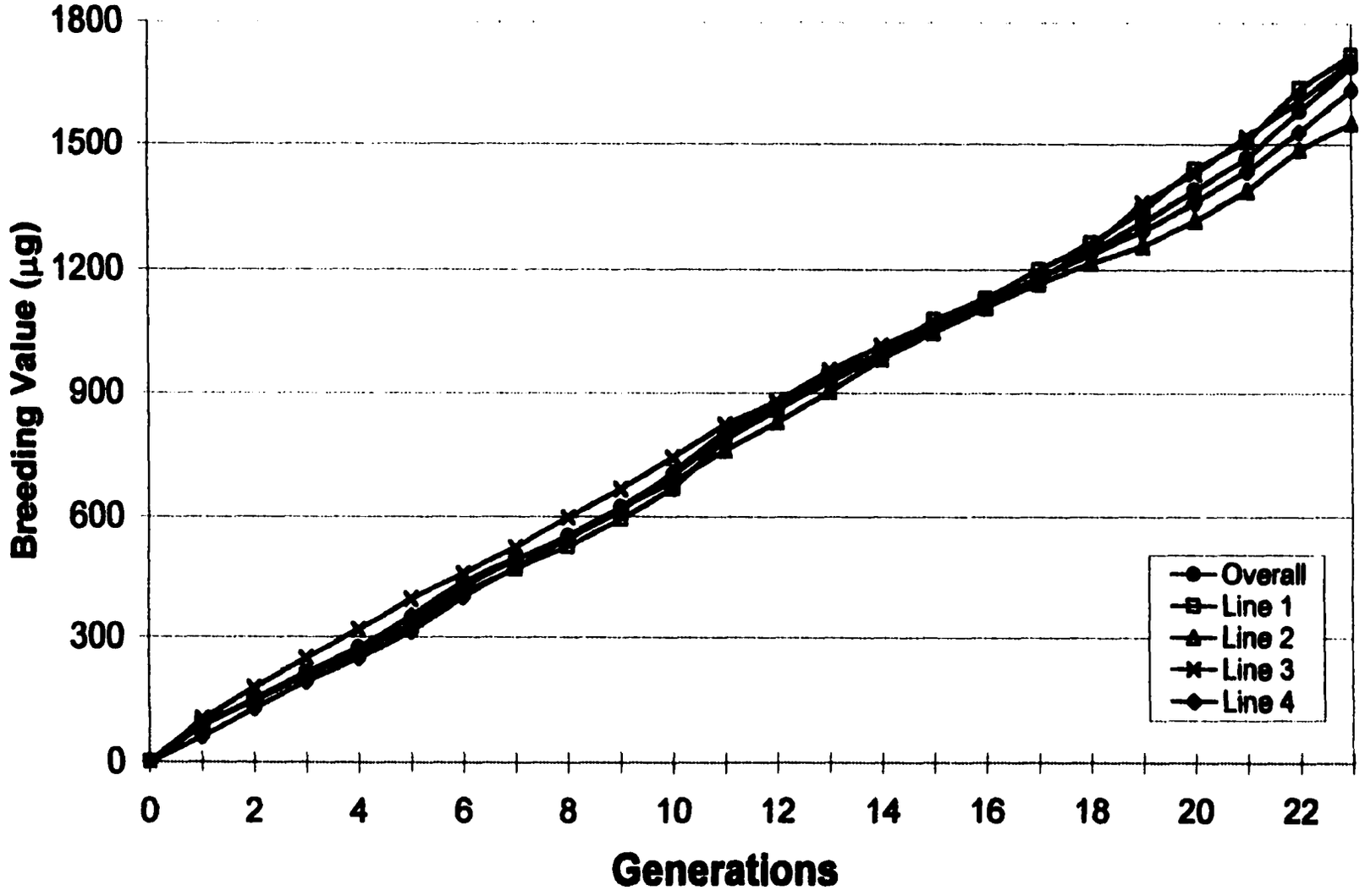

Fig. 4. Genetic trends for pupa weight (µg) in four lines under different environmental conditions: L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein, L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein, Overall (—●—).

within an environment. However, it can be argued that different genetic trends in different environments can be the result of genotype by environment interactions. VAN VLECK (1963) has stated that different estimates of parameters in different environments are another form of genotype by environment interaction.

Variance components and parameters

Estimates of variance components and parameters for the base population and across lines for the whole experiment are given in Table 4.

Total phenotypic variance was greater from the analysis including all data following 23 generations of selection than in the base population. Error and common environmental variance were substantially larger in generations where selection occurred than in the base population, 87 and 85% larger, respectively. Increase in total phenotypic variance can be attributable to increases in common environmental and error variance.

Analysis showed that the common environmental effect is a consistent factor contributing to the total phenotypic variance of PWT. Increase in error (within family) variance can be attributable partly to competition among full-sibs in a bottle. Selection increased the body weight of the insects and their demands for food. However, during the experiment, amount of food per family have been kept the same. This might have caused competition among insects in a bottle, consequently the increase in error variance.

The estimate of additive genetic variance after selection for the whole experiment was less than the estimate in the base population. However, both the estimates were still very close to each other considering the magnitude of the standard error of the estimate of additive genetic variance for the whole experiment. Thus, the additive genetic variance remained

Table 4. Estimates of variance components and genetic parameters for pupa weight in the base population, and all lines and generations combined after selection.

Data	Base population	All lines combined
Variance Comp:		
Additive variance	19,157 ± ——	16,178 ± 1,435
Common environmental variance	9,578 ± 2,394	17,700 ± 709
Error variance	23,946 ± 1,431	44,794 ± 827
Total phenotypic variance	52,781 ± ——	78,672 ± ——
Heritability (h^2)	0.36 ± 0.02	0.21 ± 0.02
c^2	0.18 ± 0.04	0.22 ± 0.01
e^2	0.46 ± 0.03	0.57 ± 0.01

[a] c^2 is the fraction of common environmental variance in total variance, e^2 is the fraction of error variance in total variance.

relatively stable in part due to the particular mating scheme used in this experiment, i.e., mating of one sire from every resource population to three females in each target environment. ENFIELD et al. (1966) reported no significant effect of selection on changing genetic variance from the results based on 12 generations of selection for increased 21-day PWT. LIN (1997) reported that the phenotypic variance increased after 16 generations of selection for increased PWT. Elsewhere, KAUFMAN et al. (1977) reported that both phenotypic and additive genetic variance decreased after 95 generations of stabilizing selection.

The model was believed to satisfy all requirements to obtain estimates unbiased by the effects of selection because the insects in the base population were unselected, the model included all data on which the selection was based, and the additive genetic relationship matrix was complete (SORENSEN and KENNEDY 1984; MEYER and THOMPSON 1984;

GIANOLA and FERNANDO 1986; GIANOLA et. al. 1988; FERNANDO and GIANOLA 1990; VAN DER WERF and DE BOER; 1990 MEYER 1991). The additive genetic variance may be expected to decrease with selection (BULMER, 1971; ROBERTSON 1977). Theoretical expectations, however, are difficult to verify under experimental conditions.

Estimates of heritability were 0.36 ± 0.02 and 0.21 ± 0.02 for the base population and for all data over all lines after selection, respectively. A decrease in heritability over selected generations was explained mainly by the increase in common environmental and residual variance. LIN (1997) reported heritability estimates of 0.33 and 0.23 for two similar replicated populations. BERGER (1977) and CAMPO and DE LA BLANCE (1988) reported heritability estimates of 0.36. BELL and BURRIS (1973) reported a realized heritability of 0.30.

Estimates of the proportion of total variance due to common environmental variance, c^2, were 0.18 and 0.22 in the base population and in the data combined over all lines, respectively. LIN (1997) reported smaller estimates of 0.07 and 0.14 for c^2.

The effect of exchanging male germplasm among environments on variance components and parameters for pupa weight and correlated response of a reproductive success within lines requires further study.

References

BELL, A. E., 1969: The nature of selection responses in *Tribolium*. Japan. J. Genet. **44**(1): 299-309.

BELL, A. E.; BURRIS, M. J., 1973: Simultaneous selection for two traits in *Tribolium*. Genet. Res. Camb. **21**: 29-46.

BELL, A. E.; MOORE, C. H., 1972: Reciprocal recurrent selection for pupal weight in Tribolim in comparison with conventional methods. Egyp. J. Genet. Cytol. 1(1): 92-119.

BENYI, K.; GALL, G. A. E., 1978: Genotype -environment interaction effects on growth and development in *Tribolium castaneum*. The Journal of Heredity. **69**: 71-76

BENYI, K.; GALL, G. A. E., 1981: Genotype-environment interaction effects on reproductive performance in *Tribolium cataneum*. Theor. Appl. Genet. **59**: 123-128.

BERGER, P. J., 1977: Multiple-trait selection experiments: Current status, problem areas and experimental approaches. In: Int. Conf. Quant. Genet. p. 191-204. Iowa State Univ. Press, Ames, IA.

BOLDMAN, K. G.; KRIESE, L. E.; VAN VLECK, L. D.; VAN TASSELL, C. P.; KACHMAN, S. D., 1995: A manual for use of MTDFREML. A set of programs to obtain estimates of variance and covariances [draft]. USDA-ARS, Lincoln, NE.

BULMER, M. G., 1971: The effect of selection on genetic variability. Am. Nat. **105**: 201-211.

CAMPO, J. L.; DE LA BLANCE, A. S., 1988: Experimental comparison of selection methods to improve a non-linear trait in *Tribolium*. Theor. Appl. Genet. **75**: 569-574.

DODENHOFF, J.; VAN VLECK, L. D.; KACHMAN, S. D.; KOCH, R. M., 1998: Parameter estimates for direct, maternal, and grandmaternal genetic effect for birth weight and weaning weight in Hereford cattle. J. Anim. Sci. **76**: 2521-2527.

ENFIELD, F. D., COMSTOCK, R. E.; BRASKERUD, O., 1966: Selection for pupa weight in *Tribolium castaneum*. I. Parameters in base populations. Genetics. **54**: 523-533.

FALCONER, D. S., 1952: The problem of environment and selection. Am. Nat. **86**: 293-298.

FERNANDO, R. L.; GIANOLA, D., 1990: Statistical inferences in populations undergoing selection or nanrandom mating. *In* D. Gianola and K. Hammond (eds.) *Statistical Methods for Genetic Improvement of Livestock*, pp. 437-453. Springer-Verlag, NY.

GIANOLA, D.; FERNANDO, R. L., 1986: Bayesian methods in animal breeding theory. J. Anim. Sci. **63**: 217-244.

GIANOLA, D.; IM, S.; FERNANDO, R. L., 1988: Prediction of breeding values under Henderson's selection model: a revisitation. J. Dairy Dci. **71**: 2790-2798.

HARDIN, R.T.; ROGLER, J.C.; BELL, A. E., 1967: Genetic and environmental interaction in growth of *Tribolium castaneum*. Can. J. Zoology. **45**: 139-147.

KATZI, A. J.; ENFIELD, F. D., 1977: Response to selection for increased pupa weight in *Tribolium castaneum* as related to population structure. Genet. Res. Camb. **30**: 237-246.

KAUFMAN, P. K.; ENFIELD, F. D.; COMSTOCK, R. E., 1977: Stabilizing selection for pupa weight in *Tribolium castaneum*. Genetics **87**: 327-341

KRESS, D. D.; ENFIELD, F. D.; BRASKERUD, O., 1971: Correlated response in male and female sterility to selection for pupa weight in *Tribolium castaneum*. Theor. Appl. Genet. **41**: 197-202.

LIN, E. C., 1997: Estimates of genetic parameters from a selection experiment for growth and reproductive success in *Tribolium castaneum* by using different statistical methods. Ph.D. Dissertation; Iowa State University, Ames, IA.

MEYER, K., 1991: Estimating variances and covariances for multivariate animal models by restricted maximum likelihood. Genet. Sel. Evol. **23**: 67-83.

MEYER, M. M.; ENFIELD, F. D., 1975: Experimental evidence on limitations of the heritability parameter. Theor. Appl. Genet. **45**: 268-273.

MEYER, K.; THOMPSON, R., 1984: Bias in variance component estimators due to selection on a correlated trait. Z. Tierz. Zuchtungsbiol. **101**: 33-50.

MINVIELLE, F.; GALL, G. A. E., 1980: Artificial selection for 18-day pupa weight and opposing simulated natural selection in *Tribolium castaneum*. Theor. Appl. Genet. **56**: 49-55.

ROBERTSON, A., 1977: The effect of selection on estimation of genetic parameters. Z. Tierzuchtg. Zuchtgsbiol. **94**: 131-135.

SORENSEN, D. A.; KENNEDY, B. W., 1984: Estimation of genetic variances from unselected and selected populations. J. Anim. Sci. **59**: 1213-1233.

SORENSON, D. A.; KENNEDY, B. W., 1986: Analysis of selection experiments using mixed model methodology. J. Anim. Sci. **63**: 245-258.

VAN VLECK, L. D., 1963: Genotype and environment in sire evaluation. J. Dairy Sci. **46**: 983-987.

VAN DER WERF, J. H. J.; DE BOER, I. J. M., 1990: Estimation of additive genetic variance when base populations are selected. J. Anim. Sci. **68**: 3124-3132.

VIA, S; CONNER, J., 1995: Evolution in heterogeneous environments: genetic variability within and across different grains in Tribolium castaneum. Heredity. **74**: 80-90.

YAMADA, Y.; BELL, A. E., 1969: Selection for larval growth in *Tribolium* under two levels of nutrition. Genet. Res. Camb. **13**: 175-195.

Department of Animal Science, Iowa State University, Ames, Iowa, USA

CHAPTER 3. VARIANCE COMPONENT ESTIMATES FOR PUPA WEIGHT IN TRIBOLIUM CASTANEUM IN FOUR ENVIRONMENTS[2]

A paper to be submitted to Journal of Animal Breeding and Genetics

By S. KONCAGUL and P. J. BERGER

Summary

A 2-by-2 factorial design of environmental treatments was used to study the effects of selection for increased pupa weight (PWT) in different environmental settings (lines): (line 1 (L1), 67% relative humidity (RH) - 5% yeast-fortified whole wheat flour; line 2 (L2), 67% RH - flour diet; line 3 (L3), 80% RH - 5% yeast-fortified diet; and line 4 (L4), 80% RH - flour diet). The best male from each line was mated to females in each of all lines every generation. Other males were mated to females within their line of birth.

This research models the beef or dairy cattle world where there is an exchange of elite male germplasm to enhance performance in other populations. Main objectives of this paper are to estimate variance components and parameters within four lines, and to investigate if there is a genotype by environment interaction that may influence the choice of an appropriate environmental setting for selection and performance testing of breeding animals.

---

[2] Journal Paper Number J- of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project number 3538, and supported by Hatch Act and State of Iowa funds.

Effects of environmental fluctuations on estimates of variance components and parameters are discussed.

Data were analyzed within each line by using multitrait derivative-free restricted maximum likelihood procedures (MTDFREML) with animal models that either included or excluded effects to account for genetic merit of sires used across environments. Models that failed to account properly for males used across environments seriously underestimated the additive genetic variance. Genetic groups for unknown sires were shown to be necessary components of the model for genetic prediction.

Diet had a larger impact on the relative magnitude of variance component estimates among environmental settings than RH. The optimum environment, L3, and the poorest environment, L2, set the maximum and minimum limits on estimates of phenotypic and additive genetic variance. Estimates of common environmental variance and residual variance were similar for each diet across both levels of RH.

It was concluded that males should be selected in the environment where they are expected to be used for future matings, or they can be used to mate to females in better environments than where they are selected.

Key words: animal model, environment, pupa weight, response, selection and *Tribolium castaneum*.

Introduction

With the implementation of animal models for genetic prediction and genetic parameter estimation it is usually assumed that all animals over all generations are descendants from a common base population. With the exchange of elite males across populations, as is

frequently done with the sale of semen in species of livestock, ancestors for sires from outside the population may be unknown. Sires with unknown ancestors can effectively have a different level of genetic merit than other sires within each population due to prior selection. Therefore, these different levels of merit of sires need to be considered to properly define the model to partition predictors of genetic merit among all breeding animals within each population.

Parents not having genetic ties to previous generations can be defined as unknown parents. They can be assigned to fixed genetic groups in the model to account for genetic trend (QUASS and POLLAK 1981; WESTELL et al. 1988). On the other hand, THOMPSON (1979) suggested that the relationship matrix can be used instead of grouping, and HENDERSON (1975) stated that there is no need to include group effects if all relationships among animals are included in the analysis. However, it is not always possible to have a complete genetic relationship matrix among animals with data, therefore, having groups in the model can complete the relationship among animals (WIGGANS et al. 1988).

Groups are still needed, even if all relationships are included in the model, particularly if all animals in the data set are not from the same base population (POLLAK et al. 1977; TONG et al. 1980). Moreover, the necessity of grouping unknown parents increases when migration from other environments or populations to the population of interest is larger than 5% (KENNEDY 1981). Grouping of unknown parents can provide a more precise way of evaluating the data generated by selection (WESTELL and VAN VLECK 1987).

Many different strategies can be used to define groups. ROBINSON (1986) and WESTELL et al. (1988) gave a list of steps for grouping unknown parents. In practice, there is no exact definition for a uniform way of defining groups for unknown parents, but groups

"should logically account for different genetic means from different time periods or subpopulations" (VAN VLECK 1990). In this paper, empirical evidence is provided showing how unknown sires can affect estimates of additive genetic variance and genetic parameters within environments or countries, and how they can be modeled when data within environment or country are analyzed alone.

Genotype and environment each have an effect on the ultimate mean level of performance achieved by individual animals or insects. Existence of genotype by environment interactions is difficult to identify by sound scientific methods of enquiry. Scientific enquiry is complicated by the fact that there are many seemingly different biological phenomena that can be classified as genotype by environment interactions. For example, GARRICK and VAN VLECK (1987) describe six different possible manifestations of biological phenomena that can be described as causing genotype by environment interactions. Five of the six occur in the presence of a perfect genetic correlation between genotype and environment.

In the presence of genotype by environment interaction, additional points of interest arise. Researchers have conducted investigations to find an answer to the following question: "should animals be selected under optimum environmental conditions or under poorer conditions for future performance?" There is no general agreement among researchers about the proper environmental conditions for selection. HAMMOND (1947); FRIARS et al. (1971) and MARKS (1980) reported that animals should be selected under environmental settings that make them express their full potential for a trait of interest, and then they can be moved to other environments. On the other hand, FALCONER (1960) concluded that selection in an adverse environment should be preferred if selected animals are intended to be used in

various environments. However, YAMADA and BELL (1969) and GEARHEART and GOODWILL (1990) concluded that animals should be selected in the environment where they will live in future. This paper provides further empirical evidence on proper environmental conditions for selection.

The main purposes of this paper are two-fold. First, to estimate variance components and parameters for pupa weight within different environmental settings by modeling the modern beef or dairy cattle world where there is a constant exchange of male germplasm among environments. Conditions leading to underestimates of additive genetic variance due to failure to account for incomplete pedigree information are discussed. Second, to investigate if there is a genotype by environment interaction due to the effects of environmental fluctuations on estimates of variance components and genetic parameters. The experiment gives insight about appropriate environmental conditions for selection.

Materials and methods

Experimental design

Design of the breeding program was similar to one widely used to enhance genetic merit across populations in species of livestock. Germplasm of elite males was used across four lines to enhance the performance of animals or insects under different environmental conditions. Details of the experimental design have been reported earlier (KONCAGUL and BERGER 2001). Briefly, insects from the base population were randomly assigned to four environments defined by two levels of two environmental factors, relative humidity (RH) and diet. Line 1 (L1) had 67% RH and a diet of 5% yeast-enriched whole wheat flour; line 2 (L2)

had 67% RH with flour alone; line 3 (L3) had 80% RH and the yeast-enriched flour diet; and line 4 (L4) had 80% RH with flour alone.

There were 324 insects per generation, 162 insects of both sexes, in each line. Selection intensity was the same for all lines. Fifteen males and fifty-four females were selected within each line to produce the next generation. Males were mated to three females within their lines. The best-ranked male from each line was also mated to three females in each of the four lines.

Each line stands for a different environmental opportunity to express performance of two traits. Traits were pupa weight (PWT), measured on both males and females, and family size (FST) measured only on females. Within lines, phenotypic mass selection was for increased PWT. Prior to selection, PWT was adjusted for generation, set and sex. Correlated response in FST, defined as the number of pupa produced by a female insect, will be reported in subsequent paper.

Statistical analysis

Multi-Trait Derivative-Free Restricted Maximum Likelihood (MTDFREML) procedure was used to obtain estimates of variance components and genetic parameters (BOLDMAN et al. 1995). In the present experiment no control population was used to allocate more resources to the lines under selection. In the absence of control populations, populations under selection can efficiently be analyzed by using mixed model genetic prediction procedures (SORENSON and KENNEDY 1986). Unbiased estimates of both fixed and random effects can be obtained by applying Restricted Maximum Likelihood (REML) procedures in the analysis of populations under selection (GIANOLA and FERNANDO 1986; MEYER 1991). The use of

REML with an animal model is desired to obtain unbiased estimates of parameters and variance components from data generated by selection (MEYER and THOMPSON 1984).

The model for estimating variance components, parameters and breeding values within lines was:

$$PWT_{ijkl} = gs_i + sex_k + anim_{ijkl} + pe_{ij} + e_{ijkl} \quad \text{(no grouping)} \qquad [1]$$

where

PWT_{ijkl} pupa weight of l^{th} insect with k^{th} sex in the j^{th} family in the i^{th} generation-set,

gs_i fixed effect of i^{th} generation-set combination,

sex_k fixed effect of k^{th} sex,

$anim_{ijkl}$ direct random genetic effect of $ijkl^{th}$ animal,

pe_{ij} random effect of ij^{th} family, common environment, and

e_{ijkl} random residual.

In matrix notation,

$$\mathbf{y} = \mathbf{X}_1\mathbf{b}_1 + \mathbf{X}_2\mathbf{b}_2 + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{e}$$

where

$\mathbf{y}$ is the vector of observations, $\mathbf{X}_1$, $\mathbf{X}_2$, $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are known incidence matrices relating observations to vectors for unknown fixed effects ($\mathbf{b}_1$ and $\mathbf{b}_2$) and random effects ($\mathbf{u}_1$ and $\mathbf{u}_2$), and $\mathbf{e}$ is the vector of random residuals.

Expectations and variances of random effects in the equation were

$$E(\mathbf{y}) = \mathbf{X}_1\mathbf{b}_1 + \mathbf{X}_2\mathbf{b}_2, \quad E(\mathbf{u}_1) = E(\mathbf{u}_2) = E(\mathbf{e}) = \mathbf{0}$$

$$V(\mathbf{u}_1) = \mathbf{A}\sigma^2_{u1} \qquad V(\mathbf{u}_2) = \mathbf{I}pe\sigma^2_{u2} \qquad V(\mathbf{e}) = \mathbf{I}e\sigma^2_e$$

$$Cov(\mathbf{u}_1,\mathbf{u}_2) = Cov(\mathbf{u}_1,\mathbf{e}) = Cov(\mathbf{u}_2,\mathbf{e}) = \mathbf{0}$$

A, additive genetic relationship matrix among insects in the data,

Ipe, identity matrix with order equal to number of families,

Ie, identity matrix with order equal to number of observations.

Within each line the data also were analyzed by using a model including a fixed effect for groups. Groups were identified by the line and generation of sires used across lines (e.g., in this experiment groups were identified by the line and generation of sires from a line other than the particular one being analyzed) (WESTELL et al. 1988). Because some sires were mated to females across lines every generation, these sires were considered to be unknown sires due to the fact that they had no genetic tie to insects in earlier generations of lines other than their line of birth.

The model used to analyze the data within lines was:

$$PWT_{ijkl} = gs_i + sex_k + \sum_{r=1}^{n} p_{lr} g_r + anim_l + pe_{ij} + e_{ijkl} \quad \text{(with grouping)} \qquad [2]$$

where

p_{lr} is the additive genetic relationship between l^{th} animal and ancestor in r^{th} group, and g_r is the fixed effect of r^{th} group; all other terms are the same as defined above for equation [1]. The data also were analyzed separately for each sex.

In the model defined by equation [2], the predicted breeding value of animal *l* is defined as $\sum_{r=1}^{n} p_{lr} g_r + anim_l$ (WESTELL and VAN VLECK 1987). Grouping started in generation two, because all sires in generation one had genetic ties to the previous generation due to the reason that all insects in the base population were included in all analyses. There

were three groups every generation within a line, because each sire from the other lines was considered to be representative of a different level of genetic merit (i.e., in line 1, sires from line 2, line 3 and line 4 were assigned to different groups in each generation).

Genetic trends were calculated as regression of average breeding values of insects on generation numbers. Realized heritabilities were calculated as regression of mean breeding values on cumulative selection differential.

Results and discussion

Groups for unknown sires

Within-line estimates of variance components and genetic parameters by equation [1] are given in Table 1. There was more phenotypic variance in L1 and L3 (i.e. those receiving a yeast-enriched diet) than in the other two lines, L2 and L4. Variances were similar across both sexes. Perhaps the most striking result in this table is the almost total absence of additive genetic variance relative to the total variance within lines. Heritability estimates for PWT were 0.02, 0.01, 0.04 and 0.02 in each of the four lines, respectively. Keep in mind that these heritability estimates are within lines, using only data from within a line and known relationships within each line. i.e., imported sires have unknown parents. These estimates are obviously unrealistic, because there was good a priori evidence that there was substantial additive genetic variance for PWT in this population (See estimates reported in Chapter 2 and KONCAGUL and BERGER 2001). They reported that heritability for PWT was estimated to be 0.36 and 0.21 in the base population and across all lines and generations, respectively. In addition, the heritability estimates obtained by equation [1] do not reflect the significant

Table 1. Estimates of variance components and genetic parameters for pupa weight. Within-line analysis using an animal model, without genetic group for unidentified parents from other lines, common base population for all lines and data from 23 generation of selection: model defined by equation [1].

Data	Line 1	Line 2	Line 3	Line 4
Humidity	67% RH	67% RH	80% RH	80% RH
Diet	5% yeast-flour	flour diet	5% yeast-flour	flour diet
Variance Comp:				
Phenotypic var., μg^2	82,988	52,213	95,351	65,734
Males	77,905	52,441	98,138	62,258
Females	87,140	51,810	90,843	68,484
Additive var., μg^2	1,863 ± 1,397	769 ± 787	3,623 ± 1,605	1,044 ± 994
Males	2,027	906	3,619	0.1335
Females	7,321	3,170	10,525	4,812
Com. Env. Var., μg^2	26,773 ± 1,604	17,231 ± 1,031	28,388 ± 1,756	21,820 ± 1,285
Males	24,465	19,303	31,304	23,433
Females	24,470	15,094	22,366	20,281
Error var., μg^2	54,351 ± 1,168	34,213 ± 724	63,340 ± 1,351	42,871 ± 899
Males	51,412	32,232	63,215	38,825
Females	55,348	33,546	57,952	43,392
Parameters:[1]				
$b_{Gi,Pi}$ (h^2_r)	0.010 ± 0.0002	0.006 ± 0.0002	0.015 ± 0.0004	0.006 ± 0.0001
Estimated (h^2)	0.02 ± 0.017	0.01 ± 0.015	0.04 ± 0.017	0.02 ± 0.015
Males	0.03	0.02	0.04	0.00
Females	0.08	0.06	0.12	0.07
c^2	0.32 ± 0.015	0.33 ± 0.015	0.30 ± 0.015	0.33 ± 0.015
Males	0.31	0.37	0.32	0.38
Females	0.28	0.29	0.25	0.30
e^2	0.65 ± 0.016	0.66 ± 0.015	0.66 ± 0.016	0.65 ± 0.015
Males	0.66	0.61	0.64	0.62
Females	0.64	0.65	0.64	0.63

[1] $b_{Gi,Pi}$ = Regression coefficient of mean breeding values on mean phenotypic values pooled over generations. c^2 is the fraction of common environmental variance in total variance, e^2 is the fraction of error variance in total variance, realized heritability was calculated as regression of average breeding value on cumulative selection differentials.

responses reported by KONCAGUL and BERGER (2001), which are presented again in Table 4. They reported that mean PWT almost doubled in all lines during 23 generations of selection for increased PWT.

Table 2. Estimates of variance components and genetic parameters for pupa weight. Within-line analysis using an animal model, genetic group for sires with unknown pedigree information from other lines, common base population for all lines and data from 23 generations of selection: model defined by equation [2]

Data	Line 1		Line 2		Line 3		Line 4	
Humidity	67% RH		67% RH		80% RH		80% RH	
Diet	5% yeast-flour		flour diet		5% yeast-flour		flour diet	
Variance Comp:								
Phenotypic var., μg^2	85,265		51,956		100,327		68,974	
Males		80,083		52,314		101,816		62,333
Females		87,229		51,279		95,088		73,155
Additive var., μg^2	25,893		9,977		37,455		28,194	
Males		27,420		10,109		35,260		18,976
Females		20,680		10,557		40,468		33,812
Com. Env. Var., μg^2	17,744		12,560		17,362		12,197	
Males		14,917		14,738		20,378		14,234
Females		18,626		11,135		13,144		12,157
Error var., μg^2	41,627		29,419		45,506		28,584	
Males		37,745		27,466		46,179		29,123
Females		47,923		29,587		41,476		27,185
Parameters:[1]								
Heritability (h^2)	0.30		0.19		0.37		0.41	
Males		0.34		0.19		0.35		0.30
Females		0.24		0.21		0.43		0.46
c^2	0.21		0.24		0.17		0.18	
Males		0.19		0.28		0.20		0.23
Females		0.21		0.22		0.14		0.17
e^2	0.48		0.57		0.45		0.41	
Males		0.47		0.53		0.45		0.47
Females		0.55		0.58		0.44		0.37

[1] c2 is the fraction of common environmental variance in total variance; e^2 is the fraction of error variance in total variance.

Groups to account for genetic merit of unknown sires were added to the model used in the analyses. Estimates of variance components and parameters from the model defined by equation [2] are given in Table 2. Average of estimates of additive genetic variance, and of estimates of heritabilities from equation [2] were similar to the estimates from data pooled over lines reported by KONCAGUL and BERGER (2001). This shows that model [2] fits the

data better by properly accounting for genetic differences among all insects. Thus, groups for unknown sires are necessary components of the model being used in the analyses, as in the case represented here, due to males being used across lines that are not direct descendants of insects from the previous generation. These results support the need for including groups in the model to account for genetic trend (QUASS and POLLAK 1981; WESTELL et al. 1988). By including groups in the model the analysis also provides more precise evaluation of sires (HENDERSON 1975).

The results further explain changes that can occur in estimates of variance components when unknown sires from different base populations are to be included in the analysis. Despite the fact that all insects within a line were included in each analysis and all insects were included in the relationship matrix, some grouping was still needed to account for different levels of genetic merit for sires from outside the population. WIGGANS et al. (1988) concluded that groups in the model could complete the relationship matrix.

The existing theory and the empirical evidence presented in this paper strongly show that groups for unknown parents must be included in the model if the data contain parents that do not have ancestors linking them to previous generations. In selection experiments with closed populations, all animals with records generally have known relationships with previous generations, except in some cases such as reciprocal semen exchange among experimental populations. In field data, however, breeding companies and farmers in one region may buy semen from farmers in other regions, or even countries may buy semen from other countries, and this makes grouping necessary for accurate evaluation of animals within a particular region or a particular country. The importation of sires over several generations from different populations can have important consequences on genetic prediction of

breeding values and estimation of genetic parameters using an animal model if the model fails to recognize distinct lines of ancestry. Estimates of additive genetic variance from animal models seriously underestimate the true additive genetic variance if imported sires are not assigned to groups as unknown parents.

If unknown parents come from a different population, it would be a mistake to group them based on some function of time alone. Grouping of unknown parents should be made according to environment or the population where they were born, and to the time when they entered into the population of interest because they can effectively have different genetic merits depending on the time and the population from which they come.

Because the need for including genetic groups for unknown parents in the model was clearly supported by experimental evidence and existing theory, the remaining results to be reported were obtained with equation [2], including genetic group effects for within-line analyses.

Variance components and parameters

There are some notable differences among lines in estimates of variance components for this experiment (Table 2). Diet had a larger impact on the relative magnitude of variance between lines than RH. The optimum environment, L3, and the poorest environment, L2, set maximum and minimum limits on estimates of phenotypic and additive genetic variance (see Table 2 for actual values of variance components and Table 3 for the relative value of variance components across lines). Estimates of common environmental and residual variance were similar for each diet across both levels of RH. Estimates of variance

Table 3. Relative value of variance component estimates from Table 2 in relation to the optimal environmental conditions of line 3.

Data	Line 1	Line 2	Line 3	Line 4
Humidity	67% RH	67% RH	80% RH	80% RH
Diet	5% yeast-flour	flour diet	5% yeast-flour	flour diet
Var (p)	0.85	0.52	1.0	0.69
Var (a)	0.69	0.27	1.0	0.75
Var (ce)	1.02	0.72	1.0	0.70
Var (e)	1.16	0.71	1.0	0.66
CV (%)[1]	10.2	8.0	11.1	9.2

[1] CV = coefficient of variation in relation to the mean of the base population.

components and parameters for both sexes fluctuated from line to line. There is no clear pattern in differences between the estimates of variances and parameters to argue that sex-linked genes determine PWT.

MEYER and ENFIELD (1975) reported estimates of phenotypic variance ranging from 55,572 to 61,488 μg^2 in an F_3 population of 19 single generation selection experiments for pupa weight. Their estimates are similar to the estimates for L2 and L4 in this experiment. Elsewhere, KAUFMAN et al. (1977) reported estimates of phenotypic variance ranged from 34,555 ± 554 to 43,399 ± 1150 μg^2; and estimates of additive genetic variance ranged from 6,762 ± 927 to 10,762 ± 2124 μg^2. Their estimates of additive genetic variance were smaller than the estimates from this experiment, except for the estimate in L2, 9,977 μg^2. LIN (1997) reported additive genetic variances of 35,376 and 17,737 in replicate 1 and 2, respectively.

Estimates of heritabilities varied from line to line. The lowest estimate was in L2, and the highest estimate was in L4. ENFIELD et al. (1966) estimated the heritability by parent-offspring regression. They reported estimates of 0.34 from sire-son regression and 0.36 from

sire-daughter regression. KATZI and ENFIELD (1977) reported heritability estimates from parent-offspring regression ranging from 0.09 to 0.20. BERGER (1977) and CAMPO and DE LA BLANCE (1988) reported similar heritability estimates of 0.36. LIN (1997) reported heritability estimates, 0.33 and 0.23 in two replicated populations selected for pupa weight.

The results show that estimates of variance components and parameters depend on joint effect of humidity and plane of nutrition, which defined specific environments for growth of insects. Estimates of additive genetic and total variance were considerable larger in L3, which had the optimum levels of diet and RH, than in L2 with the poorest levels of diet and RH. This shows that the variance components, especially additive genetic and total variance, may not be homogeneous across environments or subpopulations. Estimates of variance components are generally assumed to be known and homogeneous across environments with application of animal models. Evidence is beginning to emerge indicating that variance components may not be homogeneous across populations with different environmental opportunity. For example, dairy herds with high milk yield tend to have higher variance than herds with low milk yield (VAN VLECK 1966; HILL et al. 1983; BOLDMAN and FREEMAN 1990).

There is clear evidence for existence of genotype by environment interaction. All four lines were derived from a common base population and raised in different environments, but after 23 generations of selection we had different estimates of parameters. Result reported for this experiment showed that the ratios of additive genetic variance to total phenotypic variance can be expected to be different in different environments. Because estimates of variance components were larger in some environments than in others, this was interpreted as clear evidence of the existence of a genotype by environment interaction. VAN

VLECK (1963) also reported that a different estimate of parameters in different environments is a form of genotype by environment interaction.

Genetic response

Additional evidence of genotype by environment interaction also can be seen in Fig. 1, showing the genetic responses in all lines across generations. Average rates of changes in mean breeding values across generations are given in Table 4. Genetic responses were different among lines despite an attempt to maintain equal selection intensities across lines. L4 had the largest genetic response per generation, followed by L3, L1 and L2, respectively. The lines were derived from the same base population and subjected to the same experimental conditions except for different environmental settings. The genetic responses, however, were different in all lines, and this indicates an existence of genotype by environment interaction.

Realized parameters

Cumulative selection differentials are plotted against generation numbers in Fig. 2. Average cumulative selection differentials are given in Table 4. Although selection intensity was expected to be equal in all lines, some divergence among lines in realized cumulative selection differentials was evident by generation 7. By generation 22 it was largest for L3 followed by L1, L4 and L2, respectively.

Estimates of realized heritability followed similar patters of magnitude as genetic responses: highest in L4, about equal in L1 and L3 and lowest in L2 (Table 4). BELL and BURRIS (1973) reported estimates of realized heritability of 0.30. ENFIELD et al. (1966)

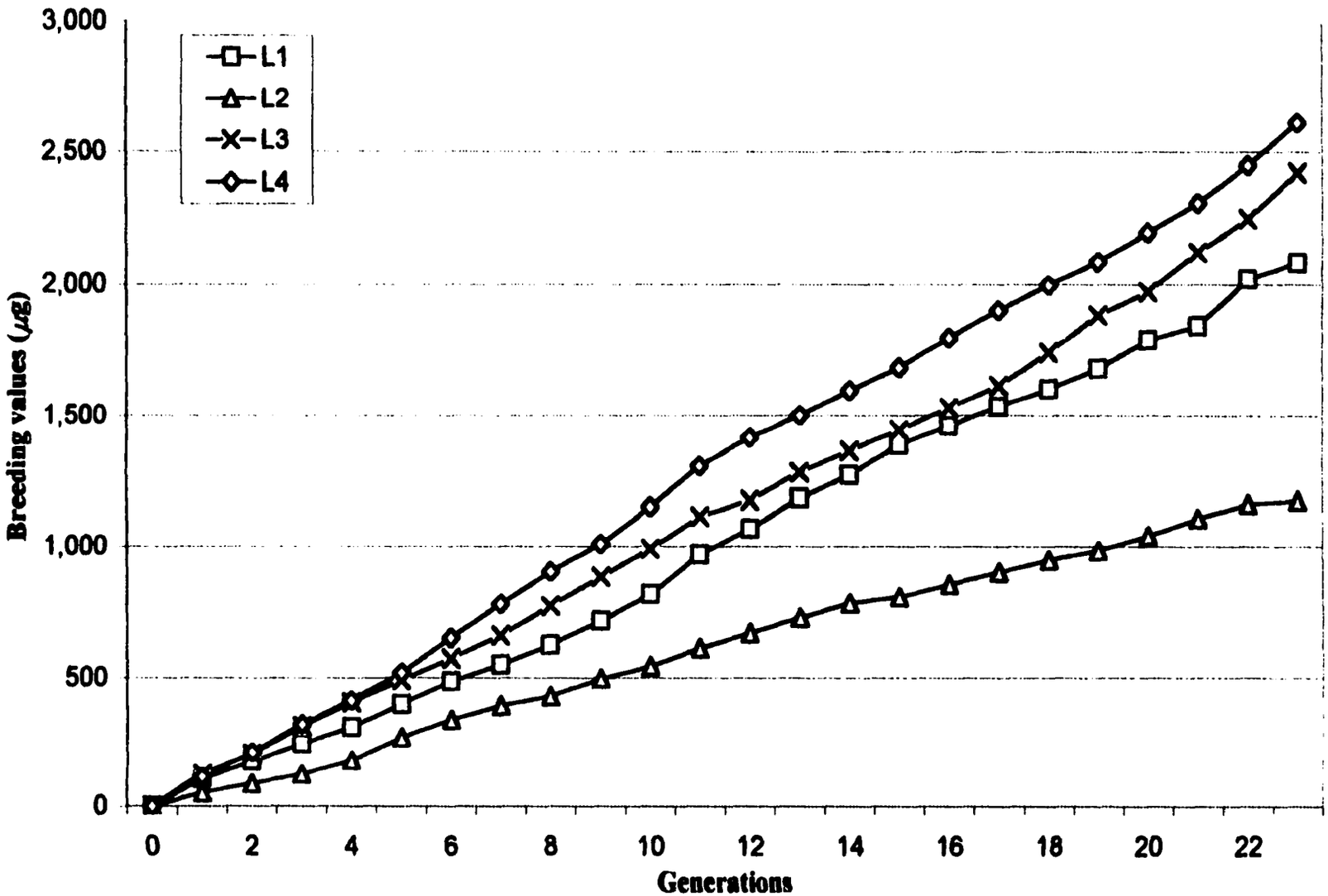

Fig. 1. Genetic trend for pupa weight based on analyses within line:
L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein,
L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein.

Table 4. Phenotypic (ΔP) and genetic (ΔG) changes in pupa weight after 23 generations of selection, cumulative selection differentials (ΔCSD) and realized heritabilities.

	ΔP/gen.[1]	ΔG/gen.[2]	ΔCSD/gen[3]	Realized (h^2)
Line 1	96.1 ± 2.8	89.9 ± 0.7	280.2 ± 3.8	0.33 ± 0.005
Line 2	70.5 ± 2.8	53.9 ± 0.7	239.7 ± 1.5	0.22 ± 0.004
Line 3	94.0 ± 2.8	100.2 ± 0.7	295.0 ± 4.2	0.34 ± 0.002
Line 4	71.3 ± 2.8	112.8 ± 0.7	263.4 ± 1.6	0.43 ± 0.003
Overall	82.6 ± 2.7	97.7 ± 1.7	271.6 ± 2.2	

[1] ΔP/gen.= average change in phenotype by generation.
[2] ΔG/gen.= average change in breeding value by generation.
[3] ΔCSD/gen.= average change in cumulative selection differentials by generation.
**all regression coefficients are significantly different from zero ($P < 0.0001$).

reported realized heritability of 0.37 and 0.34 in two replicates, respectively. MEYER and ENFIELD (1975) reported realized heritabilites, from 19 single generation selection experiments, of 0.16, 0.20 and 0.14 with 10%, 30% and 50% selection percentages, respectively. KATZI and ENFIELD (1977) reported realized heritabilities of 0.13 and 0.14. KAUFMAN et al. (1977) reported realized heritability estimates ranging from 0.05 to 0.31. MINVIELLE and GALL (1980) reported realized heritability estimates from 0.14 to 0.26.

Proper environmental setting for selection

An assessment of average breeding values of progeny of elite sires in each of the four environments is given in Table 5. Each value is the average change in mean breeding value for offspring of elite sires over 23 generations of selection (i.e., regression coefficient for mean breeding value of progeny within generation on generation number). Rows identify the environment of females mated to elite sires; columns identify the source of elite males.

We can make use of Table 5 in three ways. First, sires from different environments can be compared in the same environment, i.e., we can compare the values in each row. Second, sire from a particular environment can be compared in different environments, i.e.,

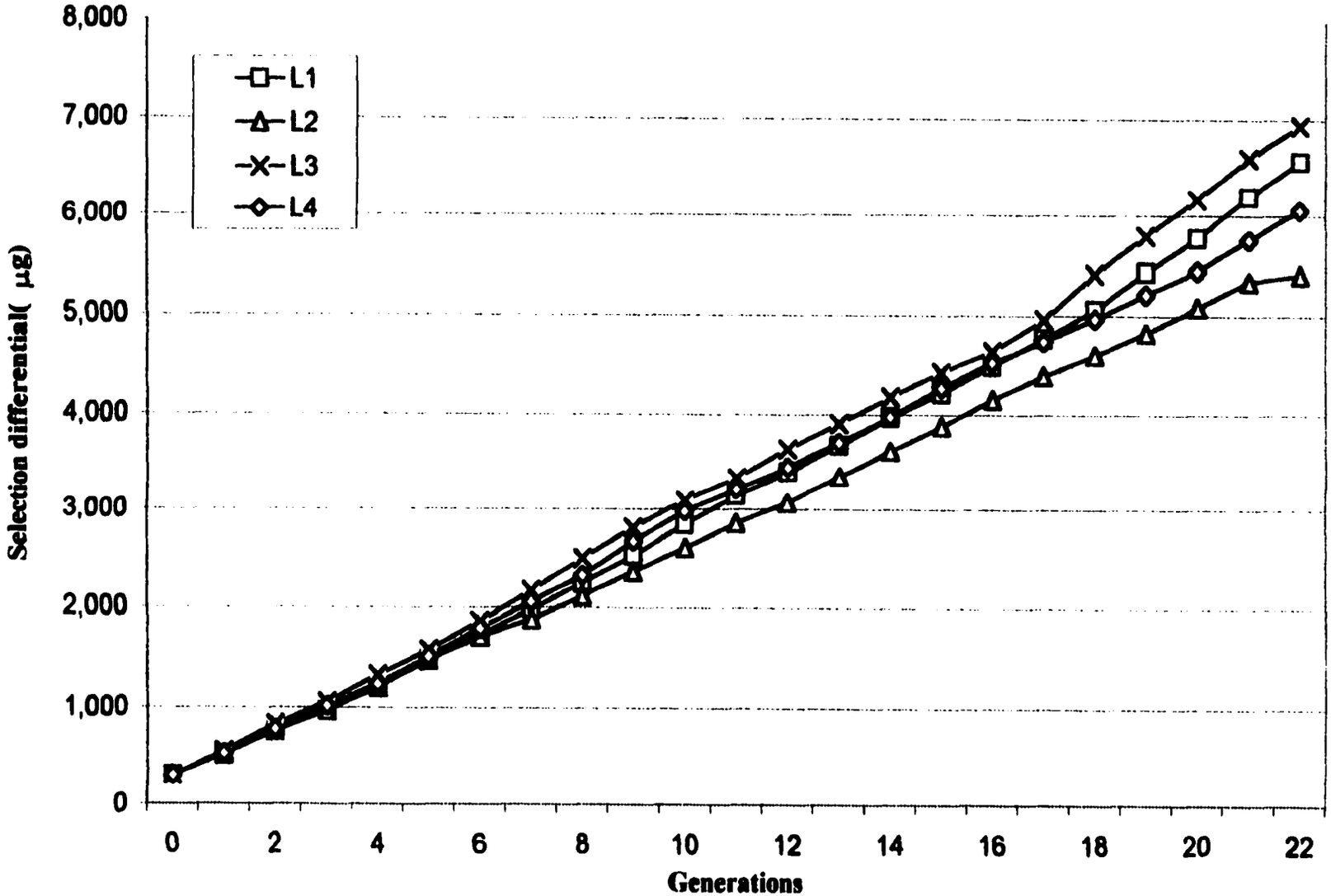

Fig. 2. Cumulative selection differentials for pupa weight within lines by generations: L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein, L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein.

Table 5. Rate of genetic change in pupa weight (μg) per generation in mean breeding value of progeny of elite sires used across environments.

Environmental setting for female parent and progeny	Source environment of elite sires: Line 1 67% RH 5% yeast - flour	Line 2 67% RH flour diet	Line 3 80% RH 5% yeast - flour	Line 4 80% RH flour diet	Mean
Line 1	**91.40 ± 2.64**	92.68 ± 5.30	87.26 ± 3.89	93.24 ± 4.44	91.15
Line 2	54.15 ± 3.53	**50.11 ± 3.07**	48.91 ± 4.30	57.39 ± 3.31	52.64
Line 3	107.62 ± 6.34	97.42 ± 1.88	**93.75 ± 2.89**	98.39 ± 5.45	99.30
Line 4	114.91 ± 4.69	108.89 ± 4.02	100.08 ± 4.40	**112.50 ± 3.22**	109.10
Mean	92.02	87.28	82.5	90.38	88.04

- all are significantly different from zero($P<0.0001$)

we can compare the values in each column. Lastly, average performance of sires from different environments can be compared over a range of target environments, i.e., we can compare the column means.

Comparing the values in the rows of Table 5 by taking the standard errors of the regression coefficients into consideration, it is seen that sires from different environments (from L1, L2, L3 and L4) performed similarly in a given environment (in L1, L2, L3 or L4). There are no apparent differences among the performances of sires from different environments when they are used in the same environmental settings.

Other interesting comparisons are given by differences between individual values within a column. For example, sires from L1 had progeny with higher average breeding values when mated to females in L3 and L4 than when they were mated to females within their own environment of origin (i.e., comparison of values in the first column of Table 5). That is, sires born under conditions of low RH, L1, had progeny with higher mean breeding values under the more optimal conditions of RH, L3 and L4.

The values in column two of Table 5 give the mean change in breeding values for progeny of sires from L2 when mated to females in all environments. Here progeny of sires selected in this less than optimal environmental setting of L2 had higher average breeding values in all other environments.

In column three, sires selected under the optimal environmental setting of L3, had progeny with lower mean breeding values in L1 and L2, higher mean breeding values in L4. This indicates that selection under optimal environmental conditions is unlikely to always yield progeny with equal or better performance in a poorer environment.

In the fourth column, mean breeding values of progeny of sires from L4 are highest within the environment of L4, nearly equal under better dietary conditions of L1 and L3, and lowest in L2. That is, for a given level of the same diet, sires born under conditions of optimum RH, L4, had progeny with much smaller mean breeding values under the conditions of low RH, L2.

In general, the estimates of responses in Table 5 can be interpreted to indicate that selected animals should be used in the environment in which they were selected, i.e., L3 has greater responses across all environments, except the environment of L4; or that animals selected in an less than optimal environment can be used in mating to animals in better environments, i.e., sire from L2 has greater response in all other environments. Unfortunately, these results add very little to our understanding of the effects of response to selection in good and poor environments. The responses in Table 5 agree with results reported by YAMADA and BELL (1969); GEARHEART and GOODWILL (1990); partially agree with FALCONER (1960); and disagree completely with HAMMOND (1947); FRIARS et al. (1971); MARKS (1980).

These results agree with the results reported by YAMADA and BELL (1969); GEARHEART and GOODWILL (1990). The results do not support the findings reported by HAMMOND (1947); FRIARS et al. (1971); MARKS (1980). They reported that animals should be selected in an optimum environment regardless of the environment selected animals are moved into. The results partially agree with FALCONER (1960)'s conclusion. He concluded that selection in an adverse environment gave better response if selected animals are to be used in various environments.

References

BELL, A. E.; BURRIS, M. J., 1973: Simultaneous selection for two traits in *Tribolium*. Genet. Res. Camb. **21**: 29-46.

BERGER, P. J., 1977: Multiple-trait selection experiments: Current status, problem areas and experimental approaches. In: Int. Conf. Quant. Genet. pp. 191-204. Iowa State Univ. Press, Ames, IA.

BOLDMAN, K. G.; FREEMAN, A. E., 1990: Adjustment for heterogeneity of variances by herd production level in dairy cow and sire evaluation. J. Dairy Sci. **73**:503-512.

BOLDMAN, K. G.; KRIESE, L. E.; VAN VLECK, L. D.; VAN TASSELL, C. P.; KACHMAN, S. D., 1995: A manual for use of MTDFREML. A set of programs to obtain estimates of variance and covariances [draft]. U.S. Dept. of Agriculture, Agriculture Research Service. Lincoln, NE.

CAMPO, J. L.; DE LA BLANCE, A. S., 1988: Experimental comparison of selection methods to improve a non-linear trait in *Tribolium*. Theor. Appl. Genet. **75**: 569-574

ENFIELD, F. D.; COMSTOCK, R. E.; BRASKERUD, O., 1966: Selection for pupa weight in *Tribolium castaneum*. I. Parameters in base populations. Genetics **54**: 523-533.

FALCONER, D. S., 1960: Selection of mice for growth on high low planes of nutrition. Gen. Res. **1**: 91-113.

FRIARS, G. W.; NAYAK, B. N.; JUI, P. Y.; RAKTOE, B. L., 1971: An investigation of genotype x environment interaction in relation to selection experiment in *Tribolium castaneum*. Can. J. Genet. Cytol. **13**: 144-154.

GARRICK, D. J.; VAN VLECK, L. D., 1987: Aspects of selection for performance in several environments with heterogeneous variances. J. Anim. Sci. **65**: 409-421.

GEARHEART, W. W.; GOODWILL, R. E., 1990: Divergent selection for pupal weight *of* *Tribolium castaneum* in optimum and adverse environments. J. Anim. Breed. Genet. **107**: 249-253.

GIANOLA, D.; FERNANDO, R. L. 1986: Bayesian methods in animal breeding theory. J. Anim. Sci. **63**: 217-244.

HAMMOND, J., 1947: Animal breeding in relation to nutrition and environmental conditions. Biol. Rev. **22**: 195-213.

HENDERSON, C.R., 1975: Use of relationship among sires to increase accuracy of sire evaluation. J. Dairy Sci. **58**(11): 1731-1738.

HILL, W. G.; EDWARDS, M. R.; AHMED, M. -K. A.; THOMPSON, R., 1983: Heritability of milk yield and composition at different levels and variability of production. Anim. Prod. **36**: 59-68.

KATZI, A. J.; ENFIELD, F. D., 1977: Response to selection for increased pupa weight in *Tribolium castaneum* as related to population structure. Genet. Res. Camb.

30: 237-246.

KAUFMAN, P. K.; ENFIELD, F. D.; COMSTOCK, R. E., 1977: Stabilizing selection for pupa weight in *Tribolium castaneum*. Genetics **87**: 327-341.

KENNEDY, B. W., 1981: Bias and mean square error from ignoring genetic groups in mixed model sire evaluation. J. Dairy Sci. **64**: 689-697.

KONCAGUL, S.; BERGER, P. J., 2001: Response to selection for increased pupa weight in *Tribolium castaneum* in four environments. J. Anim. Breed. Genet. (submitted).

LIN, E. -C., 1997: Estimates of genetic parameters from a selection experiment for growth and reproductive success in *Tribolium castaneum* by using different statistical methods. Ph.D. Dissertation, Iowa State University, Ames, IA.

MARKS, H. L., 1980: Feed efficiency of selected and nonselected Japanese quail lines. Poult. Sci. **59**: 6-10.

MEYER, K., 1991: Estimating variances and covariances for multivariate animal models by restricted maximum likelihood. Genet. Sel. Evol. **23**: 67-83.

MEYER, M. M.; ENFIELD, F. D., 1975: Experimental evidence on limitations of the heritability parameter. Theor. Appl. Genet. **45**: 268-273.

MEYER, K.; THOMPSON, R., 1984: Bias in variance component estimators due to selection on a correlated trait. Z. Tierz. Zuchtungsbiol. **101**: 33-50.

MINVIELLE, F.; GALL, G. A. E., 1980: Artificial selection for 18-day pupa weight and opposing simulated natural selection in *Tribolium castaneum*. Theor. Appl. Genet. **56**: 49-55.

POLLAK, E. J.; UFFORD, G. R.; GROSS, S. J., 1977: Comparison of alternative models for within herd genetic evaluation of beef cattle. J. Anim. Sci. **45**(5): 1010-1014.

QUASS, R. L.; POLLAK, E. J., 1981: Modified equations for sire models with groups. J. Dairy Sci. **64**: 1868-1872.

ROBINSON, G. K., 1986: Group effects and computing strategies for models for estimating breeding values. J. Dairy Sci. **69**: 3106-3111.

SORENSON, D. A., KENNEDY, B. W., 1986: Analysis of selection experiments using mixed model methodology. J. Anim. Sci. **63**: 245-258.

THOMPSON, R., 1979: Sire evaluation. Biometrics **35**: 339-353.

TONG, A. K. W.; KENNEDY, B. W.; MOXLEY, J. E., 1980: Potential errors in sire evaluation from regional genetic differences. J. Dairy Sci. **63**: 627-633.

VAN VLECK, L. D., 1963: Genotype and environment in sire evaluation. J. Dairy Sci. **46**: 983-987.

VAN VLECK, L. D., 1966: Change in variance components associated with milk records with time and increase in mean production. J. Dairy Sci. **49**: 36-40.

VAN VLECK, L. D., 1990: Breeding value prediction with maternal genetic groups. J. Anim. Sci. **68**: 3998-4013.

WESTELL, R. A.; VAN VLECK, L. D., 1987: Simultaneous genetic evaluation of sires and cows for a large population of dairy cattle. J. Dairy Sci. **70**: 1006-1017.

WESTELL, R. A.; QUASS, R. L.; VAN VLECK, L. D., 1988: Genetic group in an animal model. J. Dairy Sci. **71**: 1310-1318.

WIGGANS, G. R.; MITZAL, I.; VAN VLECK, L. D., 1988: Animal model evaluation of Ayrshire milk yield with all lactations, herd-sire interaction, and group based on unknown parents. J. Dairy Sci. **71**: 1319-1329.

YAMADA, Y.; BELL, A. E., 1969: Selection for larval growth in *Tribolium* under two levels of nutrition. Genet. Res. Camb. **13**: 175-195.

Department of Animal Science, Iowa State University, Ames, Iowa, USA

CHAPTER 4. CORRELATED RESPONSE IN REPRODUCTIVE SUCCESS TO SELECTION FOR PUPA WEIGHT IN TRIBOLIUM CASTANEUM IN FOUR ENVIRONMENTS[3]

A paper to be submitted to Journal of Animal Breeding and Genetics

BY S. KONCAGUL and P. J. BERGER

Summary

Correlated responses of family size (FST) are reported for four lines maintained under diverse environmental conditions (lines): L1, 67% relative humidity (RH) and yeast-enriched whole wheat flour; L2, 67% RH and flour; L3, 80% RH and yeast-enriched whole wheat flour; and L4, 80% RH and flour, respectively. Selection was for increased pupa weight (PWT) over 23 generations. The best-ranked male from each line was bred to three females in every line similar to practices frequently used in commercial breeding programs.

The main objectives of this paper are to examine the correlated response in FST when selection was on PWT, and to examine genetic correlation between FST and PWT across four different environmental settings.

Analyses were carried out by using a multiple-trait derivative free restricted maximum likelihood procedure (MTDFREML) with animal models for data within lines and for data

---

[3]Journal Paper Number J- of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project number 3538, and supported by Hatch Act and State of Iowa funds.

combined over all lines. Analyses included both FST and PWT. The model for within line analyses included group effects for elite sires that were mated to females across all lines.

The mean phenotypic value of FST declined in all lines. The mean breeding value of FST increased (0.35 pupa per generation) in L3, but decreased in the other lines. Experiment-wise, heritability for FST was estimated to be 0.13, and the genetic correlation between FST and PWT was -0.10. Heritability estimates (and genetic correlations) were 0.13 (-0.25), 0.17 (-0.43), 0.9 (0.14) and 0.18 (-0.49) in L1, L2, L3 and L4, respectively. The results indicated that there is clear evidence of interaction between genotype and environment by obtaining different estimates of heritability and genetic correlation in different environmental conditions.

Key words: Correlated response, Family size, Genotype by environment interaction, and *Tribolium castaneum*.

Introduction

Selection for one character can cause a correlated response for another character. The magnitude and direction of the correlated response depends on genetic and environmental correlations between selected and unselected characters, and the genetic part is due to pleiotropy (Falconer and Mackay, 1996). Several studies across many species have shown that there is a negative correlation between growth and reproductive traits when there was selection on a growth trait; in mice (ROBERTS 1979; WILSON et al. 1971), in *Tribolium castaneum* (BERGER 1977; BERGER and LIN 1992), in pigs (LEGAULT 1971), and in Jersey cattle (BONCZEK et al. 1992), but others reported a positive correlation; in mice (FOWLER and EDWARDS 1960; RAHNEFELD et al. 1966; LAND 1970; HANRAHAN and EISEN 1974; EISEN

1978; DURRANT et al. 1980; RIOS et al. 1986); in pigs (MORRIS 1975); in *Tribolium* (CAMPO and DE LA BLANCE 1988; LIN 1997), while BRADFORD (1971) reported no significant relationship between litter size and body weight in mice.

This paper describes the correlated responses in FST at 19 d. to selection for increased PWT. FST was recorded at 19 d. to reflect the number of insects in a family that corresponded with the pupa weights recorded on the same day. Based on *a priori* information it was assumed that there was an antagonistic genetic relationship between FST and PWT. The selection experiment was designed to model the direct and correlated responses achieved from a selection and mating scheme frequently occurring in commercial populations of livestock. For example, in dairy cattle artificial insemination makes it possible to exchange semen of elite bulls across many countries. In this experiment different lines were established to represent a diversity of environmental opportunities for expression of genetic merit for PWT and family size or FST. Direct responses to selection for PWT have been reported earlier (KONCAGUL and BERGER 2001 submitted. See Chapter 2 for genetic responses across lines and Chapter 3 for genetic responses within lines).

The main purpose of the present study was to examine if the genetic correlation between PWT and FST was the same in all environments. The experiment also made it possible to examine changes in the genetic correlation across generations within lines with selection for PWT.

Materials and methods

Experimental design

A detailed description of the experiment has been presented earlier (KONCAGUL and BERGER 2001 submitted. See Chapter 2.). Briefly, insects in the base population were randomly assigned to four environments defined by two levels of two environmental conditions (lines): line 1 (L1), 67% relative humidity (RH) and yeast-enriched whole wheat flour diet; line 2 (L2), 67% RH with flour alone; line 3 (L3), 80% RH and flour-yeast diet; and line 4 (L4), 80% RH with flour alone (L4). Each line stands for a different environmental opportunity. Pupa weight (PWT) was measured on both males and females, and family size (FST) was measured only on females. Within line phenotypic mass selection was for increased PWT. The correlated response for FST was defined as the number of pupa produced by a female insect.

Statistical analysis

A distinction is made between two types of analysis procedures; 1) combined analysis implies a complete analysis of all data across all lines; the relationship matrix is complete for all insects; and 2) within line analyses implies using only data from a single line; the relationship matrix is incomplete in the sense that some male insects from outside the line have no direct ancestors within the line, fixed genetic groups are included in the model to account for genetic effects due to unknown ancestors. Results from a combined analysis give a general overview of experiment-wise results, whereas results from within line are specific to the line and environment.

A Multi-Trait Derivative-Free Restricted Maximum Likelihood (MTDFREML) procedure was used to obtain estimates of (co) variance components and genetic parameters (BOLDMAN et al., 1995). The model used in the analysis fits in the general class of multiple trait models having unequal design matrices (PWT had additional fixed effects not appearing in the model for FST), and missing records for some traits. FST was a trait of the females producing families therefore only some females had FST. The model used in the combined analysis is described as follows;

$$\begin{bmatrix} \mathbf{y}_{pwt} \\ \mathbf{y}_{fst} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{gls\_pwt} & \mathbf{X}_{sex\_pwt} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{X}_{gls\_fst} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{gls\_pwt} \\ \mathbf{b}_{sex\_pwt} \\ \mathbf{b}_{gls\_fst} \end{bmatrix} +$$

$$\begin{bmatrix} \mathbf{Z}_{a\_pwt} & \mathbf{Z}_{pe\_pwt} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_{a\_fst} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{a\_pwt} \\ \mathbf{u}_{pe\_pwt} \\ \mathbf{u}_{a\_fst} \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{pwt} \\ \mathbf{e}_{fst} \end{bmatrix} \qquad [1]$$

$$\mathbf{y} = \mathbf{X}\,\mathbf{b} + \mathbf{Z}\,\mathbf{u} + \mathbf{e}$$

where

$\mathbf{y}_{pwt}$ and $\mathbf{y}_{fst}$ are vectors of observations for PWT and FST; **X** and **Z** are incidence matrices for the corresponding fixed and random effects ($\mathbf{b}_{gls\_pwt}$, generation-line-set for PWT; $\mathbf{b}_{sex\_pwt}$, sex for PWT and $\mathbf{b}_{gls\_fst}$, generation-line-set for FST) and random effects ($\mathbf{u}_{a\_pwt}$ additive genetic effect for PWT, $\mathbf{u}_{pe\_pwt}$ permanent environmental effect for PWT, explained by the practice of raising full-sibs in the common environment of a single bottle until 19 d, and $\mathbf{u}_{a\_fst}$ additive genetic effect for FST, and $\mathbf{e}_{pwt}$ and $\mathbf{e}_{fst}$ are the vectors of residuals for PWT and FST.)

Expectations and (co) variances for the model were:

$$E\begin{bmatrix}\mathbf{y}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{Xb}\\ \mathbf{0}\\ \mathbf{0}\end{bmatrix},\ V\begin{bmatrix}\mathbf{y}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{ZGZ'}+\mathbf{R} & \mathbf{ZG} & \mathbf{R}\\ \mathbf{GZ'} & \mathbf{G} & \mathbf{0}\\ \mathbf{R} & \mathbf{0} & \mathbf{R}\end{bmatrix}$$

where

$$\mathbf{G}=\begin{bmatrix}\mathbf{A}\sigma^2_{a\_pwt} & \mathbf{A}\sigma_{a\_pwt\_fst} & \mathbf{0}\\ \mathbf{A}\sigma_{a\_fst\_pwt} & \mathbf{A}\sigma^2_{a\_fst} & \mathbf{0}\\ \mathbf{0} & \mathbf{0} & \mathbf{I}_c\sigma^2_{pe\_pwt}\end{bmatrix},$$

$$\mathbf{R}=\begin{bmatrix}\mathbf{I}_n\sigma^2_{e\_pwt} & \mathbf{I}_n\sigma_{e\_pwt\_fst}\\ \mathbf{I}_n\sigma_{e\_fst\_pwt} & \mathbf{I}_n\sigma^2_{e\_fst}\end{bmatrix}$$

A is the additive genetic relationship matrix, $\mathbf{I}_n$ and $\mathbf{I}_c$ are identity matrices of order equal to the total number of insects and number of families, respectively.

Data combined over all lines and generations were analyzed by using the model defined by equation [1]. Secondly, data within each line were analyzed by a model containing an additional fixed effect of groups for unknown sires, identified by the line and generation of insects with unknown sires (e.g. in this experiment groups were identified by the line and generation of sires from another lines than the particular line being analyzed) (WESTELL et al. 1988). Because some sires were mated to females across lines every generation these sires were considered to be unknown sires due to the fact that they have no genetic tie to relatives in earlier generations of lines other than their line of birth.

Equations for the second model used to analyze the data within lines were:

$$pwt_{ijkl} = gs_i + sex_k + \sum_{r=1}^{n} p_{lr}g_r + anim_l + pe_{ij} + e_{ijkl} \qquad [2a]$$

$$fst_{il} = gs_i + \sum_{r=1}^{n} p_{lr}g_r + anim_l + e_{il} \qquad [2b]$$

where p_{lr} is the additive genetic relationship between l^{th} animal and ancestor in r^{th} group, g_r is the unknown fixed effect for unknown sires from the r^{th} group, gs_i is fixed effect of i^{th} generation-set combination, and all other terms in the model are the same as defined above for equation [1]. In the model defined by equations 2a and 2b, the breeding value of animal *l* is defined as $\sum_{r=1}^{n} p_{lr}g_r + anim_l$ (WESTELL and VAN VLECK, 1987). Grouping started in generation two because all sires in generation one had genetic ties to the previous generation due to the reason that all insects from the base population were included in every within line analysis. There were three groups every generation within a line because each sire from other lines was considered to be representative of a different level of genetic merit, i.e., in L1, sires from L2, L3 and L4 were assigned to different groups in each generation.

The models defined by equations 1 and 2 included the complete additive genetic relationship matrix among all insects in the data being analyzed, and all records on which selection was based were also included in the analyses. These conditions were necessary to obtain estimates unbiased by selection (VAN DER WERF and DE BOER, 1990).

Segmented or piece-wise regression (FULLER 1969; NETTER et al. 1996 p474) and broken-line regression (Robbins, 1986; SAS, 1990) procedures were used to characterize phenotypic, genetic and environmental changes in FST over generations. This procedure was necessary because one continuous regression function with one slope could not explain all

changes in responses over generations. In segmented regression, it is assumed that you know from prior knowledge the end-point of each segment, and two or more regression functions are fitted to the continuous response variable. We chose generations 5, 10, 13 and 22 as end-points based on changes in the phenotypic response in FST shown in Figure 1a. Broken-line regression is a more comprehensive analysis procedure, because it allows for simultaneous estimation of join-points and slopes for the regression function explaining the response in the continuous dependant variable. It is assumed that the data can be described by some increasing or decreasing function. The point joining the function on the continuous scale of response is also unknown. Regression coefficients calculated by a continuous regression function with one slope are also provided for comparison.

Results and discussion

Phenotypic response

Phenotypic means for combined data as well as data within each line are plotted against generation numbers in *Fig.* 1a and b, respectively. Regression coefficients obtained by using the segmented regression procedure are given in Table 1.

For the combined data, there was considerable variability in phenotypic changes in FST between generations. There was an increase in FST up to generation 5, a decrease from generation 6 to 10 ($P < .05$), no significant change from generation 11 to 13, and a significant decrease from generations 14 to 22 ($P < .001$). From generation 14 to 22, the mean phenotypic value of the population declined, 1.70 pupae per generation. The mean of 6 pupae per family at generation 22 was a 70% reduction of FST from the base population with a mean of 21 pupae per family.

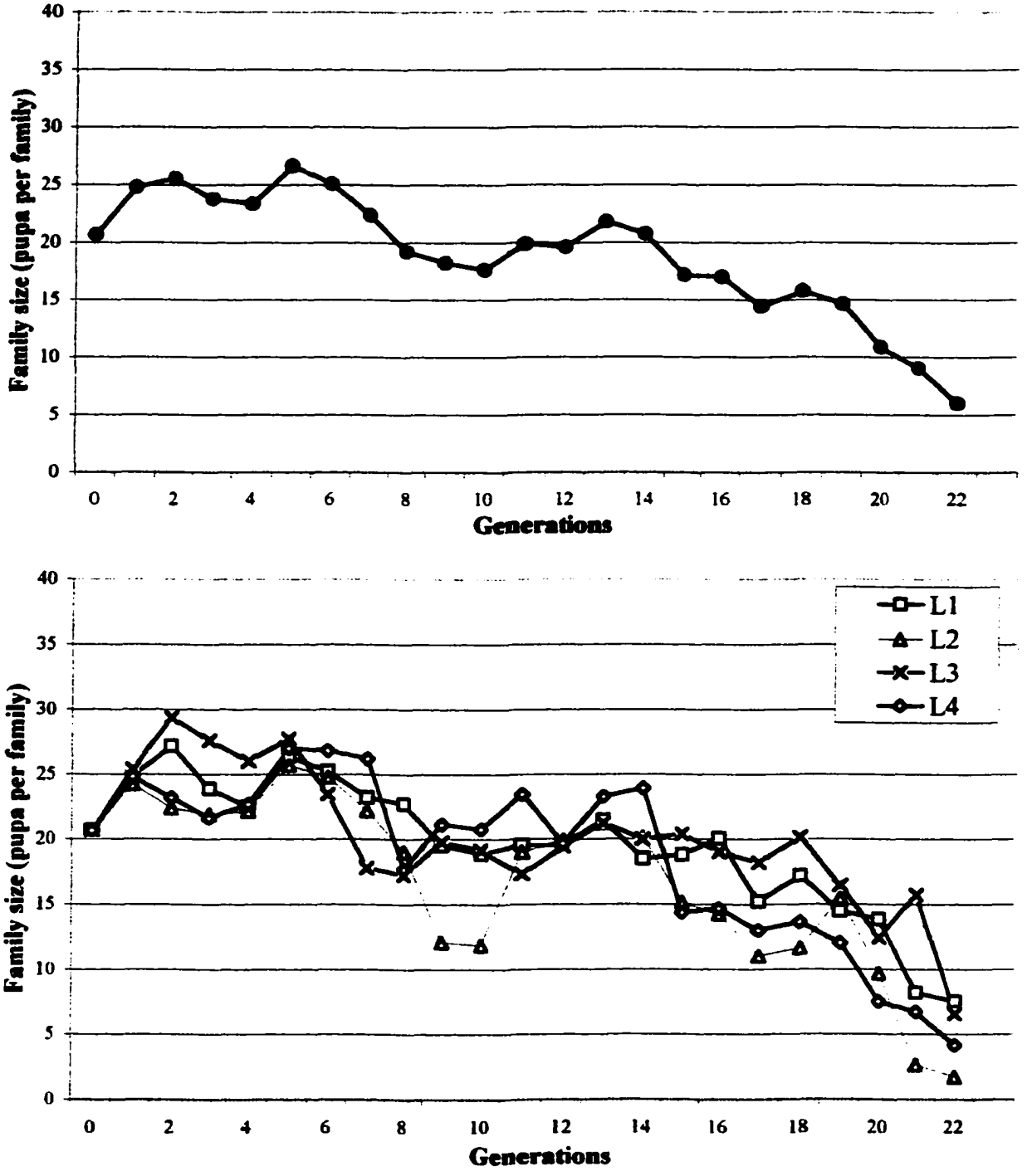

Fig. 1. Phenotypic trend for family size trait,
a) for data combined across lines (above), b) for data within lines by generation (below):
L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein,
L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein.

Table 1. Phenotypic trends in family size at 19 d. within lines and combined across lines for early, mid, and late generations of selection.

	Generation	Combined	Line 1[1]	Line 2	Line 3	Line 4
ΔP	0 to 5	0.65 ± 0.31^{+}	0.52 ± 0.39	0.33 ± 0.50	1.34 ± 0.48*	0.35 ± 0.47
	6 to 10	-0.92 ± 0.31*	-0.58 ± 0.39	-1.81 ± 0.50*	-0.91 ± 0.48^{+}	-0.39 ± 0.47
	11 to 13	-0.79 ± 0.56	-1.05 ± 0.70	-0.78 ± 0.90	-1.05 ± 0.87	-0.31 ± 0.86
	14 to 22	-1.70 ± 0.16**	-1.58 ± 0.20**	-2.13 ± 0.25**	-1.21 ± 0.24**	-2.09 ± 0.24**

$^{+}P < 0.10$
$^{*}P < 0.05$
$^{**}P < 0.001$
[1]Line 1 = 67% relative humidity (RH) and yeast-enriched flour diet; Line 2 = 67% RH and flour alone; Line 3 = 80% RH and yeast-enriched flour diet; and Line 4 = 80% RH and flour alone.

Few slopes of the segmented regression from the within line analyses were significantly different from zero up to generation 13. After generation 13, however, the within line analyses supported a significant decline in FST ($P < .001$).

Over all generations, correlated response in FST to direct selection for PWT was negative, –0.69 insects per generation (Table 2, Linear regression). The largest decreases were for FST in L2 and L4, respectively. Similar, but smaller trends were observed in L1 and L3. Lin (1997) reported a correlated response in family size of -1.29 pupae per generation. Berger (1977) reported a reduction of 1.11 pupae per generation.

The broken line regression model showed that the lines started to differentiate around generation 7 for L1, L2, and pooled data, and around generation 12 for L4 (Table 2, Non-linear regression). The broken-line regression model did not converge for L3. Until the break point the trends were not significantly different from 0, but after the break point they were highly significant ($P < 0.001$) and negative.

Genetic response

Consideration of genetic changes across all lines combined, or within individual lines, *Fig.* 2 gives a very different perspective on the genetic changes that occurred in this experiment. The broken-line analysis helped to identify the generation in which shifts in genetic response occurred and the rate of the genetic changes in FST during different generations of selection (Table 2).

Experiment-wise there was one uniform rate of genetic change in FST for the entire 23 generations, -0.10 pupae per family, obtained from both broken-line and linear regression

Table 2. Regression coefficients for phenotypic, genetic, and environmental changes in family size at 19 d. from linear, and non-linear regression analysis with one break point.

		Non-linear regression				Linear regression
		1st interval	Break point (95% CI)[1]		2nd interval	
	Data	b ± SE	Estimates	(LB, UB)	b ± SE	Generation 0 to 22
ΔP	L1	0.22 ± 0.37	7	(3, 12)	-0.85 ± 0.14**	-0.65 ± 0.08**
	L2	0.57 ± 0.73	7	(0, 14)	-0.94 ± 0.21**	-0.79 ± 0.13**
	L3	1.33 ± 1.33[a]	5	(5,5)	-0.55 ± -0.55[2]	-0.58 ± 0.11*
	L4	-0.09 ± 0.23	12	(9, 14)	-1.81 ± 0.26**	-0.80 ± 0.12**
	Combined	0.53 ± 0.44	7	(2, 12)	-0.82 ± 0.13**	-0.69 ± 0.08**
						Generation 0 to 23
ΔG	L1	-0.07 ± 0.19	7	(4, 9)	-0.73 ± 0.05**	-0.56 ± 0.04**
	L2	-0.32 ± 0.10*	6	(4, 8)	-0.43 ± 0.02**	-0.33 ± 0.02**
	L3	0.05 ± 0.52	2	(0, 4)	0.36 ± 0.01**	0.35 ± 0.01**
	L4	-0.77 ± 0.00**	0	0	-0.65 ± 0.02**	-0.65 ± 0.02**
	Combined	0.09 ± 0.00**	1	(0, 4)	-0.10 ± 0.004**	-0.10 ± 0.003**
						Generation 0 to 22
ΔE	L1	0.10 ± 0.09	20	(19, 21)	-3.37 ± 1.58*	-0.07 ± 0.09
	L2	-0.47 ± 0.26+	13	(8, 17)	-1.49 ± 0.39*	-0.46 ± 0.12*
	L3	1.08 ± 1.02	5	(0, 13)	-0.91 ± 0.15**	-0.92 ± 0.11**
	L4	0.13 ± 0.14	19	(15, 23)	-1.76 ± 1.46	-0.12 ± 0.12
	Combined	0.25 ± 0.39	7	(1, 13)	-0.74 ± 0.15**	-0.60 ± 0.09**

+P<0.10, *P<0.05, **P<0.001

[1]95% confidence interval

[2]analysis did not converge

LB= lower bound, UB= upper bound

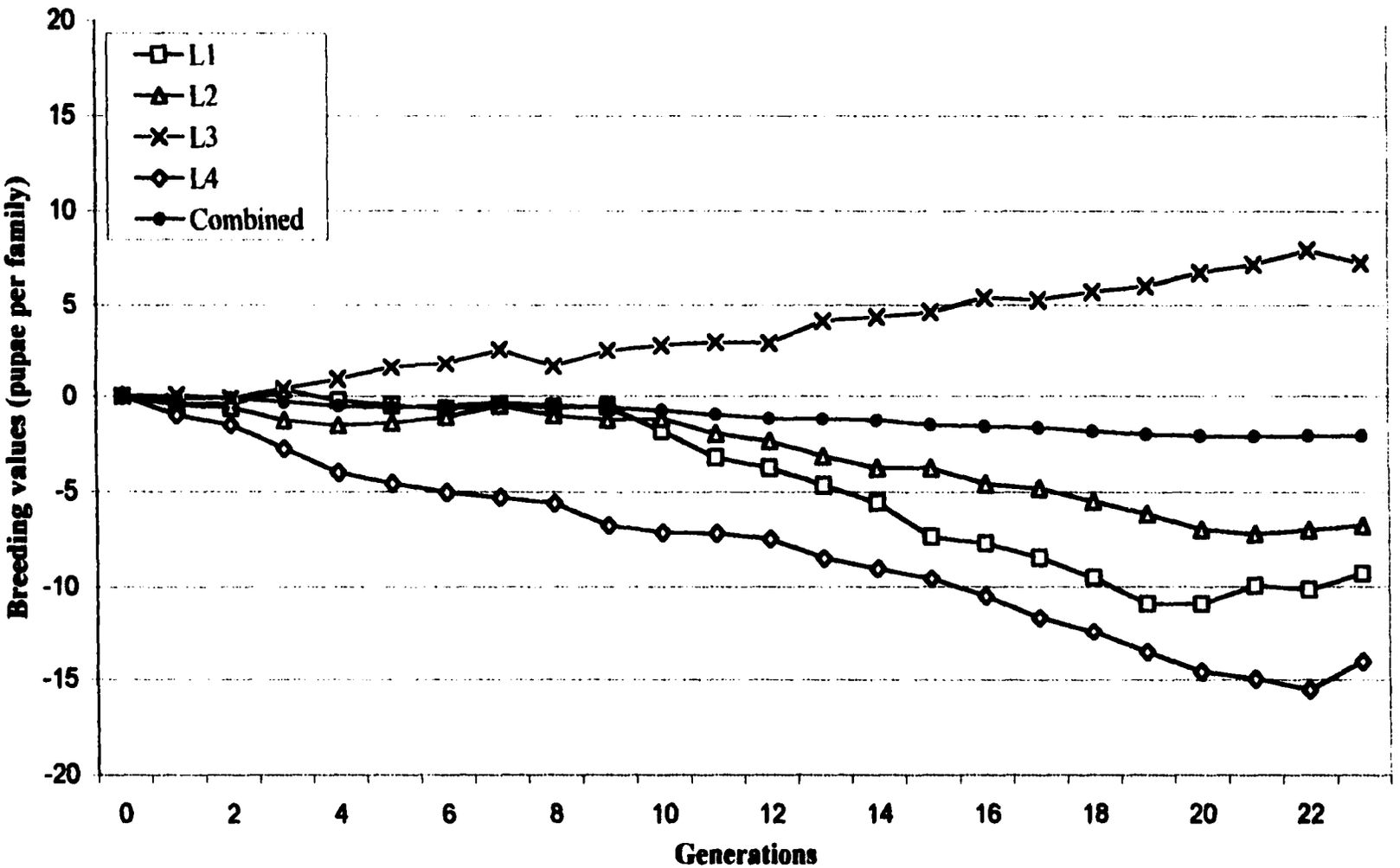

Fig. 2. Genetic trends for family size trait for data combined across lines and for data withinlines by generation: L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein, L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein, Combined (—●—).

procedures (See row 10 of Table 2). Similarity between the regression coefficients indicates that there was uniformity of response over all generations.

Within lines, however, there were markedly different patterns of genetic response. Break points for L3 and L4 were at generation 2 and 0, respectively. Linear regression coefficients over all generations and the regression coefficients for the second interval were nearly identical when the break points were estimated to be at or near the beginning of the experiment. This implies that there was one uniform rate of genetic response over all generations in L3 and L4; L3 increased 0.36 pupae per generation and L4 decreased –0.65 pupae per generation. L1 and L2 showed no correlated response in FST up to generations 7 and 6, respectively. Afterward there were significantly negative ($P < 0.001$) trends in FST of –0.73 and –0.43 pupae per generation in L1 and L2, respectively.

Environmental response

Environmental values are plotted against generation number in Fig. 3a and b for combined data and within line data, respectively. Regression coefficients are given in Table 2. Environmental values fluctuated generation to generation.

Experiment-wise there were highly variable non-significant changes in the mean effect of environment on FST up to generation 7. Thereafter, there was a significant ($P < .01$) decrease in environmental effects on FST, –0.74 pupae per family per generation.

Within lines, however environmental effects changed at widely different places. Significant changes in environmental effects occurred at generation 20 for L1, at generation 13 for L2, at generation 5 for L3, and there were no significant changes in environmental effects in FST in L4.

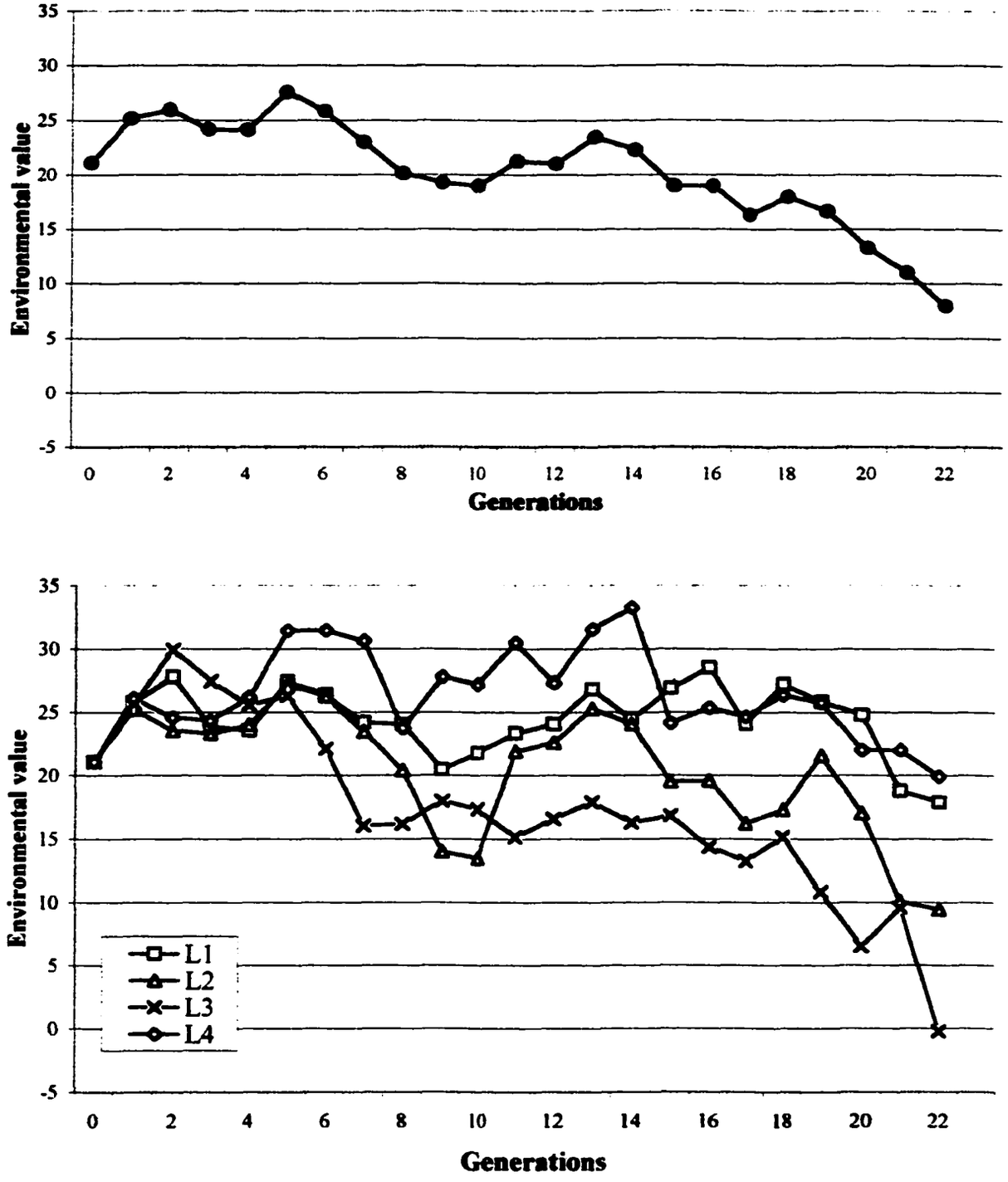

Fig. 3. Environmental trend for family size trait,
a) for data combined across lines (above), b) for data within lines by generation (below): L1 (—□—) low humidity - high protein, L2 (—Δ—) low humidity - low protein, L3 (—x—) high humidity, high protein, and L4 (—◊—) high humidity - low protein.

Variance components and parameters

Combined analysis

Estimates of covariance components between PWT and FST, and parameter estimates for data in the base population as well as for all data combined across lines after selection are given in Table 3. Estimates of phenotypic and error variance were larger using all data than the estimates from the base population. Estimate of the additive genetic variance for FST was 56% smaller using all data than the estimate in the base population. Phenotypic variance for FST was about 8% larger in all data than in the base population; error variance for FST was 39% larger.

After selection for 23 generations, the heritability estimate for FST was 0.13. This estimate of heritability is slightly higher than estimates reported by other researchers; 0.09 (CAMPO and DE LA BLANCE 1988), 0.11 (BERGER 1977), 0.09 with a univariate model and 0.09 with a multivariate approach (BERGER and LIN, 1992), and similar to the estimates reported by LIN (1997), 0.09 and 0.13. The higher heritability estimates for FST in this experiment than in other studies indicated that there was greater genetic variability among lines in this study than in earlier studies. Possibly, the greater genetic variability demonstrated here might be due to exchange of male germplasm across environments.

Across all generations of selection for increased pupa weight the genetic correlation was nearer to zero than in the base population, -0.10 versus –0.26, respectively. The environmental correlation was slightly larger across all generations than in the base population, -0.08 versus –0.06. Magnitude of the difference between genetic and environmental correlations was much less in combined data. Results from correlated

Table 3. Variance components and parameter estimates for family size at 19 d and pupa weight trait for data in base population and for data pooled across lines after selection.

Data	Base Population			Combined		
Trait	FST	PWT	Cov.	FST	PWT	Cov
Variance Components						
Phenotypic	50.65	50,810.97	-201.77	54.47	78,669.82	-155.60
Additive	16.57	18,842.08	-146.05	7.22	16,117.04	-34.65
Common		8,133.93	.		17,735.07	
Error	34.09	23,834.96	-55.73	47.26	44,817.71	-120.95
			Parameters			
Heritability (h^2)	0.33	0.37		0.13	0.20	
Genetic Correlation (r_g)		-0.26			-0.10	
Permanent Environment (c^2, %)		0.16			0.23	
Error (% of total)	0.67	0.47		0.87	0.60	
Env. Corr.(r_e)		-0.06			-0.08	

responses in FST support a hypothesis of an antagonistic genetic relationship between PWT and FST. BERGER (1977) and BERGER and LIN (1992) reported a higher negative genetic correlation between PWT and FST, -0.43 and -0.35, respectively. Whereas, CAMPO and DE LA BLANCE (1988) reported a positive genetic correlation of 0.13 ± 0.14, and LIN (1997) reported genetic correlations of 0.04 and 0.15 in replications 1 and 2, respectively, when selection was for increased pupa weight.

Within-line analyses

Variance-covariance components and parameter estimates for correlated responses of FST from within line analyses are given in Table 4. The largest estimate of phenotypic variance was obtained in the best environment, i.e. in the high protein diet and 80% RH (L3). Lowest estimate of phenotypic variance was obtained in the poorest environment, low level of protein diet and low RH (L2). The additive genetic variances for FST in L1 and L2 were

Table 4. Variance components and parameter estimates for family size at 19 d and pupa weight from within line analyses with an animal model including fixed effect of unidentified sires imported from different environments.

		Variance components				Parameter estimates				
Trait	Data[1]	Phenotypic	Additive	Common	Error	h^2	r_g	c^2	e^2	r_e
FST	L1	58.23	7.35		50.88	0.13			0.87	
	L2	42.37	7.33		35.04	0.17			0.83	
	L3	65.87	5.70		60.16	0.09			0.91	
	L4	48.98	8.76		40.22	0.18			0.82	
PWT	L1	85,258	25,909	17,725	41,625	0.30		0.21	0.49	
	L2	52,010	10,410	12,381	29,219	0.20		0.24	0.56	
	L3	100,152	36,684	17,592	45,877	0.37		0.18	0.46	
	L4	69,136	29,045	11,884	28,207	0.42		0.17	0.41	
FST,PWT	L1	-264.49	-110.52		-153.98		-0.25			-0.11
	L2	-129.98	-118.54		-11.44		-0.43			-0.01
	L3	-337.89	61.99		-399.88		0.14			-0.24
	L4	-58.50	-248.46		189.92		-0.49			0.18

[1]L1, data in line 1; L2, data in line 2; L3, data in line 3; L4, data in line 4

almost identical. A slightly lower estimate of the additive genetic variance was obtained in L3, and the highest estimate was in L4. Error variance in L2 was the lowest, and the highest in L3.

The heritability estimate for FST was the smallest in the lines receiving the high protein diet, L1 and L3, and highest in lines receiving the low protein diet, L2 and L4. Except for the estimate in L3, heritability estimates for FST in other lines were higher than the estimates reported by BERGER (1977); CAMPO and DE LA BLANCE (1988); BERGER and LIN (1992); LIN (1997).

The sign and magnitude of genetic and environmental correlations varied from one environment to another environment. Except for L4, estimates of environmental correlations were negative in the other lines. Except for L3, genetic correlations between PWT and FST were negative and different in all lines. One possible explanation for getting different genetic correlation estimates in different environments could be that pleiotropic effects of genes are environmentally dependent. Another possible explanation could be that different genes are responding differently in different environments, and this leading us to select different sets of genes in depending on environmental conditions and genetic nature of traits affected by selection.

In a review of several laboratory experiments, Roberts (1979) concluded that selection for growth increases body size and demand for food intake, and animals eat more and become fatter. Thus, fat animals are less willing to breed. Because animals are fat this results in some reproductive deficiencies. He concluded that correlated response in fitness is partly due to physiological difficulties, as well as, linkage and pleitrophic effects of genes. Good nutrition allows one to select heavier female animals, but heavier females could have

fatter reproductive organs and this might cause a reduction in reproductive success. Physiological problems, however, could be overcome by restricting food, and it would still be possible to select favorable genes for growth.

In this selection experiment, we believe that physiological difficulties in fitness due to food intake were overcome due to the fact that each full-sib family had a fixed amount of food during the experiment. This, however, might have caused greater competition among insects within a family, because insects were getting larger due to selection for pupa weight. Under a hypothesis of competition, larger insects might have eaten more while smaller insects might have eaten less. Consequently, this could be a reason of larger error variance estimates by using all data after selection than by using the data in the base population.

Another implication that can be drawn from these results is the clear evidence for the existence of genotype by environment interaction. All four lines were generated from a common base population and there was gene transfer from one environment to others, but different environments lead to different parameter estimates.

In conclusion, the correlated response of FST was negative when selection was for increased PWT. The magnitude of the genetic and environmental correlations depended on the environment in which selection was performed. Environment, in terms of diet or temperature and humidity, has an important role determining the magnitude of correlated response in reproduction.

The results indicated that good a environment, allowing insects to show their limit of genotypic ability, increased the phenotypic and environmental variances, while decreasing the additive genetic variance. The effects of different environments lead to estimates of variance components and parameter estimates strongly implying an interaction between

genotype and environment. Genotype by environment interaction can also have a large role in defining the optimum environment for growth and reproduction.

This experiment draws attention to the fact that under certain environmental conditions an undesirable correlated response in reproductive success can be associated with selection for growth, i.e., all environments except L3. Correlated response in reproductive success can no longer be ignored, or left unmeasured, in cattle and pigs when there is intense selection for growth without proper identification of optimum environmental conditions for reproductive success.

References

BERGER, P. J., 1977: Multiple-trait selection experiments: Current status, problem areas and experimental approaches. In: Int. Conf. Quant. Genet. p. 191-204. Iowa State Univ. Press, Ames.

BERGER, P. J.; LIN, E.-C., 1992: Comparison between estimates of genetic parameters from univariate and multivariate animal models. NCR-21 Quantitative Genetic Annual Meeting. Clemson University, Clemson, SC. Mimeo. pp:6.

BOLDMAN, K. G.; KRIESE, L. E.; VAN VLECK, L. D.; VAN TASSELL, C. P.; KACHMAN, S. D., 1995: A manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances [draft]. U.S. Dept. of Agriculture, Agriculture Research Service. Lincoln, NE.

BONCZEK, R. R.; RICHARDSON, D. O.; MOORE, E. D.; MILLER, R. H.; OWEN, J. R.; BELL, B.

R., 1992: Correlated responses in reproduction accompanying selection for milk yield in Jersey. J. Dairy Sci. **75**: 1154-1160.

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

CAMPO, J. L.; DE LA BLANCE, A. S., 1988: Experimental comparison of selection methods to improve a non-linear trait in *Tribolium*. Theor. Appl. Genet. **75**:569-574.

DURRANT, B. S.; EISEN, E. J.; ULBERG, L. C., 1980: Ovulation Rate, embryo survival and ovarian sensitivity to gonadotrophins in mice selected for litter size and body weight. J. Reprod. Fert. **59**: 329-339.

EISEN, E. J., 1978: Single-trait and antagonistic index selection for litter size and body weight in mice. Genetics **88**: 781-811.

FALCONER, D. S.; MACKAY, T. F. C., 1996: Introduction to quantitative genetics. (4^{th}. Ed.). Logman. Malaysia.

FOWLER, R. E.; EDWARDS, R. G., 1960: The fertility of mice selected for large or small body size. Genet. Res. Camb. **1**: 393-407.

FULLER, W. A., 1969: Grafted polynomials as approximating functions. Australian J. Agr. Econ. **13**: 35-46.

GARNETT, I.; RAHNEFELD, G. W., 1976: Mass selection for post-weaning growth in swine. V. Correlated response of reproductive traits and pre-weaning growth. Can. J. Anim. Sci. **56**: 791-801.

HANRAHAN, J. P.; 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.

KONCAGUL, S.; BERGER, P. J., 2001: Response to selection for increased pupa weight in

Tribolium castaneum in four environments. J. Anim. Breed. and Genet. (submitted).

LAND, R. B., 1970: Genetic and Phenotypic Relationships between ovulation rate and body weight in the mouse. Genet. Res. Camb. **15**: 171-182.

LIN, E.-C., 1997: Estimates of genetic parameters from a selection experiment for growth and reproductive success in *Tribolium castaneum* by using different statistical methods. Ph.D. Dissertation. Iowa State University, Ames, Iowa.

LEGAULT, C., 1971: Relationship between fattening and carcass performance and litter performance in pigs. Ann. Genet. Sel. Anim. **3**: 153-160.

MORRIS, C. A., 1975: Genetic relationships of reproduction with growth and with carcass traits in British pigs. Anim. Prod. **20**(1): 31-44.

NETER, J.; KUTNER, M. H.; NACHTSHEIM, C. J.; WASSERMAN, W., 1996: Applied Linear Statistical Models. Fourth Ed. McGraw Hill, NY.

RAHNEFELD, G. W.; COMSTOCK, R. E.; SINGH, M.; NAPUKET, S. R., 1966: Genetic Correlation between growth rate and litter size in mice. Genetics **54**: 1423-1429.

RIOS, J. G.; NIELSEN, M. K.; DICKERSON, G. E., 1986: Selection for postweaning gain in rats: II. Correlated response in reproductive performance. J. Anim Sci. **63**: 46-53.

ROBBINS, K. R., 1986: A method, SAS program, and example for fitting the broken line to growth data. Research Report 86-09. University of Tennessee, Agric. Expt. Sta., Noxville, TN.

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

SAS Institute Inc., 1990: SAS/STAT User's Guide, Version 6 Volume 2 (4^{th} ed.) Cary, N.C.: SAS Insytitute Inc.

VAN DER WERF, J. H. J.; DE BOER, I. J. M., 1990: Estimation of additive genetic variance when base populations are selected. J. Anim. Sci. **68**: 3124-3132.

WESTELL, R. A.; VAN VLECK, L. D., 1987: Simultaneous genetic evaluation of sires and cows for a large population of dairy cattle. J. Dairy Sci. **70**: 1006-1017.

WESTELL, R. A.; QUASS, R. L.; VAN VLECK, L. D., 1988: Genetic group in an animal model. J. Dairy Sci. **71**: 1310-1318.

WILSON, S. P.; GOODALE, H. D.; KYLE, W. H.; GODFREY, E. F., 1971: Long term selection for body weight in mice. J. Hered. **62**: 228-234.

CHAPTER 5. GENERAL CONCLUSIONS

PUPA WEIGHT

Response to selection

It was possible to define four environments that could have a measurable effect on pupa weight at 19 d. Selection increased the mean phenotypic values for pupa weight in all populations regardless of differences in environments.

Phenotypic, genetic, and environmental responses were greater on a high protein diet than on a low protein diet. As a factor used to modify or create different target environments, diet (i.e., high versus low protein) has a larger effect on growth and development than two levels of humidity (i.e., 67 and 80% relative humidity).

Variance components and parameters

Combined analysis

Total phenotypic variance was greater from the analysis including all data following 23 generations of selection than in the base population. The increase in total phenotypic variance was attributable to increases in error and common environmental variances across generations of selection. Error and common environmental variances were substantially larger in generations where selection occurred than in the base population. The increase in error (within family) variance can be attributable partly to competition among full-sibs in a bottle. The common environmental effect was a consistent factor contributing to the total phenotypic variance of pupa weight.

The estimate of heritability was smaller after selection than before selection. A decrease in heritability over selected generations can be explained mainly by the increase in common environmental and residual variance.

Within-line analyses

Estimates of variance components and parameters depended on joint effects of humidity and plane of nutrition, which defined specific environments for growth of insects. The optimum environment and the poorest environment set maximum and minimum limits on estimates of phenotypic and additive genetic variance. The variance components, especially additive genetic and total variances may not be homogeneous across environments or subpopulations.

Estimates of variance components and parameters for both sexes fluctuated from line to line. This shows that pupa weight does not depend on sex-linked genes.

FAMILY SIZE

Response to selection

In general, selection for pupa weight resulted in reduced mean family size, about 70% in 23 generations. However, there were markedly different patterns of genetic response within lines. Lines under high level of protein started to exhibit a different rate of response in FST in very early generations than lines under a low level of protein. Estimates of correlated responses by using linear and broken-line regression procedures led us to conclude that genetic changes in family size occurred at different generations depending on the environmental conditions for each line.

This experiment draws attention to the fact that an undesirable correlated response in reproductive success is frequently associated with selection for growth. Correlated response in reproductive success can no longer be ignored, or left unmeasured, in cattle and pigs when there is intense selection for growth.

Variance components and parameters

Combined analysis

Estimates of phenotypic and error variance were larger using all data than the estimates from the base population. However, the estimate of the additive genetic variance was 56% smaller using all data across all lines and generations than the estimate in the base population.

The higher heritability estimates in this experiment than in other studies indicates that there was greater genetic variability among lines in this study than in earlier studies. Possibly, the greater genetic variability demonstrated here might be due to exchange of male germplasm across environments.

Within-line analyses

The largest estimate of phenotypic variance was obtained in the optimum environment, and the lowest estimate of phenotypic variance was obtained in the poorest environment. Heritability estimates, however, were the smallest in the lines receiving the high protein diet, and highest in lines receiving the low protein diet. The sign and magnitude of genetic and environmental correlations varied from one environment to another.

Based on results presented for this experiment we concluded that pleiotropic effects of genes were environmentally dependent, or that different genes were responding differently in different environments, and this led us to select different sets of genes depending on environmental conditions.

MODELING EFFECTS OF MIGRATION

The importation of sires over several generations from different populations can have important consequences on genetic prediction of breeding values and estimation of genetic parameters using an animal model. Imported parents need to be assigned to groups because their unknown ancestors cannot be assumed to be at the same level of merit as the other insects in the population. Animal models seriously underestimate the true additive genetic variance if parents imported into the population are not assigned to groups as an additional fixed effect in the model.

Grouping of unknown parents is somewhat arbitrary and should be made according to environment or the population where the unknown parents were born. It would be a mistake to group unknown parents based on some function of time alone if they come from different populations and possibly from different genetic backgrounds.

GENOTYPE BY ENVIRONMENT INTERACTION

The result of this experiment showed that the ratio of additive genetic variance to phenotypic variance was different for different environments, and that these differences were larger in some environments than others. This was interpreted as clear evidence of existence of genotype by environment interaction.

Genotype by environment interaction can also have a large role in defining the optimum environment for growth and reproduction. Results were reported showing that the target environment for progeny of selected parents should be the same or better than the environment from which the parents were selected.

ACKNOWLEDGMENTS

I wish to express my gratefulness to all taxpayers in Turkey. I could not be here without their tax money.

Sincere appreciation is expressed to Dr. P. J. Berger for his guidance, patience, and flexibility as the major Professor. My sincere appreciation is also expressed to his wife, Fran. I first tasted American hospitality in their house.

Thanks to Drs. Rohan Fernando, Doyle E. Wilson, Edward Pollak, and Kendall R. Lamkey as committee members, and to all of my teachers who taught me from primary school to the conclusion of this dissertation.

Thanks to my wife, Yeliz, my son, Firat (diseased), my daughter, Filiz, my father, Mustafa (diseased) , my mothers, Nezaket (diseased) and Inci (diseased), my brothers, Seyit Ahmet and Mirati, my sisters, Sevil and Irep, for their spiritual support.