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QUANTITATIVE GENETICS OF ANTHROPOMETRIC VARIATION IN THE SOLOMON ISLANDS

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# Quantitative Genetics of Anthropometric Variation in the Solomon Islands

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## Abstract

This work follows the direction set by Sewall Wright in applying path analysis, and other multivariate statistical techniques, to the study of anthropometric variation. Two themes concerning anthropometric variation are examined. The first concerns the need to partition phenotypic covariation between traits into genetic and environmental components. The second theme emphasizes the difference between within- and between-group heritability. Data on anthropometric variation in six Solomon Island populations is analyzed using statistical models appropriate to these themes.

The correlation structure of 27 anthropometric measurements is examined by cluster analysis and principal components analysis. The six populations show a common pattern (in both males and females) which echoes earlier studies. The correlation matrix of measurements is then partitioned into genetic and environmental components and the genetic correlation matrix is examined, once again by cluster analysis and principal components analysis. There is a fairly close agreement between the genetic correlation structure and the phenotypic correlation structure. The environmental correlation matrix is not examined further because it is very poorly estimated.

The partitioning of phenotypic correlations into genetic and

environmental components is based on a multivariate generalization of a path model for the heritability of a continuous trait proposed by C.C. Li. The parameters estimated in the single trait model include additive genetic heritability, common home environment, and genetic correlation between spouses. In order to fit this model observations are required on parent-offspring, spouse-spouse, and sib-sib correlations.

The heritability of each measurement is obtained (pooled within each sex and population) and some comparisons are made with values obtained from other studies. Heritability values for the Solomons are markedly lower than those reported elsewhere. However, when total heritability (ignoring subpopulation structure) is estimated for the six Solomons populations, the values are higher and form a more familiar pattern. The striking difference between the two kinds of heritability in the Solomon Islands re-emphasizes the danger of using total heritability estimates obtained from several subpopulations or a national sample.

The within-group heritability of a trait has been used elsewhere as a means of identifying anthropometric (and psycometric) variables for which between-group variation has a primarily genetic basis. It is, however, the between-group heritability which should be used for this purpose.

The between-group component of heritability for each measurement is compared to the within-group heritability and to levels of

between-group phenotypic variation. Between-group heritability presents a different picture from that of within-group heritability. The data demonstrate that high within-group heritability for a given trait does not imply that between-group variation in that trait is genetic in origin.

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# Chapter 1

## Some Multivariate Approaches to Anthropometric Variation

### 1.1 Prologue

The study of variation in physical form within and between human groups has long occupied a central position in physical anthropology. The analysis of human biometric variation has also attracted the interest of statisticians who have made major contributions to the development of statistical techniques. Among these contributors are many well known names: Galton (1886), Pearson (Pearson and Lee 1903), Mahalanobis (1936), Fisher (1918), Wright(1931), and C.R. Rao (Majumdar and Rao 1960). This long history of cooperation between statisticians and anthropologists has certainly been of mutual benefit. One of the areas in which progress has been conspicuous is multivariate statistical techniques.

The predeliction of physical anthropologists to include a number of correlated variables in their between-group comparisons presents a problem for data analysis using univariate statistical techniques. The analysis of correlated variables using

univariate approaches is less than satisfactory for two reasons. First, the calculation of probabilities becomes distorted when each variable is counted as if it were an independent piece of evidence. Second, treating each variable as a separate piece of evidence ignores much interesting information concerning the relationship between the variables themselves. Multivariate approaches to estimation and hypothesis testing were developed by Fisher (1936) and Mahalanobis (1936), although computationally simpler techniques were more often used before the advent of modern computers. The multivariate techniques commonly in use today represent broader generalizations of their univariate counterparts, including the multivariate general linear model which emphasizes the common threads running through a variety of techniques (Bock 1975; Finn 1974; Harris 1975).

This work is an attempt to follow the lead set by Sewall Wright in the use of path analysis for the study of biometrical variation (Wright 1920, 1932, 1934, 1960, 1968, 1969, 1977, 1978a, 1978b). Path analysis is primarily a set of techniques which allow an investigator to determine if a given causal model is consistent with a set of observed correlations. In its simplest form it resembles multiple regression on standardized variables, but the method can be used to study any linear model. Essential to the use of path analysis is a path diagram which provides a picture of the causal relationships among the variables in a particular model. Although path analysis is as old as many other multivariate techniques used in biometry, it is

less widely known and utilized. Commenting on the reasons for the slow development of path analysis, C.C. Li observes:

> The path method has been "underutilized" in biology (and in other fields), partly because we are overwhelmed by the beauty and logic of formal statistical methods and partly because we wish to be relieved of responsibility of using a concept of our own. Consequently, many, if not most, of the so-called "analyses" are simply based on pre-programmed procedures, regardless of the particular meaning of each of the variables under study, still less on their possible step by step relationships. (Li in Morton and Chung (eds) 1978:86).

However, the book from which this quote is taken is ample evidence of renewed interest in path analysis. Much of this interest is found in sociological applications, and more recently in epidemiology. Although Morton and Rao have been vocal proponents of the use of path analysis for the study of biometrical variation in man (Morton and Rao 1978; Morton, et al. 1975) their work has centered primarily on modeling the genetic and environmental determinants of intelligence test scores. This has had one very fortunate effect. The models and estimation procedures developed by Morton and his associates have been subjected to far more careful scrutiny and criticism (cf. Goldberger 1978) than would studies on the genetic determinants of leg length. This work on anthropometric variation benefits

greatly from the attention which has been lavished on the I.Q. debate.

Two central themes will unfold as this work progresses. The first is the need for understanding the genetic and environmental factors which combine to produce both biometric variation and covariation. A path model is developed in the second chapter which may be used to this end. The second theme concerns the difficulty of understanding the causes of between-group variation, especially in the absence of a good understanding of within-group variation. Standard multivariate statistical techniques for the study of between-group and within-group variation can be improved by the development and testing of associated path models.

## 1.2 Within Group Variation

The application of traditional methods from biometrical genetics to the study of quantitative variation in man has proceeded along two relatively independent fronts. Some workers have made estimates of the heritability of different anthropometric traits treating each variable independently (Clark 1956 ; Osborne and DeGeorge 1959 ; Vandenberg 1962; Mueller

1976, 1977, 1978; Mueller and Titcomb 1977; Susanne 1975, 1977; Rao, et al. 1975). Other workers have used multivariate techniques (such as PCA or factor analysis) to examine the phenotypic correlation of anthropometric traits (Burt 1944; Burt and Banks 1947 ; Thurstone 1946, 1947; Hammond 1942; Heath 1952; Howells 1951; Vandenberg 1968; Rhoads 1972).

The merging of these two approaches in the area of multivariate morphometrics (Blackith and Reyment 1966) has had to wait for the development of faster computers and generally available programs. Work in this area is increasing, and reported studies include work by researchers at Indiana Univeristy on dental, dermatoglyphic, and craniofacial variation (Potter, et al. 1968,1976; Nakata, et al. 1974a, 1974b, Susanne and Sharma 1978; DeFrise-Gussenhoven and Susanne 1978), and the pioneering study of anthropometric variation by Howells (1953). A recent attempt at examining multivariate patterns in heritability for nonmetric traits in Rhesus monkeys has also been reported (Cheverud and Buikstra 1981a, 1981b). The study by Howells examined the correlation between brothers on factor scores. Although the examination of phenotypic correlations based on sib pairs is not sufficient to partition formally genetic and environmental causes of covariation, this study did demonstrate family resemblance in a multivariate framework. Similar techniques have been used by the Indiana group. In addition they have applied the methods described by Vandenberg (1965; Bock and Vandenberg 1968; see also Defrise 1970) for

multivariate twin studies. This multivariate generalization of the identical vs. fraternal twin method suffers from the same problems of low sample sizes and lack of control for dominance, family environment, and gene-environment covariation which plagues all twin studies (Kamin 1974; Lewontin 1975).

As more sophisticated models for single trait heritability are developed these may be extended to a multivariate study. However, no studies have as yet attempted to partition the phenotypic correlation between metric traits into genetic and environmental components in a human population.

Anthropologists may be forgiven for not examining the genetic and environmental components of covariation between traits, for this area has received relatively little attention from biologists and biometricians as well (Bailey 1956; Leamy 1977; Misra 1966; Rouvier 1966; Falconer 1960; Searle 1961; Cheverud and Buikstra 1981a,b; Smith et al. 1962; Hashiguchi and Morishima 1969). The results of several empirical studies will be reviewed once the concepts of path analysis have been introduced in the second chapter. The study of genetic covariation between traits can only begin after the genetic and environmental basis of single traits is better understood. This has always been a serious problem in the study of man, where estimates of heritability must be made without the opportunity for controlled breeding, selection experiments, or randomized

environments. In addition, many misconceptions concerning the meaning of heritability still persist.

### 1.2.1 The concept of heritability

The heritability of a trait is commonly defined in two different ways. Heritability in the broad sense is taken to be the ratio of genetic variance to total phenotypic variance in a population (Li 1978; Falconer 1960). For use in plant and animal breeding a second version called narrow heritability is more useful. The narrow heritability of a trait is the ratio of additive genetic variance to total phenotypic variance. This latter formulation is based on the additive genotypic (breeding) value of an organism (Falconer 1960) and is relevant to practical concerns such as developing bigger eggs and fatter cows. In both definitions the total phenotypic variance is a result of genetic plus environmental variation. Biometric variation in natural populations is never due to genes or environment acting alone. Both types of heritability are based on the components of variance present in a population. Heritability has no meaning at the individual level. If an individual is 170 cm tall it makes no sense to talk about what proportion of his/her height is due to genes. Since all heritability estimates are a function of the amount of environmental variation present in the population, heritability will change from one population to another even when

the genetic basis for the trait is the same. Heritability likewise depends upon the amount of genetic variation present in a given population. Thus the heritability of a trait such as arm length is an attribute of a particular population in a particular environmental regime. Heritability is not an attribute of arm length itself.

Estimates of narrow heritability are useful in plant and animal breeding where the goal is to predict the result of selection for desired traits while maintaining a constant environment. Heritability estimates do not always provide reliable predictions for the phenotypic change which results from an environmental change (Lewontin 1974, 1975). This limitation on our ability to predict phenotypic response to environmental change arises because we cannot be sure that the response is linear. Non linear response seems probable because the environment itself is a complex set of elements (temperature, humidity, food resources, etc.) which interact with the genotype. If a controlled laboratory experiment can sample the phenotypic response of a population across a large range of environmental conditions then the norm or range of reaction for that population can be estimated for each set of environmental factors. In the study of natural populations, estimates of heritability are local rather than global estimates of a population norm of reaction (Lewontin 1974, 1975). Linear extrapolation from a response to small environmental changes along one dimension may be completely misleading. These remarks

on heritability imply that the concept is of no use in developing educational strategies (Morton 1972, 1974; Goldberger 1978; Lewontin 1970a, 1970b, 1974, 1975). The examination of heritability estimates for anthropometric traits remains a useful exercise, with the proviso that no recommendations concerning environmental intervention strategies will be made from the results. The only way to estimate the result of an intervention (be it protein supplements for physical growth or early childhood education for mental growth) is to conduct an experiment (Kempthorne 1978).

One of the more instructive misinterpretations of heritability is found in the literature on child growth (Newman 1975; Mueller 1977; Mueller and Titcomb 1977; Russell 1976). The fallacy is that "reduction of heritabilities of growth status might be expected in societies where protein-calorie malnutrition coupled with infection increase the likelihood and intensity of environmentally caused growth delays" (Mueller 1977:134). But in fact undernutrition and disease may affect the timing and rate of growth (hence achieved size for a given age) without lowering the heritability at all. The fallacy of reduced heritability arises from a confusion between measures of means and variances, and between populations and individuals.

By definition heritability estimates are based solely on the ratio of two variances. Heritability estimates are independent

of means. Correlations between relatives are also based solely on covariance and ignore mean differences. In a "good" environment children may grow faster than in a "poor" environment, but at a given age this is a difference in phenotypic means not variance. The "good" environment may have a higher mean protein and calorie intake than the "poor" one, but this does not affect a heritability estimate based solely on variances. Unless there is a difference in genetic or environmental variation between the two populations, the contrast between "good" and "poor" environments need not lead to a difference in heritability. This is an unfortunate consequence of the definition of heritability, which argues strongly in favor of studying population norms of reaction rather than heritability (Lewontin 1970a, 1970b, 1974, 1975).

The use of the term "environmental variation" is itself premature, since quantitative assessments of "environment" are elusive. Crude measures of environment may be based on parent's education and socioeconomic status. Yet there is considerable uncertainty regarding just what is being measured, and how an index of environment can be related to measures of phenotype (Cloninger, Rice and Reich 1979). Given our ignorance, we should not find it unreasonable that Mueller (1976) and Mueller and Titcomb (1977) report similar heritability estimates for well-nourished and malnourished children. In the absence of direct measures of environmental variation from one study to another, we can only guess at the relative variability of

different environments. As Mueller (1976) correctly points out, there are further complications which arise when children and their parents grow up in different environments. Studies in regions where rapid acculturation has occurred in the past few decades remain problematic.

Although it is difficult to measure environments, or even come to a suitable definition of what factors constitute "environment", it is quite possible to demonstrate the influence of environment on anthropometric traits. One form of "environmental influence" which has been clearly demonstrated is the "cohabitation effect" reported by Garn and his workers (Garn, et al. 1979). Studies of both metric and biochemical similarity between spouses and between parent-adopted offspring pairs, demonstrate that common family environment has a measurable effect. The similarity of unrelated persons who live together also increases with longer cohabitation. This implies that attempts to measure heritability which do not account for the effect of common family environment will produce inflated heritability estimates.

### 1.2.2 Heritability in practice

Studies of the heritability of anthropometric traits may be conveniently divided into those based on: (1) twin studies, (2) sib correlations and parent-offspring correlations, and (3) midparent-offspring regression or more complex models. This ordering reflects increasing information content of the data sets with reference to the estimation of heritability. As will be seen, there is a predictable inflation of heritability estimates in the poorer designs. The term heritability is used throughout the remainder of this chapter in the narrow sense, although most data sets can only estimate broad heritability.

Vandenberg (1962) reviewed the results of six twin studies. He notes that the information content available from monozygotic versus dizygotic twins is insufficient to estimate heritability. Twin studies confound other factors (dominance, common family environment, assortative mating, gene-environment covariance, genotype-environment interaction, correlation between the environments of parent and offspring) with heritability estimates. These other factors may cause the heritability estimate to be inflated. Rather than use the data to estimate heritabilities with unrealistic equations, Vandenberg retreats to comparing DZ/MZ F ratios. He is studying family resemblance in the broad sense and not relative degrees of genetic determination

in different traits. Vandenberg demonstrated greater family resemblance for linear measurements than for width and girth measurements as a general trend across the six studies. The genetic component of this family resemblance is unknown.

A number of studies examine sib-sib and parent-offspring correlations for anthropometric traits (Howells 1953, 1966; Susanne 1975; Mueller 1977). As in twin studies, where workers are reduced to using F ratios, there is a temptation to interpret the correlation coefficients themselves rather than calculate heritabilities using suspect methods. The retreat to using the correlation coefficients themselves is appealing because they are closer to the empirical "facts." Yet there is a tendency to forget the distinction which must be made between calculating the observed correlations and acting as if such correlations tell us about the relative importance of genes. If the model by which sib-sib and parent-offspring correlations produce heritability estimates is considered unrealistic, then we are again studying family resemblance in the broad sense.

Howells (1966) examines the intraclass correlation of siblings in a homogeneous population isolate (the Hutterites) for a number of anthropometric traits. This study produced an ordering of traits reflecting decreasing family resemblance: linear measurements, transverse diameters, and measures of fatty tissue. Howells notes that the measures containing a greater

proportion of fat (upper arm circumference versus wrist diameter) show lower family resemblance. This observation is consistent with the idea that environmental causes play a major role in determining fatness.

The correlation studies by Susanne (1975) and Mueller (1977) have been extended by the use of better models in their other publications (Susanne 1977; Mueller 1976), so we shall not review the correlation results here. In the other studies by Mueller (1976; Mueller and Titcomb 1977) and Susanne (1977) two different methods for the estimation of heritability have been employed. Susanne uses the method of Fisher (1918) which requires information on spouse-spouse, parent-offspring, and sib-sib correlations. This method takes into account assortative mating and dominance effects, but a separate estimate of common family environment is not available. Similarity of sibs may be incorrectly ascribed to dominance effects, and an inflated estimate of heritability will be obtained if any other complications exist (gene-environment covariance, correlation of parent and offspring environments, epistasis, gene-environment interaction). Mueller (1976; Mueller and Titcomb 1977) uses midparent-offspring regression which is similar to Fisher's model. Midparent-offspring regression does not estimate the effects of common home environment. Dominance and assortative mating do not seriously inflate the regression estimates, but further complications which Fisher's model leaves out are also left out of the midparent-offspring regression model. These

methods do offer an improvement over the simpler models underlying twin studies or simple parent-offspring correlation. Accordingly, they generally give lower estimates than models based on less information.

Susanne (1977) presents a decreasing order of heritability for: linear measurements, diameters of pelvis and weight, and circumference of limbs. This echoes the results from twin studies and correlation studies. Mueller (1976) reports a range of heritability estimates from 0.31 to 0.58 for stature. He notes that these are lower than estimates made by doubling the parent-offspring correlation (0.44-0.88) and considerably lower than estimates from twin studies (0.9-1.28). The value of 0.788 given by Susanne (1977:575) for stature falls outside the range reported by Mueller (1976). The higher estimate obtained by Susanne (1977) may be due to many causes, and these serve to warn us about comparing heritability estimates from different populations. Lower environmental variation in the Belgian sample might account for the higher heritability estimate. A higher heritability value might also be due to the genetic makeup of the Belgian sample. One "genetic" explanation for a higher estimate is that genetic variation in the Belgian sample is inflated because it represents a number of sub-populations. As Howells (1966) discovered, treating samples from European countries as homogeneous will produce inflated estimates. Despite the high value obtained by Susanne, the general relationship between sophistication of model and heritability estimate remains a

useful explanation for some of the systematic differences between studies. Inflated estimates of heritability are reduced as more factors are included in the model. More information is necessary in order to estimate the greater number of parameters required by more realistic models. This information can come from adding an observed measure of environment, or including observations on the phenotypic resemblance of relatives other than the nuclear family set (parent-offspring, spouse-spouse, and sib-sib). Both kinds of additional information may be combined.

A path model presented by C.C. Li (1976, 1978) adds the phenotypic correlation between half sibs and allows a partitioning of the effects of dominance and common home environment. A simplified form of this model (ignoring dominance effects) will be presented in more detail in Chapter 2 as it forms the basis for some of the models used in this study.

Morton and his associates (Rao, et al. 1975) have fitted a different path model to data on height and weight of children and adults in Brazil. This model assumes that assortative mating, gene-environment covariance, and dominance effects are negligible. One important new feature is that they add an index of common family environment to the array of observed correlations. This index is formed via multiple regression of the phenotype (separately for height or weight) on a set of variables which are indicators of environment. In their study

they use social and medical information including parental literacy, social level, longitude, latitude, local density, and occurrance of certain diseases. By attempting to measure the common family environment itself, they take an important step toward testing more realistic models. The estimates for heritability of stature and weight averaged over all ages are about 0.44 and 0.42, respectively. These estimates for heritability are in the centre of the range reported by Mueller (1976). In both measures, common family environment contributes an additional 0.18 to the correlation between siblings. It would appear the common family environment does significantly increase familial correlations.

The inclusion of an environmental index also allows the path model to be overdetermined. This implies that there are more equations to be solved than there are parameters to be estimated (or alternatively it assumes that some parameters are zero). A maximium likelihood solution is used by Morton and co-workers (Morton 1974) which allows single degree of freedom significance tests for parameters based on a large sample chi square approximation. However, Li (1976) points out the the use of this approach at an early stage of investigation may be counterproductive.

The use of significance tests on individual parameter values assumes that the basic form of the path model is known, and the

study is simply undertaken for the sake of parameter estimation. The maximum likelihood method finds a solution by minimizing the differences between observed and expected parameter values. If the expected values are incorrect because the 'true' model is not being fitted then the fitting technique will not give a correct solution. In fact, the solution will hide any large discrepencies in one or two parameter estimates which might otherwise appear.

An additional problem with the use of environmental indexing is deciding what to measure in the environment. The variables which form the environmental index used in the study of height and weight in Brazil (Rao, et al. 1975) are a hodgepodge of factors. What are longitude and latitude doing in an equation predicting phenotype over an area the size of Brazil? They could be a proxy for many things including genetic differentiation between regional populations! There is little attempt to justify the use of a particular set of variables, and no understanding of the causal pathways from the index variables to phenotype. It seems that environmental indexing is, for now, nothing but a very clever mathematical device for creating over-determined sets of equations.

The model used by Rao, et al. (1975) also allows the heritability estimates to be different in the parent and offspring generations. Once the possibility of different

heritability estimates was allowed for in path models, differences in heritability were found between generations for both anthropometric and I.Q. data (Rao, et al. 1975; Rao and Morton 1978). Rao, et al. (1975) seem to feel the genetic basis of height and weight is somehow threatened by differences in heritability estimates from one generation to the next. Although it is embarrassing for those who believe incorrectly that heritability is an attribute of a trait, there is nothing suprising in variable estimates. Rao, et al. (1975) also imply that high heritability estimates are in some way incompatible with secular trend, and are relieved to discover lower estimates for heritability in their own data. Thus Rao, et al. (1975) join those who confuse means and variances, and also those who believe that heritability can predict the effect of an environmental change. They make the latter mistake again in the I.Q. debate, when they suggest that adult education programmes may be more succesful than early childhood programmes because adult heritability for I.Q. is lower than that for children. (Rao, Morton and Yee 1976: 238).

### 1.2.3 Further complications in familial correlations

Changes in the heritability of anthropometric traits with age present a challenge to the analysis of data on child growth, but such changes may also help to explain the patterns of

variation in parent-offspring and sib-sib correlations at different ages (Bayley 1954; Cawley, et al. 1954; Morton 1955; Tanner and Israelsohn 1963; Furusho 1963, 1964, 1968; Mueller 1977, 1979). The general trend for correlations appears to be: (1) sib-sib correlations decline with increasing difference in age between sibs, and (2) parent-offspring correlations increase as the child grows older, or when the parents are younger. A further complication is brought about by higher values for mother-offspring versus father-offspring correlations (maternal effects) and higher values for some like-sex sib-sib correlations (sex effects). The observed phenotypic correlation for parent-offspring and sib-sib pairs confounds all of these factors, and it is not yet possible to study each effect separately.

The action of age-limited genes and transient environmental effects have been advanced to account for the decreasing resemblance of sibs separated in age by greater numbers of years (Bouchard 1980). Mueller (1977, 1979) reviews results for school-aged sibs versus adult sibs, and suggests that transient environmental effects must be responsible for the pattern of differences between adult sibs. The pattern for sib-sib correlations for adult sibs follows the general pattern of greatest correlations for bone measurements, lower correlations for circumferences and mass, and lowest for skinfolds. In school-aged sibs the correlations for all measurements are more similar to those for bone measurements, except suprailliac and

medial calf skinfolds, and relative sitting height. Among those adult sibs separated by more than seven years in age, correlations for all but bone measurements decrease. Thus it appears that there is more variation between adult sib pairs than between school-aged pairs in all but bone measurements.

Temporal variation in parent-offspring correlations has also been observed (Mueller 1976; Furusho 1964; Rao, et al. 1975). A common approach has been to attempt to correct for the age-related variation statistically, or study children at a single age. This has not led to a better understanding of the reasons for temporal variation. The operation of transient environmental effects is implied by the observation that younger parents are more highly correlated with their offspring than older ones are (Furusho 1964; Mueller 1976). Cross-sectional data confounds transient environment effects with other mechanisms since the age difference between parent and offspring is always less for older children. The resolution of this problem must await the analysis of more longitudinal data using more detailed models. Garn and Rohmann (1966) show that parent-offspring correlations do vary as children age in a longitudinal sample. This implicates factors other than transient environmental effects, perhaps including age-specific genes. Thus it appears that a model which allows for both transient environmental effects and age-limited genes will be required to explain the observations which have been reported.

Maternal effects have been observed, especially for birthweight and postnatal weight (Morton 1955; Rao, et al. 1975; Morton and Rao 1978; Mueller 1976). Maternal effects would tend to produce higher mother-offspring than father-offspring correlations in the absence of any other complicating factors. Unfortunately, an appropriate path model has not been applied which might isolate this effect in anthropometric data. Few studies have collected separate estimates of environment for mother and father, so such models could not yet be fitted. Nor, as has been discussed before, do we have an adequate knowledge of how to characterize the complex interplay of factors which we call "environment." Comparing phenotypic correlations for stature, Mueller (1976) found that the mother-child correlation was greater than the father-child correlation. However, this difference disappears when the comparison is made on the separated sex samples (fa-son vs. mo-da or mo-son vs. fa-da). In addition to the statistical problems of sample independence, values for some correlations (fa-da and mo-da) show much variability in the studies compared. The evidence for a maternal effect on weight is less ambiguous.

The effects of sex linkage have also been sought in data on child growth (Hewitt 1957a, 1957b; Tanner and Israelsohn 1963; Mueller 1976, 1977; Mueller and Titcomb 1977; Russell 1976). The expected pattern for X-linked traits is that like-sex sib-sib correlations will be greater than opposite sex sib-sib correlations, and that parent-offspring correlations for like

sexes will be less than parent-offspring correlatons for opposite sexes (Hewitt 1957a; Hogben 1931; Wright 1969:427). Evidence for such an effect is equivocal, and at least one study produced the opposite observation (Tanner 1960). This may be due to other confounding effects which are not included in the simple X-linked formulation. In the case of Y-linked regulatory genes with pleiotropic effects, the above expectations do not hold. Such an effect of regulatory genes on the Y chromosome has been suggested by Tanner (1960). Given the present evidence neither a pure Y-linked or X-linked model will fit.

In summary, studies of the heritability of anthropometric traits have made considerable progress. This progress has come about through the collection of better observations in the field, and more sophisticated and realistic models for the analysis of data. As models have improved the estimates of heritability have decreased, but many more complications affecting the expected phenotypic correlation between relatives have yet to be adequately treated.

### 1.2.4 Correlations between traits

Because the human body is made up of a number of functionally interrelated parts, it is always tempting to move from the consideration of simple traits to the multivariate study of trait complexes. The move to multivariate studies carries with it all the problems of single trait studies. There are additional complications involved which are unique to multivariate studies. In multivariate studies of anthropometric variation, we are once again limited to inspection of phenotypic correlations. However, this time we begin with the phenotypic correlation of traits within an individual rather than between relatives. The starting point for a multivariate analysis of between-group or within-group variation is often a covariance or correlation matrix. This matrix is often taken for granted as an empirical fact rather than as a result of several distinct processes.

Two traits in the same individual may be correlated because they are both influenced by the same genes (pleiotropy) or closely linked loci (Turner and Young 1969:124). This kind of correlation is called a genetic correlation. Similarly, two traits in the same individual may be correlated because the life experiences of each individual represent an environment shared by the developmental pathways of both traits. This form of

correlation is called an environmental correlation between traits. A general formulation exists for the relationship of phenotypic, genotypic, and environmental correlations of traits (Falconer 1960; Searle 1961):

$$r_P(x,y) = r_A(x,y)\, h_x h_y + r_E(x,y)\, e_x e_y \qquad [1.1]$$

This partitioning of the phenotypic correlation ($r_P$) into additive genetic ($r_A$) and environmental ($r_E$) components requires estimates of the heritability ($h^2$ in the narrow sense) and environmental ($e^2$) contribution for each trait. These heritability values are the same estimates sought in the univariate study of variation. The ties between univariate and multivariate approaches to biometrical genetics are emphasized by their similar data requirements. The above equation will be derived by path analysis in chapter 2, and a detailed discussion of it will be postponed unitl that time. At this point it should be clear that the interpretation of the results of a multivariate analysis of anthropometric measurements is confounded by the unknown mixture of these two distinct components of phenotypic correlation.

In addition to the genetic and enironmental components of

phenotypic correlation, there is a third kind of correlation which may arise because of the definition of the variables. Often anthropometric studies include some measures which are in turn segments of other variables. A simple example would be stature and leg length. Because stature includes leg length as one segment of its value, there is necessarily a correlation between the two measurements. These correlations of parts and wholes may be treated by path analysis and an example is given by Li (1975:312-313). In the search for the underlying structure of anthropometric variation these induced correlations must be treated differently from those based on some common underlying factor. They tell us about the definition of our measurements and not about the relationship of body components.

Once a correlation matrix has been produced, it can be subjected to statistical analysis. Two widely used techniques of multivariate analysis are Principal Components Analysis (PCA) and Factor Analysis (Zegura 1978). Although these techniques are mathematically similar there are quite different models lurking behind the equations. One approach views the existence of correlated variables as a nuisance which confounds model testing. By a clever mathematical technique (PCA) the correlated variables are transformed into an equal number of new uncorrelated ones, and analysis continues on these uncorrelated variables. Following this recommended approach (Zegura 1978) one would hardly expect to test ideas about why the original variables were correlated in the first place. The factor analytic model

recognizes that there may be an underlying process producing the observed correlations, and attempts to find a parsimonious set of "factors" or "causes" which reproduce the observed correlation matrix. However, the extent to which the result of such a procedure is a "true" causal picture is unknown. Given a matrix of phenotypic correlations between traits, a factor solution cannot automatically be expected to yield factors which neatly partition genetic and environmental sources of covariation. Factor analysis cannot magically untangle causation given data which is inadequate.

### 1.2.5 Studies of correlations between traits

Despite the problems inherent in interpreting a correlation matrix between traits based on phenotypic values, such matrices have been used as data in the search for the underlying structure of anthropometric variables. The general results of the early workers (Burt 1944; Burt and Banks 1947; Thurstone 1946, 1947; Hammond 1942) have been supported by later studies (Heath 1952; Howells 1951; Vandenberg 1968; Rhoads 1972). Although the ordering of the factors or components varies from one study to another, a number of dimensions of variation stand out.

In a comparison of two factor analysis studies, Vandenberg

(1968) reported the similarity of results for adult women in the U.S. and Holland. Both the Holland and U.S. (Heath 1952) samples were made for the garment industry. Factors common to both studies were: (1) long-bone lengths, (2) size of extremities, and (3) weight and girth measures. Less clearly related were a cancellous bone factor (joint and limb circumferences plus sitting height) in Heath's study and a trunk factor in Vandenberg's results. Heath's factor solution also distinguished between fatty tissue on lower trunk and legs versus girth measures of upper trunk and upper extremities. Considering the different measurements used, these studies show excellent agreement with each other, as well as with the studies by Howells (1951) and Rhoads (1972).

The study by Howells (1951) on American adult males produced the following factors: (1) general size, (2) long-bone lengths, (3) general cranial size, (4) brain size, (5) lateral cranio-facial development, (6) facial length, and (7) ear size. A simpler pattern emerges in results from two samples of adult U.S. males and a sample of male Solomon Islanders from Malaita studied by Rhoads (1972). Interpretable factors included: (1) linearity, (2) circumferential, (3) distal limb size, (4) adiposity, and (5) head size. There were some differences in the factors derived for the U.S. versus Solomon Island samples especially with regard to skinfold measures, but again the results were generally similar.

Despite the injustice which is done to these studies by comparing only the "labels" which different investigators have chosen for the factors, it does seem that there is an underlying similarity across the studies. This is all the more suprising considering the differing variable sets used, and the widely differing factoring and rotational techniques used. Perhaps there really is an underlying developmental genetic programme which integrates long bone lengths (linearity) and separates linearity from other body components such as head size, size of extremities, or weight. This observation of relative independence of development for different body segments requires closer examination, however, because statistical independence of orthogonal factors is an artifact of the analysis procedure. In biological terms there may well be a functional relationship between such factors as weight and height (Rhoads 1972). Fergusson, Horwood and Shannon (1980) have studied the stabilizing relationship between height growth and weight growth in newborn infants.

Regardless of the confidence which we may place in these factor analytic results as the number of replications increases, they leave a number of problems unexamined. All of the studies to date have used the phenotypic correlation between traits as their starting point. But, as we have seen, a phenotypic correlation between two traits may arise for several different reasons. Bailey (1956) has made an eloquent plea for the separation of genetic and environmental factors:

> The separation of the genetic and environmental portion of variance and covariance prior to extraction of the principal components is of concern for ultimate analysis and utilization of the components. Since there is no evidence available indicating the two sources of control would posess similar components, their (statistical) separation is necessary in order to avoid analyzing compounded effects which would have no obvious biological meaning. (Bailey 1956:64).

## 1.3 Between Group Variation

The analysis of between-group variation is inherently more complex than within-group variation. All the complications of within-group variation are present, multiplied by the number of groups examined. Yet studies of between-group variation are even more susceptible to taking for granted the within-group correlation matrix (or matrices). Often the final interpretation is made in terms of derived canonical variates alone, with little care being taken to examine the correlation matrix of original variables or investigate the reason for the existence of a particular correlation. This approach is reminiscent of the PCA

solution to correlated variables: create some new uncorrelated ones. Critical views on this approach are presented by Rhoads and Trinkhaus (1977) and Corruccini (1978).

Metric traits have long been used in the study of variation between human groups, although the genetic basis for this variation was unknown. As the field of Physical Anthropology has progressed, workers have become more cautious in their reading of anthropometric differences, and have come to rely more heavily on gene frequency data. The results of a number of recent studies of human variation using both biometrical and gene frequency (blood group, serum protein) data have raised questions concerning what kinds of group differences are reflected in anthropometric variables. Conventional wisdom suggested that the use of gene frequency data would provide a clearer reading of the phylogenetic relationships among local populations than would anthropometric variation. The reasons for this position undoubtedly include the observation that anthropometric variation confounds genetic and environmental differences while gene frequencies allow us to get straight to the genetic differences between groups. Thus there was some suprise when in South America (Spielman and Smouse 1976) and Melanesia (Friedlaender 1975) old fashioned anthropometric data outperformed gene frequencies in discriminating between villages. But perhaps this should not be so unexpected. Consider several explanations for the better performance of metric traits:

(1) there is simply a greater amount of variation in metric traits than in blood groups and serum proteins, thus more opportunity for discrimination between groups,

(2) metric traits are presumably based on a large number of loci so they sample a larger portion of the genome and give more reliable results,

(3) the populations studied were small enough for drift to be important in obscuring differences in gene frequencies, but polygenic (including metric) traits are less susceptible to drift.

(4) all the villages in a region occupy different environments, thus metric traits overestimate the genetic differences because they sum together genetic and environmental sources of between group variation.

Examinig these points, it seems advantageous to assess population differences on the basis of polygenic systems which have extremely low environmental input. Thus the use of fingerprint data has been gaining favour as a relatively stable polygenic system with high heritability (Freolich and Giles 1981; Rothhammer, et al. 1977; Neel, et al. 1974). Yet when anthropometric or dermatoglyphic data is being considered, it is well to remember that we don't know enough about within-group or

between-group variation to interpret the results which have been obtained in a simple fashion. This problem is particularly difficult in assessments based on a set of anthropometric variables which mix high and low heritability measures.

One approach to the interpretation of between-group anthropometric variation has been to compare the list of discriminating variables with their heritabilities estimated from American twin studies (McHenry and Giles 1971; Friedlaender 1975; Hiernaux 1963; Littlewood 1972). The expectation is that if the between-group discriminating variables are all of high heritability then the discriminant functions are reflecting genetic differences between groups. Alternatively, if the between-group discriminating variables have low heritability then they represent only environmental differences between groups. Unfortunately this expectation is false (Lewontin 1970a, 1970b, 1974, 1975; DeFries 1972). The mix of environmental and genetic sources of variation within groups does not tell us the causes of between-group variation. As Lewontin (1969a, 1969b) illustrates, it is possible for all of the variation within each of two populations to be environmental but all of the variation between these populations to be genetic. This occurs in the case of two separate highly inbred lines in identical environments. Likewise, all of the variation between two populaions may be environmental while the variation within each group is entirely genetic. These extremes are found under laboratory conditions or in thought experiments. Natural populations will represent an

intermediate situation. The point remains that even given an accurate measure of heritability for each trait in a population, these values alone cannot be compared to an ordering of between-group discriminating variables to reveal the genetic basis of between population variation.

A further problem with the work which has been reported so far is that the estimates of heritability which have been available for comparison are based on different populations in a different environments (American white twins vs. African and Melanesian blacks). Heritability estimates are specific to a given population in a given environment. Thus it is hard to be sure just what is being compared when we use a Melanesian or African data set and heritability estimates from American twins. Whatever their worth in between-group comparisons, the heritability estimates used must at least come from the same populations under study.

Although the comparison of $h^2$ estimates and between-group discriminating variables is meaningless from a theoretical standpoint, there are more satisfactory methods which have not yet been tried. These methods are based upon a partitioning of heritability into between-group and within-group components. The between-group heritability component then provides a basis for assessing the genetic proportion of between-group variation in different traits.

### 1.3.1 Between group heritability

The concept of between-group heritability (or heritability of group means) has been developed by plant and animal breeders concerned with the selection of family lines (Falconer 1960:232-4). DeFries (1972) develops the analogy between analysis of family lines and analysis of any subdivided population. The approach is based on a partitioning of the total additive genetic and phenotypic variances into within and between-group components. The phenotypic intraclass correlation between members of a group is (following Falconer 1960):

$$t = \sigma_B^2 / \sigma_T^2 \qquad [1.2]$$

This equation is solved for the between-group phenotypic variance and the within-group phenotypic variance:

$$\sigma_B^2 = t\,\sigma_T^2 \qquad [1.3]$$

$$\sigma_W^2 = (1-t)\,\sigma_T^2 \qquad [1.4]$$

Similarly, the intraclass correlation for additive genetic variance is:

$$r = \sigma^2_{gB} / \sigma^2_{gT} \qquad [1.5]$$

which leads to a similar set of equations. The total heritability is:

$$h^2 = \sigma^2_{gT} / \sigma^2_T \qquad [1.6]$$

The heritability for group means (between-group component of heritability) is:

$$h^2_B = h^2 \cdot r/t \qquad [1.7]$$

and the within-group component is:

$$h^2_W = h^2 \cdot (1-r) / (1-t) \qquad [1.8]$$

When these formulae are applied to small families a correction is

required for the error variance associated with the estimation of family means. This refinement affects only the between group calculations and takes the form:

$$h_B^2 = h^2 \cdot \frac{1 + (n-1)r}{1 + (n-1)t} \qquad [1.9]$$

DeFries (1972) attempts to apply the idea of between-group heritability to the question of genetic differences in I.Q. scores between blacks and whites. The minimum information required to make an estimate using this approach is knowledge of t, r, and $h^2$. Since he has data for whites only, DeFries does some algebraic manipulation and arrives at the following equation relating between and within-group variation:

$$h_B^2 = h_W^2 \cdot \frac{(1-t)r}{(1-r)t} \qquad [1.10]$$

Lewontin (1975) criticizes the use of this equation by DeFries when he has heritability values based on whites only. What DeFries does is the equivalent of a one way ANOVA with data from only one cell. The estimate used by DeFries represents the white within-group heritability <u>not</u> the pooled within-group heritability for blacks and whites. If the data is not available

to make an estimate of the total and within-group variance, then the total variance cannot be partitioned. To believe otherwise is to pull numbers out of thin air.

DeFries also has to borrow his values for r from studies of inbreeding in anthropological populations. Physical anthropologists are in a unique position to apply the concept of between-group heritability because they routinely collect the necessary genetic and demographic data. The data required for calculating t and $\sigma^2$ are phenotypic and observable, but the estimation of r must proceed indirectly using F statistics (Falconer 1960:233). An attempt to use between-group heritability models requires a linkage between studies of population structure (supplying F values) and biometrical variation. As Howells (1966) points out, studies of biometric variation in populations too often ignore family relationships, and treat the sample as if it were a homogeneous group of unrelated individuals. The use of between-group heritability models offers an opportunity to redress the balance.

# Chapter 2

## Path Models for the Decomposition of Phenotypic Correlations

### 2.1 A brief sketch of Path Analysis

The method of path analysis was developed by Sewall Wright in the early 1920's and has been applied to a wide variety of topics in population genetics. This is not the place for a complete introduction to the methods or history of path analysis. Fortunately, C.C. Li (1975) has presented an excellent primer on the subject which can serve as an introduction to the more technical papers by Wright (1920, 1931, 1934, 1960, 1968). In this section path analysis will only be introduced by example. Derivations of the rules may be found in Li (1975). A simple path diagram is shown in exhibit 2.1. This path diagram is consistent with the model assumed when multiple regression is used. The dependent variable is Y, and there are two correlated independent variables X1 and X2. The fact that X1 and X2 are correlated is indicated in the path diagram by the curved double-headed arrow between them. The reason for this

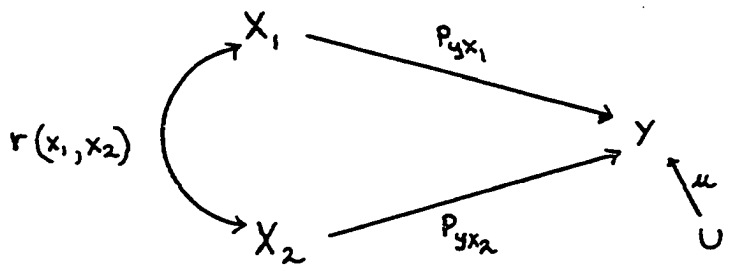



Exhibit 2.1 Path Diagram Representing Multiple Regression

correlation is not indicated in the path diagram, so r(X1,X2) is referred to as an unanalyzed correlation. The variables X1 and X2 do not completely determine Y. In order to make the diagram complete, a residual factor u is also shown. The value of this residual factor is not directly correlated with X1 or X2 since there is no arrow connecting them. The absence of an arrow is as significant as its presence, because lack of an arrow implies zero correlation. The difference between the path diagram in exhibit 2.1 and a multiple regression analysis is that in drawing an arrow from X1-->Y and X2—>Y we assert that X1 and X2 are causes of Y. A multiple regression model could be fitted for purely predictive purposes, but need not carry any causal implications. In path analysis the existence of an arrow from one variable to another always implies causation.

In the path diagram shown in exhibit 2.1 the influence of X1 on Y is measured by the path coefficient labelled p(Y,X1). The path coefficient for a given cause-->effect path is the ratio:

$$\frac{\text{(variability of effect with other causes held constant)}}{\text{(total variability)}}$$

Variability in this formulation is measured by the standard deviation (Wright 1920). This definition sounds like those of partial correlation or partial regression coefficients, and indeed there is a similarity. In the case of the path diagram of

exhibit 2.1 the value of p(Y,X1) is equal to the standardized partial regression coefficient. But path diagrams may be created where path coefficients do not take on such familiar forms. It is the generality of path analysis, coupled with the requirement that a causal model be specified explicitly, which makes path analysis a powerful analytical technique.

Once a given path diagram has been written, certain rules may be followed to derive structural equations which describe the situation depicted. These rules describe the tracing of connecting lines between variables to discover the expected correlation between variables, or the degree of determination of one variable by another. Tracing of a path proceeds by moving along single-headed arrows. Movement with the direction of an arrow is travelling "forward" and movement against an arrow is travelling "backward." These are the tracing rules: (1) the only travel permitted in tracing connections is first backward and then forward, (2) in tracing a connection one double-headed arrow (unanalyzed correlation) may also be crossed, and (3) the value of a compound path (several simple ones travelled in sequence) is the product of the path coefficients for each segment.

Applying these rules to exhibit 2.1 we can trace a path from Y to X2 moving backward along the arrow between X1 and Y (rule 1) and then along the double-headed arrow (rule 2). The value of

this compound path is: p(Y,X1)*r(X1,X2) (rule 3). These rules for tracing paths may be used in applying two additional rules: (4) the correlation between two variables is the sum of the values of all paths connecting the two variables, and (5) the degree of determination is always a round trip from effect to cause and back via some determining variables.

Thus to find the correlation between X2 and Y in exhibit 2.1 we add up all the paths connecting them. We have already found one compound path via X1, and its value was the product p(Y,X1)*r(X1,X2). There is another simple path and its value is p(Y,X2). Summing these we have:

$$r(X2,Y) = p(Y,X2) + p(Y,X1) * r(X1,X2) \quad [2.1]$$

Rule (5) really arises from applying rule (4) to the case where we find the correlation of a variable with itself. There are 5 paths which we may trace doing a round trip away from and back to Y. Each one represents a portion of the total determination of Y. These round trip paths are:

(a) p(Y,X1) * p(Y,X1) (direct effect of X1)

(b) p(Y,X1) * r(X1,X2) * p(Y,X2) (joint effect of

(c) p(Y,X2) * r(X1,X2) * p(Y,X1) X1 and X2)

(d) p(Y,X2) * p(Y,X2) (direct effect of X2)

(e) u * u (residual)

Since the determination of Y is complete in the path diagram, we may also write:

$$r(Y,Y) = 1 = p^2(Y,X1) + 2 * p(Y,X1) * p(Y,X2) * r(X1,X2) + p^2(Y,X2) + u^2 \qquad [2.2]$$

The equations in [2.1] and [2.2] represent the two kinds of fundamental relationships among variables which may be derived by the application of rules (4) and (5).

## 2.2 A model for decomposing phenotypic correlations

Equipped with the rules (1) - (5) and a suitable diagram, it is now easy to derive the equation for the genetic correlation between two traits ($r_A$) introduced in chapter 1. Consider the path diagram in exhibit 2.2 This path diagram appears complex, but the basic form is fixed by the nature of Mendelian bisexual reproduction. In this diagram Z1 and Z2 are the phenotypic values for two traits. Primes are added when these refer to the

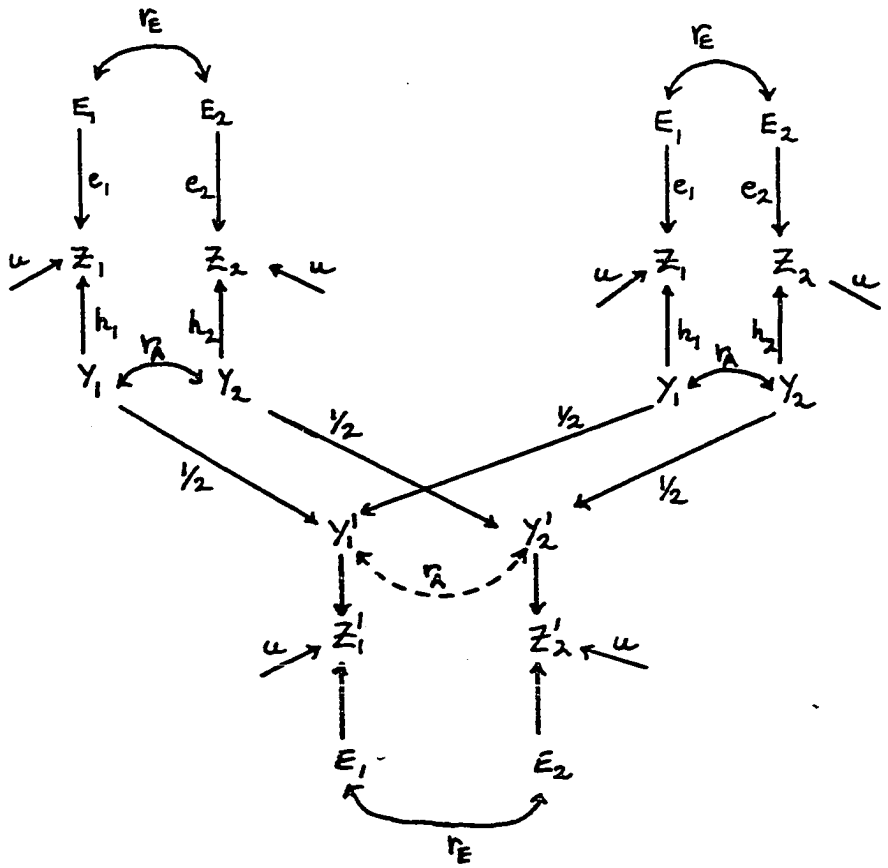



Exhibit 2.2 Path Diagram Illustrating Genetic Correlations

offspring generation. As the diagram makes clear, the phenotype is caused by 2 different factors (additive genotypic value Y; environment E) and a residual (the path labelled u). Y is the (unobserved) additive genetic value and the path from this to phenotypic value is labelled h (with subscript to indicate the trait in question). Note that the partial degree of genetic determination of the phenotype is thus $h^2$, in keeping with traditional usage for narrow heritability. Likewise the environment (E) contributes $e^2$. The formation of zygotes is summarized by the paths leading from Y-->Y'. As Wright has demonstrated, these paths are equal to 0.5. The offspring phenotype is determined in the same way as parental phenotype. Note that the h and e values don't have primes. This reflects a restriction that h and e values are equal in the two generations.

In addition to the direct paths in exhibit 2.2, there are several unanalyzed correlations. The genetic correlation between Y1 and Y2 in the adult generation is labelled $r_A$. The corresponding correlation in the offspring generation is shown as a dotted line and labelled $r'_A$. The curved arrow is dotted to indicate that this is an induced correlation (brought about by the nature of the diagram) rather than a primary correlation (see Li in Morton and Chung 1978). Thus the correlation $r'_A$ is a shorthand expression for the expected correlation r(Y1',Y2') which may be calculated directly from the diagram. A second primary correlation exists between the environments E1 and E2.

In addition to a summary of what is included in this path diagram, it is necessary to point out what is not included. Assortative mating is assumed to be absent as there is no correlation indicated between the phenotypic values of spouses. Inbreeding is assumed to be zero because there is no correlation indicated between the genotypic values of spouses. Likewise no correlations are indicated between the environments of spouses or between parent and offspring environments. Dominance is assumed negligible in this formulation, and departure from additivity would be counted as residual error. Gene-environment correlations are assumed to be zero as well. All these assumptions are explicitly represented in the path diagram by the absence of the appropriate correlation terms.

Using the rules for reading path diagrams, the basic equation partitioning the phenotypic correlation between traits may be derived by inspection from exhibit 2.2.

$$r(Z1,Z2) = h1 * h2 * r_A + e1 * e2 * r_E \qquad [2.3]$$

The path diagram makes clear the model behind this equation. In order to calculate the value of r from the observed correlations we need to trace out the following three equations from the path diagram in exhibit 2.2:

$$r(Z1,Z2') = 1/2 * h1 * h2 * r_A \qquad [2.4]$$

$$r(Z1,Z1') = 1/2 * h1 * h1 \qquad [2.5]$$

$$r(Z2,Z2') = 1/2 * h2 * h2 \qquad [2.6]$$

Solving [2.4] for $r_A$ and [2.5] and [2.6] for h we find that:

$$r_A = r(Z1,Z2')/(1/2 * h1 * h2) \qquad [2.7]$$

$$h1 = \sqrt{2 * r(Z1,Z1')} \qquad [2.8]$$

$$h2 = \sqrt{2 * r(Z2,Z2')} \qquad [2.9]$$

Substituting the values for h1 and h2 into the equation for $r_A$ we obtain the following:

$$r_A = r(Z1,Z2') / \sqrt{r(Z1,Z1') * r(Z2,Z2')} \qquad [2.10]$$

where primes refer to the trait in the offspring generation.

This is the expression given by Falconer (1960:317) although this version is in standardized units. An improved version suggested by VanVleck and Henderson (1961) uses the average of both cross trait covariances, and thus is less subject to sampling error. Their formulation is:

$$r_A = \frac{1/2\ (cov(X,Y') + cov(X',Y))}{\sqrt{cov(X,X') * cov(Y,Y')}} \qquad [2.11]$$

One caveat which must be mentioned is that the use of correlations in equation [2.10] produces the same results as

unstandardized covariances [2.11] only under the assumption that the variances of each trait are equal in the two generations ($\sigma^2_x = \sigma^2_{x'}$ and $\sigma^2_y = \sigma^2_{y'}$). Since selection is assumed to be negligible in both models, the phenotypic variance for a trait in the parent and offspring generation should be the same. However, this may not always be true in empirical studies because of sampling errors and other confounding factors (especially the rapidly changing environments of developing countries). In this instance equation [2.11] is preferred.

## 2.3 Some empirical studies of genetic correlations

The path model shown in exhibit 2.2 forms the basis for several studies which have attempted to estimate the genetic correlation between two traits through familial correlations.

Leamy (1977) examined the genetic and environmental correlations between metric traits in 200 mouse families. Estimates of genetic correlation ($r_A$) were obtained using equation 2.11. Unfortunately, the values obtained for $r_A$ were unreliable and exceeded 1 in several cases. This is most likely due to the inclusion of traits with low or zero heritability (Leamy 1977; Hill and Thompson 1978). The familiar product-moment correlation always lies between +1 and -1 as it

satisfies the Cauchy-Schwartz inequality (Kendall and Stuart 1967:288). The genetic correlation coefficient ($r_A$) is not bounded in this fashion. In fact it has the unfortunate property of exceeding unity when one or both terms in the denominator of equation [2.10] or [2.11] are close to zero. A genetic correlation matrix generated by these equations may not be positive semidefinite, and may have correlations greater than one, making it unsuitable for PCA (Seal 1966:177). In fact the probability of generating a genetic correlation matrix which contains correlations greater than one grows rapidly as the number of variables examined increases (Hill and Thompson 1978).

Despite the problems in the formulation of the matrix of $r_A$ values, Leamy (1977) is able to interpret the results for the genetic correlation matrix using a succession of nonmetric multidimensional scaling and clustering techniques. It is not possible to compare the results of a PCA on the phenotypic correlation matrix with his nonmetric cluster results. Lack of such a systematic comparison hinders understanding of the differences produced by analysing genetic versus phenotypic correlation matrices. The results of the analysis of environmental correlations between traits ($r_E$) proved even less satisfactory. This may be due to the confusion of residual and environmental variation in his analysis.

Although estimates of the path coefficient e are not

required for calculating $r_A$, they are required for a partitioning of the phenotypic correlation using eq. [2.3]. When independent estimates of e are not available there is a confounding of environmental effects (E) and residual variation (u). Both sources of variation are lumped together so that:

$$h^2 + e^2 = 1 \qquad [2.12]$$

rather than

$$h^2 + e^2 + u^2 = 1 \qquad [2.13]$$

holds true. Thus $e_1^2$ and $e_2^2$ are simply residuals found by subtraction from $h_1^2$ and $h_2^2$ using equation [2.12]. When the values for e1 and e2 are obtained in this fashion, and eq. [2.3] is then solved for $r_E$, given (r(Z1,Z2), h1, h2, $r_A$, e1, e2), there is a serious dependency between values of $r_E$ and $r_A$ as noted by Leamy (1977). The results obtained in this fashion are unreliable and an analysis of the matrix of environmental correlations between traits cannot be expected to yield interpretable results. This problem accounts, in part, for the difficulties encountered by Leamy (1977). A second problem leading to uninterpretable $r_E$ results in Leamy's work is that his estimates of $r_E$ are obtained from $r_A$ values which are themselves unreasonable (producing correlations greater than one). Since the $r_E$ values depend upon the product of $h^2$ values subject to sampling error, and unreasonable $r_A$ values, they are doubly suspect.

Cheverud and Buikstra (1981b) have recently reported the results of a study on non-metric skeletal traits in Rhesus monkeys. Using the same methods as Leamy, they report genetic and environmental correlation matrices for 13 traits. Several genetic correlations fall outside the range -1 to +1. As in Leamy's work, environmental correlations are even less well behaved than their genetic counterparts. Cheverud and Buikstra (1981b) note that the correlations falling outside the range -1 to +1 can be accounted for by sampling variation. The standard errors for many of these errant correlations are quite large. As in Leamy's work the structure of the genetic and environmental correlation matrices is explored with cluster analysis.

The results produced by these studies on two different animal populations are tantilizing. However, the unfortunate behaviour of the genetic and environmental correlations (extending outside the range -1 to +1) calls into question the value of the model and methods being used. The difficulty of interpreting the correlation matrices remains whenever there are correlations outside the normal range.

If this were the only study of genetic and environmental correlations between metric traits, the prospects for further work would appear dim. However, more than two decades earlier Bailey (1956) reported a study which fared much better. The estimates of $r_A$ and $r_E$ were not made using equations [2.3] and

[2.10] but came instead from the correlation matrices calculated from within ($r_E$) and between ($r_A$) several highly inbred lines of mice. The components obtained from an analysis of the $r_A$ and $r_E$ matrices produced biologically interpretable results, and showed a general similarity. Bailey suggested that this was consistent with the view that environmental and genetic factors influence the phenotype via similar developmental pathways.

A later study on pigs by Smith, King and Gilbert (1962) used covariance components to estimate a genetic correlation matrix for 24 traits. The patterns of principal components were again similar for both genetic and environmental correlation matrices. The genetic correlation matrix generated in this study was not positive semidefinite, although it was far better behaved than that used by Leamey (1977) and had no correlations which exceeded unity.

These two studies were performed using controlled breeding experiments. The genetic and environmental matrices were formed by special techniques which take into account the experimental breeding design. Thus it seems that the idea of genetic and environmental correlations is sound enough. However, in practice it is difficult to get reliable and reasonable estimates for $r_A$ and $r_E$ in non-experimental populations. The difficulties in using data from non-experimental populations might arise for several reasons:

(1) estimates of individual trait heritability are inaccurate,

(2) the assumptions inherent in the path diagram of exhibit 2.2 do not hold in the study population,

(3) environmental correlations are often estimated by the residuals from unreliable genetic correlations, and

(4) given the sample sizes available, the genetic and environmental correlations have quite large standard errors.

The first of these problems can be examined by using path analysis to derive some alternative formulas for estimating heritability in natural populations. Likewise the second problem demands that alternative path models be developed which include different sets of assumptions. The treatment of environmental correlations as other than residuals requires more sophisticated modelling of the environment, perhaps through the type of indexing proposed by Morton and his coworkers (Morton 1974; Gulbrandsen, Morton, Rhoads, Kagan and Lew 1977; Morton and Chung 1978; Morton and Rao 1978; Rao et al. 1975,1976). The final problem of sample size is especially serious when the heritability of a trait is small (Turner and Young 1969:127; Reeve 1955). Since sample sizes for anthropological populations are limited, we can only hope that by developing more sophisticated models we can make more accurate assessments on the

peoples we choose to study. Turning back to the first problem of heritability estimates for individual traits, we will examine in more detail the path models available for studying familial correlations.

## 2.4 Path models for phenotypic correlations between relatives

A number of different path models may be written which correspond to the various equations used for estimating the heritability of a trait. The model which forms the basis for this work is one proposed by C.C. Li (1975,1977,1978) and is illustrated in exhibit 2.3. This diagram shows the phenotypic and genotypic values for both parents and two offspring. It includes parameters for assortative mating and common family environment. The central portion is similar to that of exhibit 2.2, although it illustrates a single trait rather than two traits. The path from genotype of parent to offspring (Y-->Y') has a value of 0.5 as the offspring receives one half of his/her genes from each parent. In the parental generation there is also a correlation shown between the two parents (the curved path r(Z,Z)). The Li model treats the phenotypic correlation between spouses as causal, and due to assortative mating. Because of the non-random mating in the population (indicated by a non-zero value for r(Z,Z)) there is an induced correlation between the genotypic values of the parents. This is shown as the dotted curve r(Y,Y). The value of r(Y,Y) can be found from the path diagram to be:

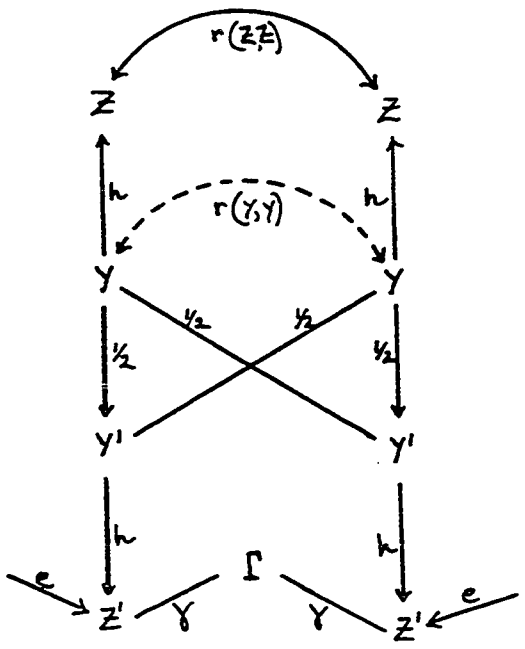



Exhibit 2.3 Path Model Proposed by C.C. Li

$$r(Y,Y) = r(Z,Z) \; / \; h^2 \qquad [2.14]$$

Li notes that there are two different ways of looking at non-random mating patterns. In systems of mating where genetic relationships are known and used to influence matings the genetic correlation between mates is causal. An example of this is systematic inbreeding in an animal herd. The key factor is that genetic relationships form the basis for decisions on mating. Although avoidance of close inbreeding in human populations may be based on biological kinship, observations in many societies suggest that phenotype rather than genotype plays a major role in mate selection. Thus Li is unsatisfied with models which treat genetic correlation between parents as causal. I find his arguments compelling. However, it seems likely that more complex models using Wright's concept of social homogamy and personal choice (Wright 1978a: 368) will become more popular as the field develops.

In the path diagram shown in exhibit 2.3 an equation for the parent offspring correlation (r(Z,Z')) may be derived given the features already discussed:

$$r(Z,Z') = 0.5 \; ( \; 1 + r(Z,Z)) \; h^2 \qquad [2.15]$$

The correlation between offspring in the same family is further influenced by a common home environment factor shown in exhibit 2.3 as $\Gamma$. The phenotypic value for each child is determined by genetic contribution from parents and common environment factor plus a residual (path e). The correlation between offspring in a family is then:

$$r(Z',Z') = 0.5 \ ( \ 1 + r(Y,Y)) \ h^2 + \gamma^2 \qquad [2.16]$$

with the common environment contributing the final term in the equation.

The path model in exhibit 2.3 gives rise to three equations ([2.14], [2.15], [2.16]) and four parameters ($h, e, \gamma, r(Y,Y)$). A fourth equation [2.12] allows a unique solution to the set of equations. However, the parameter e represents a residual path lumping together all factors not represented by h and $\gamma$. Although environmental indexing would add additional equations and allow the model to be over-determined, this proved impossible in the analysis of the data which follows. Relevant environmental data is not available in all of the six Solomon Island populations which will be studied with this path model in the next chapters.

This model assumes that dominance effects are zero, but if

they are present then they will be incorrectly ascribed to common family environment. Li (1977) illustrates a model which includes both dominance and common family environment, but it requires an additional observed correlation (half-sibs) for complete solution. Since only small numbers of half sibs are available in the analysis of the data which follows, the model including dominance is not used. Gene environment covariance is also left out of this formulation. As Li points out (1978:66) gene-environment covariance is probably not a significant factor in heritability estimators for physical measurements.

The final step in this section is to re-examine the genetic correlation between two traits introduced in exhibit 2.2, and adjust it to take into account assortative mating and common family environment.

We begin by extending the path diagram in exhibit 2.3 by adding subscripts to the Z values to distinguish between two traits. We also add the superscript 's' to distinguish the correlation between two traits in the same individual (r(Z1,Z2)) from the correlation between two traits in different individuals of the same generation ($r(Z1,Z2^{s})$). The previous equation for parent offspring correlation [2.15] appears with subscripts for trait i as

$$r(z_i, z_i') = \frac{1}{2}\left(1 + r\left(z_i, z_i^{s}\right)\right) \cdot h_i^2 \qquad [2.17]$$

The cross trait parent-offspring correlation for traits (i,j) may be derived by a change of subscripts:

$$r(Z_i, Z_j') = \frac{1}{2}\left(1 + r(Z_i, Z_j^s)\right) \cdot h_{ij}^2 \qquad [2.18]$$

where $h_{ij}^2$ is the cross trait heritability. There is a second cross trait parent-offspring correlation which is obtained by exchanging the order of subscripts:

$$r(Z_j, Z_i') = \frac{1}{2}\left(1 + r(Z_j, Z_i^s)\right) \cdot h_{ji}^2 \qquad [2.19]$$

In the equations that follow these two forms are assumed to be equal, and in model fitting the mean value is used for computations. This is also true of the symmetrical spouse-spouse and sib-sib equations.

The use of equation [2.18] removes the genetic correlation term $r_A$ from the diagram and associated equations, substituting instead a cross trait path $h_{ij}$. In order to use equation [2.18] to estimate $r_A$ it is neccessary to find a point of contact between the two path diagrams in exhibits 2.2 and 2.3. The bridge between these is found in the following equation:

$$h_i h_j r_A = h_{ij}^2 \qquad [2.20]$$

This equation ensures consistency between the two path models by requiring that the value of the paths from $Z_i \rightarrow Z_j'$ be the same

in both diagrams. Solving equation [2.20] for $r_A$ we obtain a general equation for the value of $r_A$ which is also given (but not derived) by Morton and Rao (1978).

$$r_A = h_{ij}^2 \;/\; h_i \cdot h_j \qquad [2.21]$$

Solving equation [2.18] for $h_{ij}^2$ we have

$$h_{ij}^2 = \frac{2r\left(z_i, z_j'\right)}{1 + r\left(z_i, z_j^s\right)} \qquad [2.22]$$

Expressing $r_A$ in terms of phenotypic correlations, and averaging over the two equations in [2.18] and [2.19] we see that

$$r_A = \frac{\dfrac{r\left(z_i, z_j'\right)}{1 + r\left(z_i, z_j^s\right)} + \dfrac{r\left(z_j, z_i'\right)}{1 + r\left(z_j, z_i^s\right)}}{h_i\, h_j} \qquad [2.23]$$

The value for $h_i$ is found from equation [2.17] and that for $h_j$ by appropriate substitution of subscripts.

The final equation for $r_A$ in terms of phenotypic correlations is then

$$r_A = \frac{\dfrac{r\left(z_i, z_j'\right)}{1 + r\left(z_i, z_j^s\right)} + \dfrac{r\left(z_j, z_i'\right)}{1 + r\left(z_j, z_i^s\right)}}{\sqrt{\dfrac{r\left(z_i, z_i'\right)}{1 + r\left(z_i, z_i^s\right)} \times \dfrac{r\left(z_j, z_j'\right)}{1 + r\left(z_j, z_j^s\right)}}} \qquad [2.24]$$

Notably, equation [2.24] simplifies to equation [2.11] when there is no assortative mating ($r(Z1,Z_2^S) = r(Z2,Z_1^S) = r(Z1,Z_1^S) = r(Z2,Z_2^S) = 0$) Equation [2.16] for sibling correlations can also be extended via subscripts to allow for cross trait formulations. Equation [2.16] with subscripts becomes

$$r(Z_i^t, Z_i^s) = \frac{1}{2}\left(1 + r(Y_i, Y_i^s)\right) h_i^2 + \gamma_i^2 \qquad [2.25]$$

The cross trait equation takes the form

$$r(Z_i^t, Z_j^s) = \frac{1}{2}\left(1 + r(Y_i, Y_j^s)\right) h_{ij}^2 + \gamma_{ij}^2 \qquad [2.26]$$

Given the common environment parameters $\gamma_i$ and $\gamma_j$, it is possible to estimate environmental correlations in a similar manner to that used for the genetic correlations:

$$r_\gamma = \gamma_{ij}^2 \,/\, \gamma_i \gamma_j \qquad [2.27]$$

The $r_\gamma$ parameter is given a different subscript from the earlier $r_E$ parameter because it represents effects specific to common family environment.

Thus, given observations on an array of traits in both

parents and offspring, it is possible to solve equations [2.21] and [2.27] and obtain matrices containing genetic correlations and common family environment correlations for each trait pair. These matrices are obtained in addition to the single trait heritability and home environment parameters given by the set of equations ([2.12], [2.14], [2.15], [2.16]). The model, generalized to cross trait correlations, takes advantage of cross trait phenotypic correlations which are available in data sets used for estimating the heritability of several traits individually. The added parameters to be estimated are offset by the increased number of observed phenotypic correlations, leaving the cross trait model fully determined (assuming that the associated single trait model is fully determined).

Although this model leaves out many factors which require further examination (see section 1.2.3) it provides a starting point for deriving genetic correlation matrices which take into account the complications of assortative mating and common environment effects. Further refinements must await better data sets which include larger samples and more detailed observations of the environment. What follows is a preliminary experiment.

# Chapter 3

## Anthropometric Variation in the Solomon Islands

### 3.1 Materials and Methods

The application of the methods proposed in Chapter 2 requires a set of data which includes observations on parents and offspring. This minimum data set is available in the results of the Harvard Solomon Islands Project in the western and central Solomons, and an additional population I surveyed at the eastern end of the Solomons. In order to develop a base line for evaluating the results of new techniques, it is neccessary to begin with a brief survey of the anthropometric data analyzed by the standard multivariate techniques. This initial treatment will serve to introduce the study populations and the measurements used. Patterns of within-language-group (within population) and between-population variation will be explored. Previous studies of anthropometric and other data from Bougainville groups have demonstrated that there are significant components of both between-village variation and

between-language-group variation (Rhoads 1977; Friedlaender 1975; Rhoads and Friedlaender 1975). Thus in studying variation at the level of language groups it must be understood that we are ignoring (or treating as background noise) the large proportion of phenotypic variation between individuals and between villages. This is an unfortunate consequence of the need for large sample sizes to reach reliable estimates of parameters in path models. The extremely fragmented and localized breeding structure of these Solomon Islanders makes them difficult subjects in a study of this kind.

A second caution which must be sounded concerns the effects of rapid acculturation on the patterns of growth and physical form. None of the groups studied are immune to changes in diet, medical care, and disease patterns which have accompanied the emergence of the Solomon Islands into the world economy (Damon 1974, Friedlaender and Rhoads 1981). The rate of change has also been mediated by accessibility, so that coastal groups suffer greater changes while isolated inland groups remain less affected. The impact of these changes on estimates of heritability and familial correlations is an unknown quantity. It is with these difficulties in mind that we turn to a brief introduction to the sampled populations, and the measurements taken.

### 3.1.1 The Subjects

The locations of the surveyed populations are shown in exhibit 3.1. There are two groups from Bougainville, the Nasioi from the southwestern inland plain, and the Aita from a more northerly highland region. The three groups from Malaita include one coastal population (the Lau) and two inland groups (the Baegu and Kwaio). The final group is from the Reef Islands at the extreme eastern end of the Solomon Islands. In all six populations children over five years of age, men, and women were measured. The groups on the large islands of Bougainville and Malaita were surveyed during the years 1966-1970 by members of the Harvard Solomon Islands Project (Damon 1974). The group from the Reef Islands was surveyed by me in 1978. Although more groups were examined by the Harvard teams, they are not included here because the genealogical information required to link records for parents and offspring is not yet available in suitable form. The six groups which have been included occupy a variety of physical environments which illustrate the ecological diversity of the Solomon Islands. However, all share the common economic mode of subsistence gardening with varying levels of cash cropping.

The physical anthropology of the populations on Bougainville and Malaita has been reported elsewhere. Rhoads (1977) summarizes the sampled areas, and the environments occupied by these groups. He also presents a wealth of data on genetic and anthropometric variation. Friedlaender (1975) has concentrated

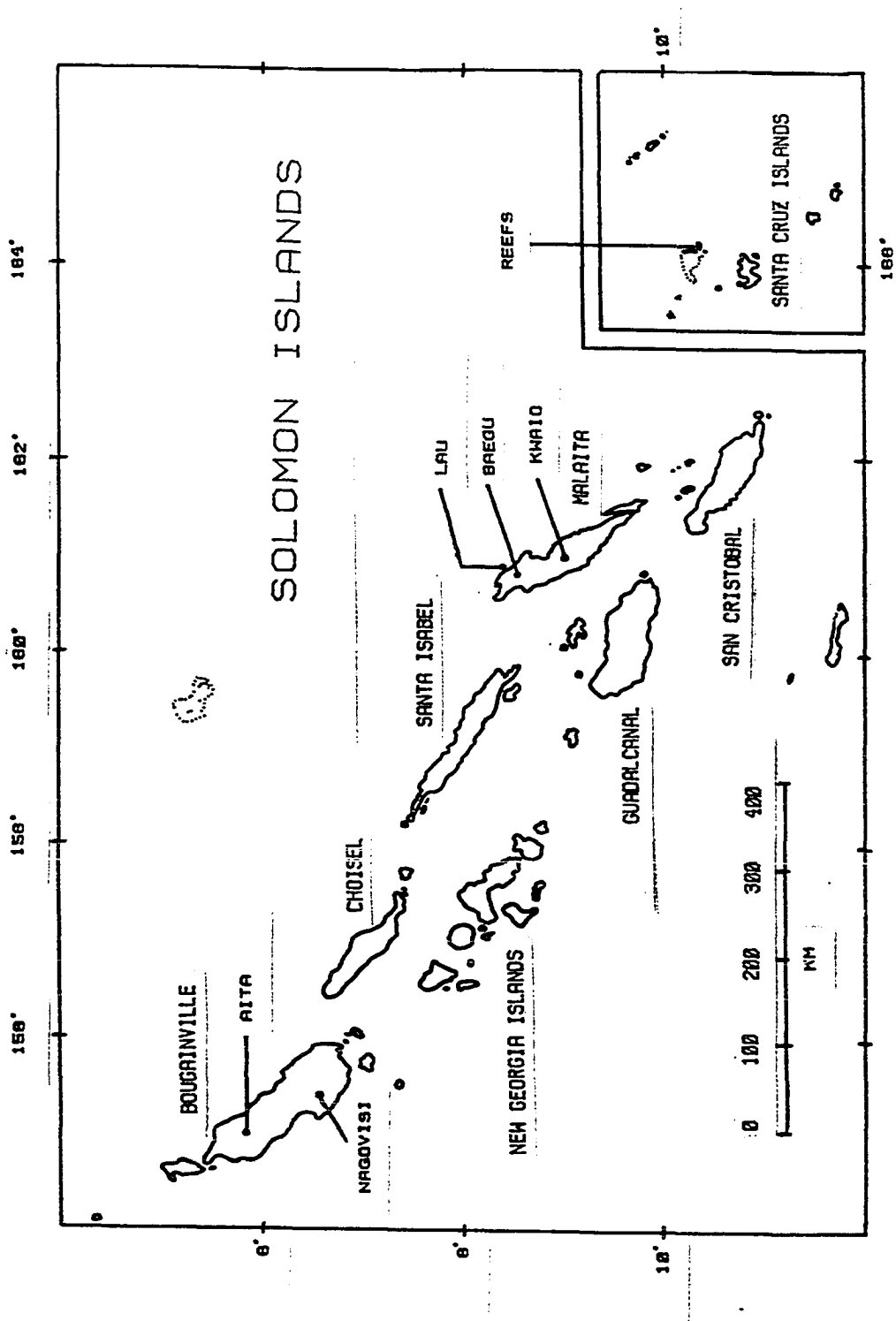



Exhibit 3.1 Map of Survey Area

on Bougainville itself, and includes demography, blood genetics, anthropometrics, dermatoglyphics, and dental variation. Both of these analyses have compared patterns of variation in different trait complexes with each other, and with that expected from distances based on linguistic, migrational, and geographical information. Up to this time, however, the information available on familial relationships has not been used to estimate heritability values for anthropometric variation in these populations. Instead, estimates of genetic control of within population anthropometric variation have been borrowed from other populations. The main thrust of later work has been more epidemiological (Damon 1974; Page, Friedlaender and Mollering 1977; Page, Damon and Mollering 1974; Friedlaender and Rhoads 1981).

Additional ethnographic material has been reported for most of these groups. The Lau have been described in a classic study by Ivens (1930), and in later work by the Marandas (E. Maranda 1970; Maranda and Maranda 1970). The Lau people are the ultimate "coast dwellers" in the Solomons, as they have built artifical islands on which to live. In contrast, the other two groups from Malaita are inland dwellers, and relatively isolated from the inroads of the modern world. As the Lau live a more maritime existence they have greater access to fish and shellfish, and consequently a higher protein intake than the inland groups (Rhoads 1977:44; Damon 1974:198). The Lau also trade their fish with other groups, and are less reliant on their

own gardens on the mainland.

Inland from the Lau are the Baegu. Ross (1973,1976) has published accounts of the Baegu which contain much useful information on demography, settlement patterns, and ecology. The Baegu present the traditional pattern of subsistance agriculturalists based on cultivation of sweet potato and taro. The Baegu, and to a greater extent the Kwaio, are less acculturated than the Lau. Roger Keesing has introduced the social structure of the Kwaio to many Pacific anthropologists through a long series of publications (Keesing 1965, 1966a, 1966b, 1967a, 1967b, 1968a, 1968b, 1970a, 1970b, 1970c, 1970d).

On Bougainville, the Nagovisi have been visited by Douglas Oliver, who brought back both biological and cultural data. Oliver collaborated with William Howells in examining the relationship between anthropometric variation and cultural patterns (Oliver 1949; Oliver and Howells 1957, 1960). More recent work has been undertaken by Mitchell and Nash (Mitchell 1971; Nash 1974; Ogan, Nash and Mitchell 1976). At the time they were surveyed (1970) they were still living primarily as subsistance agriculturalists, although some cash crops were being grown (mainly cocoa).

The Aita are another inland population from Bougainville,

but from the northern mountains. They are less acculturated than the Nagovisi due the their isolated location (Rhoads 1975:36). On the basis of shared cognates these two linguistic groups are members of the South Papuan and North Papuan phyla of Bougainville, respectively (Allen and Hurd, n.d.). This level of linguistic differentiation implies that the two populations have been isolated from one another for a significant number of generations. Thus we should not anticipate any close association between the Aita and Nagovisi groups relative to the others.

The final sample comes from the Reef Islands, at the extreme eastern end of the Solomon Islands chain. The Reef Islands have a population of over 4000 people and a land area of about 78 square km, and thus they support a population density of over 50 persons per square km. This density of settlement is one of the highest in the Solomons, although it is exceeded by the Lau on their artifical islands (Damon 1974). The Lau must be seen as a special case, however, since they maintain gardens on the mainland. Although the Reef Islands are more nearly self sufficient, there was still trade in food, utilitarian and ceremonial goods, and women in a regional network (Davenport 1964, 1969, 1975; Green 1974; Bayliss-Smith 1978). Subsistance agriculture in the Reef Islands is unusually dependent upon tree crops, with breadfruit being the favourite staple. Breadfruit is also dried and stored for consumption out of season. Root crops of yam, taro, and sweet potato are also important (Yen 1974, 1976). Fish are readily available in the lagoon area. In this

way, the Lau and the Reef Islands are similar in having a higher consumption of fish and shellfish than inland groups.

The Reef Islands are of particular interest to linguists because Polynesian- and Melanesian-speaking groups live in close proximity. The Polynesian-speaking populations are believed to have been resident in the area for over 300 years, yet they have retained their traditional language (Bayard 1976; Black 1978; Black and Green 1977). Polynesian speakers are present on several tiny coral atolls (Nupani, Nukapu, Matema, Pileni and Nifiloli) and a larger volcanic island Taomako, in the Duff Islands group. The larger raised coral atolls of the central Reef Islands are occupied by Melanesians. The sample used in this study is made up of the Melanesians from the central Reef Islands. Although some Polynesians were measured, the numbers were low and they have been excluded from this analysis.

### 3.1.2 The Measurements

The set of measurements used in this study is based on the recommended list of the International Biological Programme (Weiner and Lourie 1969). Twenty seven measurements were used, and these represent the intersection of the two sets used by the Harvard Solomon Islands Project and by me. All measurements are

in mm unless specifically noted. A brief description of each measurement follows:

Weight. Measured using a spring scale and reported in Kg. For all but the Reefs populations, weight was originally measured with a Detecto scale in pounds. The Reef Islanders were measured with a Seca scale in Kg. Measurement was made with the subjects wearing light clothing.

Sitting Height. The subject was seated on a hard surface and asked to sit at "attention" to give the maximum stretch. The distance between the surface on which the subject was seated and the highest point of the head, in the saggital plane, was measured with an anthropometer. (SITHT)

Stature. The anthropometer was used to measure the distance from the highest point of the top of the head in the sagital plane to the surface on which the subject was standing. A wooden board was used as a standing platform. The subject was standing fully erect at "attention." (STAT)

Biacromial diameter. The distance between the most lateral margins of the acromial processes of the scapulae was measured with the anthropometer as a sliding caliper. The subject was standing with arms hanging relaxed at his side. (BIACROM)

Bicristal diameter (biiliac breadth). Measured from the most

lateral point illaic crest on the left side to the corresponding point on the right side. The anthropometer was used as a sliding caliper, and pressed firmly to compress any fat tissue. (BICRIST)

Chest breadth. The transverse distance between the most lateral points on the chest, taken at about nipple level. The anthropometer was used as a sliding caliper. (CHESTB)

Foot length. Measured with the subject standing erect on a wooden board with his weight evenly distributed on both feet. An anthropometer was used as a sliding caliper to record the distance from the most posteriorly projecting point on the heel of the left foot, to the tip of the most anteriorly projecting toe. (FOOTL)

Total facial height. Measurement made with sliding caliper from nasion to gnathion. (TFACHT)

Upper facial height. Measurement made with sliding caliper from nasion to prosthion. (UFACHT)

Nose length. Measurement made with sliding caliper from nasion to subnasale. (NOSEL)

Nose breadth. The maximum transverse distance between the most laterally situated points of the subject's nose. (NOSEB)

Bicondylar humerus diameter. The maximal width across the outer margins of the distal left humeral condyles, measured with the sliding calipers. (BICHUM)

Wrist breadth. The distance across the left wrist at the level of the distal heads of the radius and ulna, measured with the sliding calipers. (WRISTB)

Hand breadth. Measured with the subject supinating the left hand palm upward and fingers together and extended. The maximal distance between the distal heads of the second and fifth metacarpals was based on their most laterally projecting points, using the spreading calipers. (HANDB)

Hand length. With the hand in the same position as that for hand breadth, the distance from the distal end of the styloid process of the radius to the tip of the third or middle finger was measured. (HANDL)

Bicondylar femur diameter. The subject was seated with the left knee bent to about a right angle. The sliding caliper was used to measure the distance across the outermost parts of the femoral condyles. (BICFEM)

Foot breadth. With the subject standing as for foot length, the sliding caliper was used to measure the distance between the outer margins of the distal heads of the first and fifth metatarsals. (FOOTB)

Head length. The distance between glabella and opisthocranion was measured using the spreading calipers. (HEADL)

Head breadth. The spreading calipers were used to find the greatest transverse diameter of the subject's head in the horizontal plane above the ears. (HEADB)

Minimum frontal diameter. The shortest distance between the temporal lines, measured with the spreading calipers. (MFRONT)

Bizygomatic diameter. The maximal distance between the most laterally projecting points on the zygomatic arches, taken with the spreading calipers. (BIZYGO)

Bigonial diameter. The maximal distance between the most laterally projecting points on the postero-inferior angle of the mandible. Measured with the spreading calipers. (BIGON)

Head circumference. The circumference at the level of the glabella and opisthocranion measured with a flexible steel tape. (HEADCR)

Upper arm circumference. Taken on the left arm hanging relaxed at the subject's side. The measurement is made at a point about halfway between the acromial point and the elbow. The flexible steel tape was in light contact with the skin, but

not depressing it. (UPARM)

Calf circumference. The subject was standing in the same position as for foot length, with weight distributed equally on both feet. The measurement was made at the maximum circumference of the lower left calf, with the flexible steel tape horizontal to the board on which the subject stood. (CALFC)

Triceps skinfold thickness. Measured using Lange skinfold calipers, on a pinch of skin taken from the posterior midline surface of the left arm about 1 cm above the level where arm circumference was taken. (TRISKN)

Subscapular skinfold thickness. The Lange skinfold calipers were applied to a pinch of skin taken about 1 cm below the base of the left scapulum. (SUBSKN)

## 3.2 Adult variation between groups

### 3.2.1 Describing group differences

There are many ways in which two or more groups may differ. The most common notion of how groups may differ is that they have different means for a given variable. However, it may be as interesting to know that two groups have different variances for a given variable. Careful researchers using analysis of variance check for differences in variance, since the assumption of homogeneous variance must be made when probability statements are based on F tests. Yet the hope is that variances are equal (or can be transformed in such a way as to make them equal) so that testing of differences between means may proceed.

When a number of variables have been measured on each subject it is possible to extend the number of ways in which two groups may differ. The basic data structures for a multivariate comparison of group differences are a variance-covariance matrix and a vector of means. When group differences are compared in a multivariate framework, these extra ways in which groups may differ are based on the off diagonal elements (covariances) of the variance-covariance matrix. Thus, in addition to a difference in means and variances, groups may exhibit different covariance structures. This makes multivariate comparisons of

group differences a more powerful tool than a series of single variable comparisons. In the analyses which follow we begin with a multivariate description of group differences, followed by an examination of individual variables when these are of particular interest.

Although the differences between groups are explored using analysis of variance models, the design does not represent a planned experiment. The execution of this research falls into what Bock (1975:415) refers to as a comparative study. The groups which we begin with are "natural groups" in the sense that they are observed rather than designed by the researcher. Since the individuals are not randomly assigned to the categories or groups we cannot, strictly speaking, ascribe the differences to any cause, and we cannot predict the effects of experimental intervention (Kempthorne 1978). Nonetheless, we can use the analysis of variance framework for describing the differences.

There are two ways of classification which will be examined: language group (also referred to as population), and sex. The comparisons are restricted to individuals over 20 years of age. The numbers of individuals falling into each of these categories is shown in exhibit 3.2. Although children were also measured, any comparisons between groups are complicated by the factor of child growth. As Gould has observed, "the justification for depicting phylogeny as a sequence of adults does not arise from a claim that only this stage is important in evolution, but merely from the mundane need to consider a sequence of processes at

MANOVA Table for 2 way design

| Effect | Wilks Lambda | F Approx. | Hypoth D.F. | Error D.F. |
|---|---|---|---|---|
| Sex | 0.14 | 235.9 | 27 | 1041 |
| Pop | 0.04 | 35.2 | 135 | 5139 |
| Sex.Pop | 0.63 | 3.7 | 135 | 5139 |

(all F values significant at $p < 0.01$)

Box's test for Homogeneity of Dispersion Matrices:

Box's M = 7260.0

Approx F = 1.53, d.f.=(4158,671246), $p < 0.01$

Chi Square Approx. = 6413.8, d.f.=4158, $p < 0.01$

Cell Counts

| | Reef | Kwaio | Lau | Baegu | Nagovisi | Aita |
|---|---|---|---|---|---|---|
| Male | 60 | 118 | 73 | 114 | 102 | 74 |
| Female | 82 | 104 | 85 | 105 | 93 | 69 |

Exhibit 3.2 MANOVA Table and Cell Counts for 2 Way Design

comparable points" (1977:212). The multivariate description of between group differences in child growth is a separate topic which would be as large again as that undertaken here. Growth curves for each of several variables for 5 of the 6 groups (without the Reef Islanders) are presented elsewhere (Rhoads 1977). The measurements made on sub-adults will be taken for granted at this point, and reappear only in the calculation of family correlations presented in chapter 4.

### 3.2.2 Multivariate analysis of variance

The result of a multivariate analysis of variance is given in exhibit 3.2. It is clear that there are significant differences in both main effects and the interaction of the two main factors. In addition there are differences in the generalized (multivariate) variance. We will return to a general consideration of differences in covariance structures in section 3.3, noting at this point that the probability levels for any F tests are distorted by unequal variance-covariance matrices. Despite the disturbing effects of unequal variances, we will accept that an interaction between sex and language group is present. The next step is to examine this interaction effect in more detail.

The interaction of sex and language group may be interpreted from two different points of view. On the one hand it can be

seen as indicating that the pattern of between-group variation is different for males and females. Alternatively, it can be demonstrating that the pattern of sexual dimorphism is different from one language group to another. We can identify the variables involved in the interaction effect by examining the univariate F ratios in exhibit 3.3. Note that this table includes both univariate F tests and Bartlett-Box tests for homogeneity of variance. The variables which appear to have differing variances in this comparison are: weight, bicristal diameter, chest breadth, upper facial height, nose length, head breadth, minimum frontal diameter, bigonial diameter, upper arm circumference, triceps skinfold, and subscapular skinfold. The variables which have a significant F ratio for between group variation are: sitting height, biacromial diameter, bicristal diameter, chest breadth, upper facial height, nose length, hand breadth, bicondylar femur, upper arm circumference, triceps skinfold, and subscapular skinfold. This set includes a single representative of overall length or linearity (sitting height). Thus linearity is somewhat underrepresented given the mix of variables measured. Transverse and breadth measurements are well represented by: biacromial diameter, bicristal diameter, chest breadth, hand breadth, and bicondylar femur. Fatness and bulk are represented by: upper arm circumference and the two skinfolds.

The variables showing either differing variances or significant F tests are chosen for further examination. Each chosen variable is discussed with reference to boxplots (Tukey

| | F Ratio | Sig | Bartlett Box F | Sig |
|---|---|---|---|---|
| WEIGHT | 1.30 | | 5.14 | *** |
| SITHT | 5.35 | *** | 1.41 | |
| STAT | 1.55 | | 1.35 | |
| BIACROM | 4.17 | *** | 1.17 | |
| BICRIST | 4.20 | *** | 5.26 | *** |
| CHESTB | 5.43 | *** | 5.63 | *** |
| FOOTL | 1.17 | | 0.95 | |
| TFACHT | 1.85 | | 1.78 | |
| UFACHT | 5.95 | *** | 4.33 | *** |
| NOSEL | 3.11 | *** | 4.73 | *** |
| NOSEB | 2.01 | | 1.29 | |
| BICHUM | 0.90 | | 1.54 | |
| WRISTB | 2.79 | | 1.49 | |
| HANDB | 4.30 | *** | 1.07 | |
| HANDL | 0.97 | | 1.66 | |
| BICFEM | 3.14 | *** | 1.31 | |
| FOOTB | 1.73 | | 1.42 | |
| HEADL | 1.74 | | 0.78 | |
| HEADB | 1.05 | | 2.40 | *** |
| MFRONT | 1.31 | | 3.12 | *** |
| BIZYGO | 0.68 | | 0.88 | |
| BIGON | 2.46 | | 3.59 | *** |
| HEADCR | 2.25 | | 1.24 | |
| UPARM | 7.29 | *** | 2.72 | *** |
| CALFC | 1.67 | | 1.44 | |
| TRISKN | 6.82 | *** | 56.07 | *** |
| SUBSKN | 7.68 | *** | 47.71 | *** |

(*** = significant at $p < 0.01$ level)

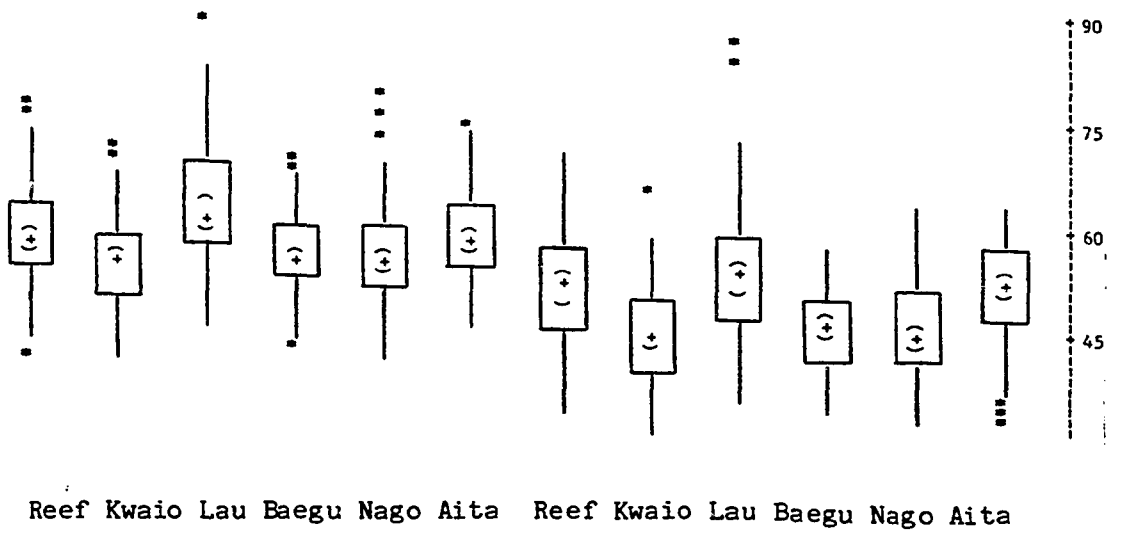
Exhibit 3.3 Univariate F Ratios for Interaction Effect

1977) showing the distribution for each of the twelve groups. The form of the boxplot used here is defined in the Minitab 81.1 Reference Manual and Command Summary, and generally follows Tukey (1977). One addition is an approximate 95% confidence interval for the population median. This is indicated by parantheses '()' on either side of the median '+'. The symbol for outliers is '0' and the symbol for values between the inner and outer fences is '*'.

The general scheme for interpreting group differences is as follows: (1) don't interpret any differences if the multivariate test is not significant at the .05 level, (2) examine univariate F tests if the multivariate test is significant and judge univariate F tests significant at the .05 level, (3) if the univariate F is significant use a robust comparison of medians based on a .05 level for each comparison. There is no correction for multiple comparisons made at the third level, but the test is protected at the previous steps against inflated significance levels (Bock 1975:422).

Group differences in weight are summarized in exhibit 3.4. Looking at the boxplots we see that there are some differences in variance, as estimated by the hinge spread (H-spread). The H-spread is a robust analogue of variance formed by the difference between the upper and lower quartiles (Tukey 1977). The H-spread is shown in boxplots by the box itself. Extreme values are the low H-spread for Baegu males and females, and the high H-spread for Lau males and females. There is also a visible

Exhibit 3.4 Boxplot for weight



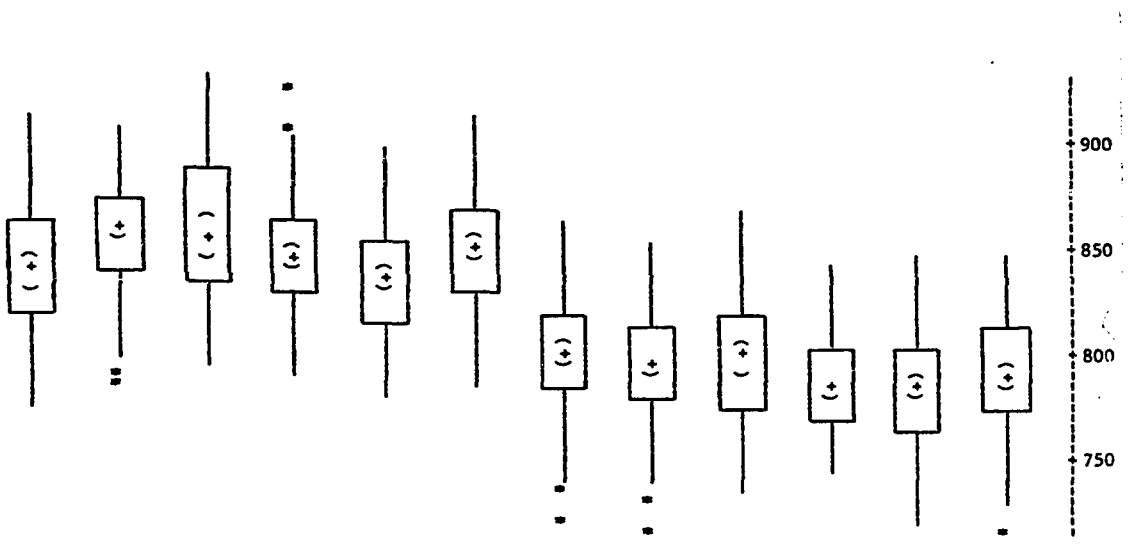
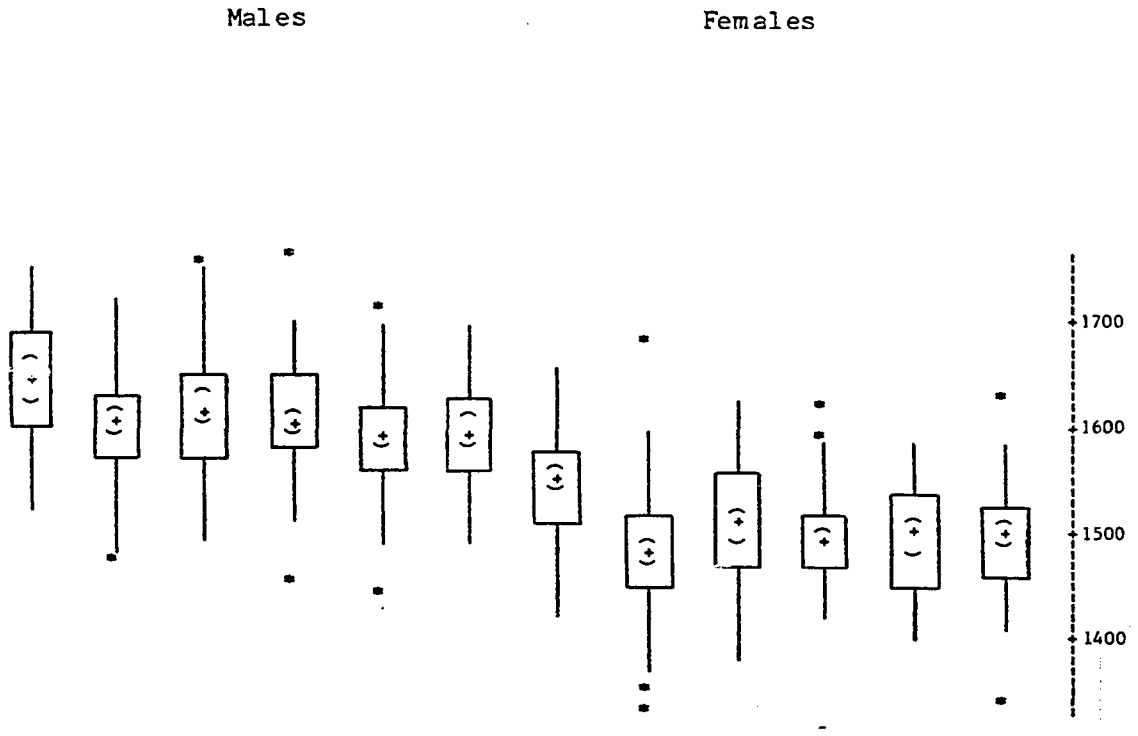




Exhibit 3.5 Boxplot for sitting height

Exhibit 3.6 Boxplot for stature



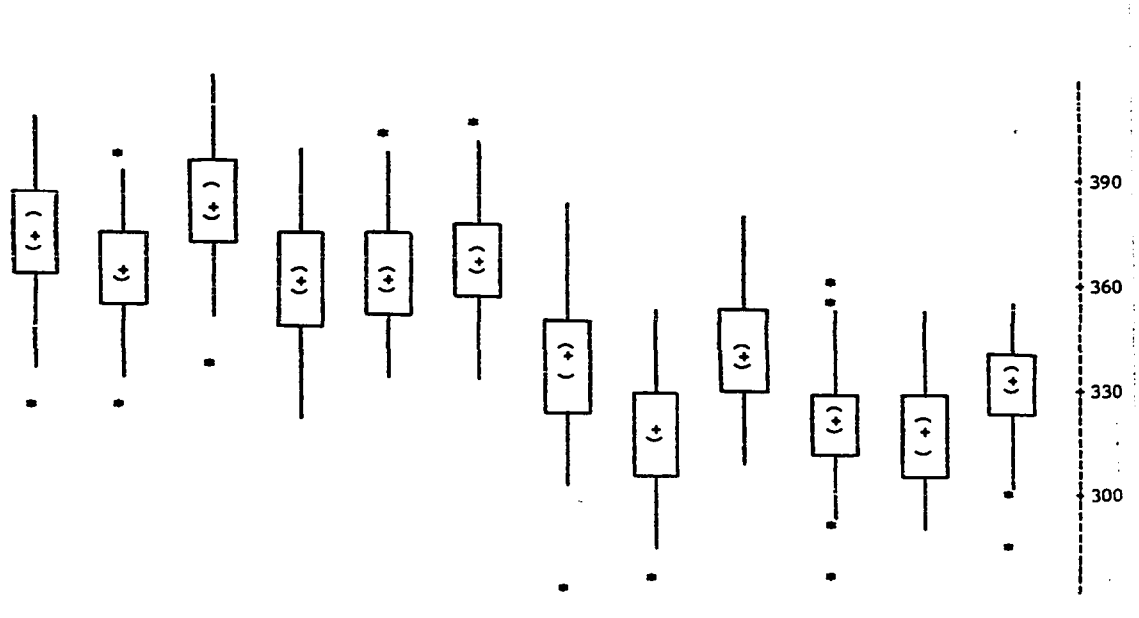
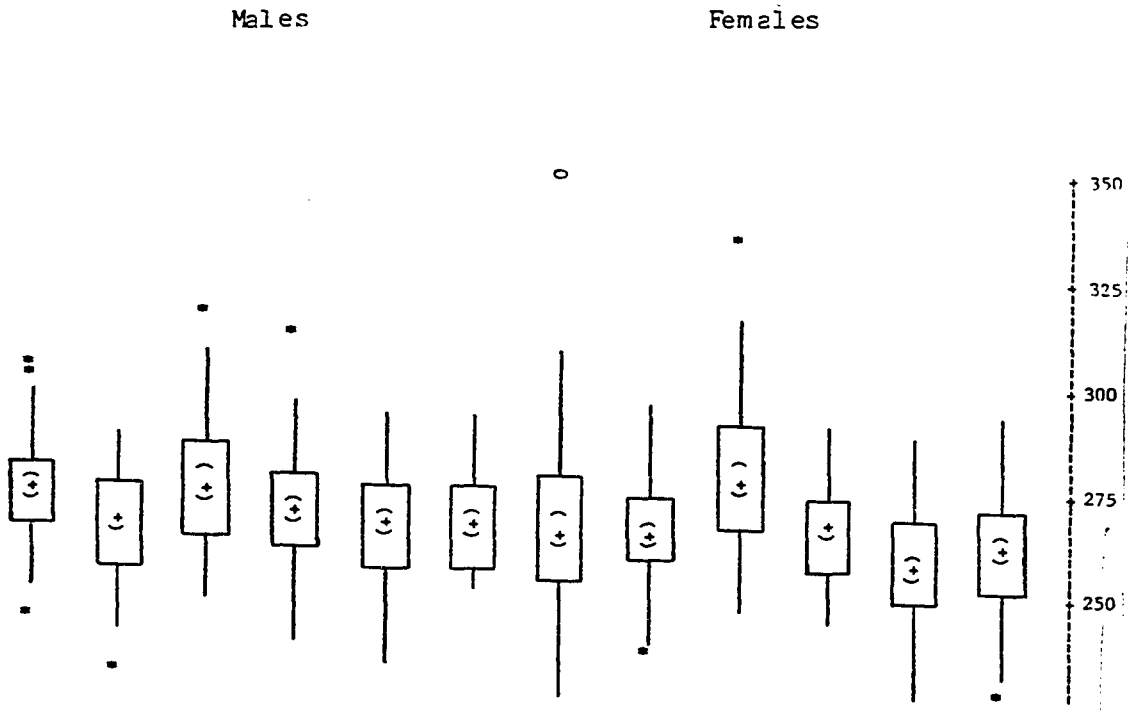




Exhibit 3.7 Boxplot for biacromial diameter

Exhibit 3.8 Boxplot for bicristal diameter



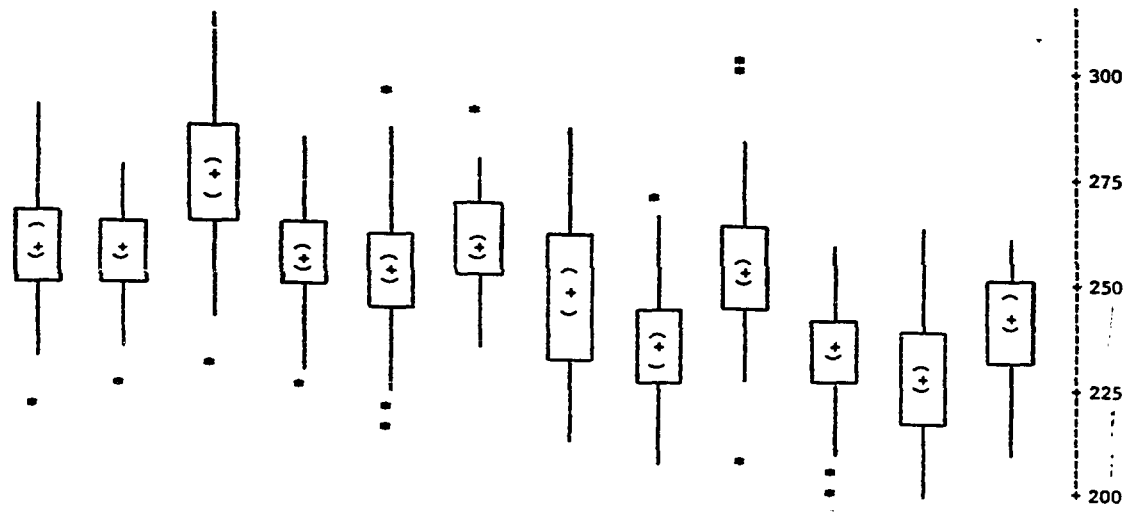
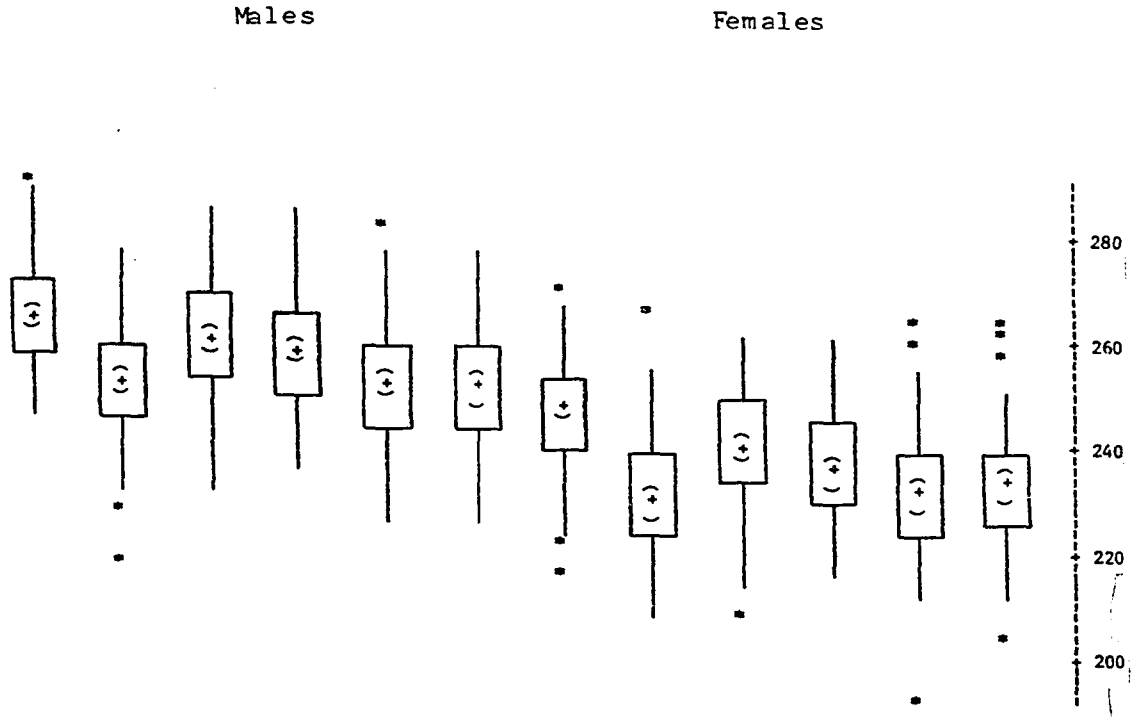




Exhibit 3.9 Boxplot for chest breadth

Exhibit 3.10 Boxplot for foot length



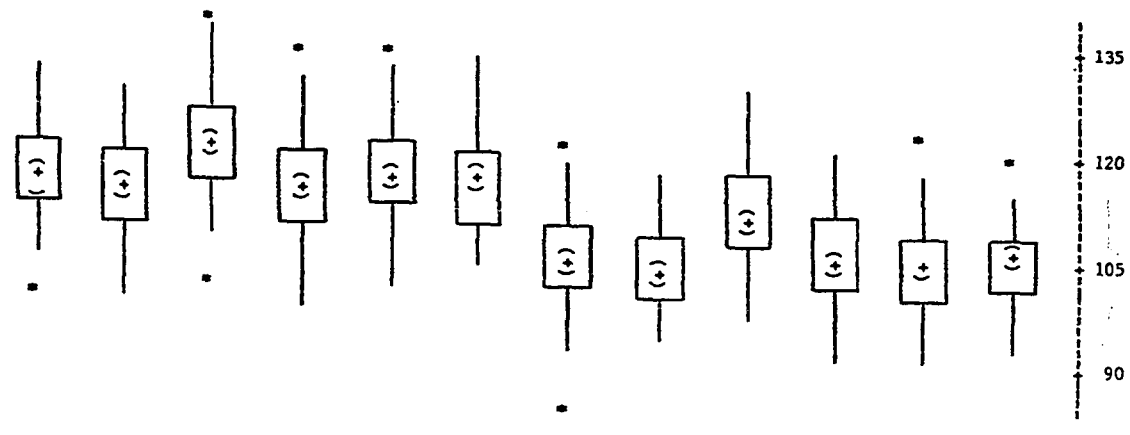
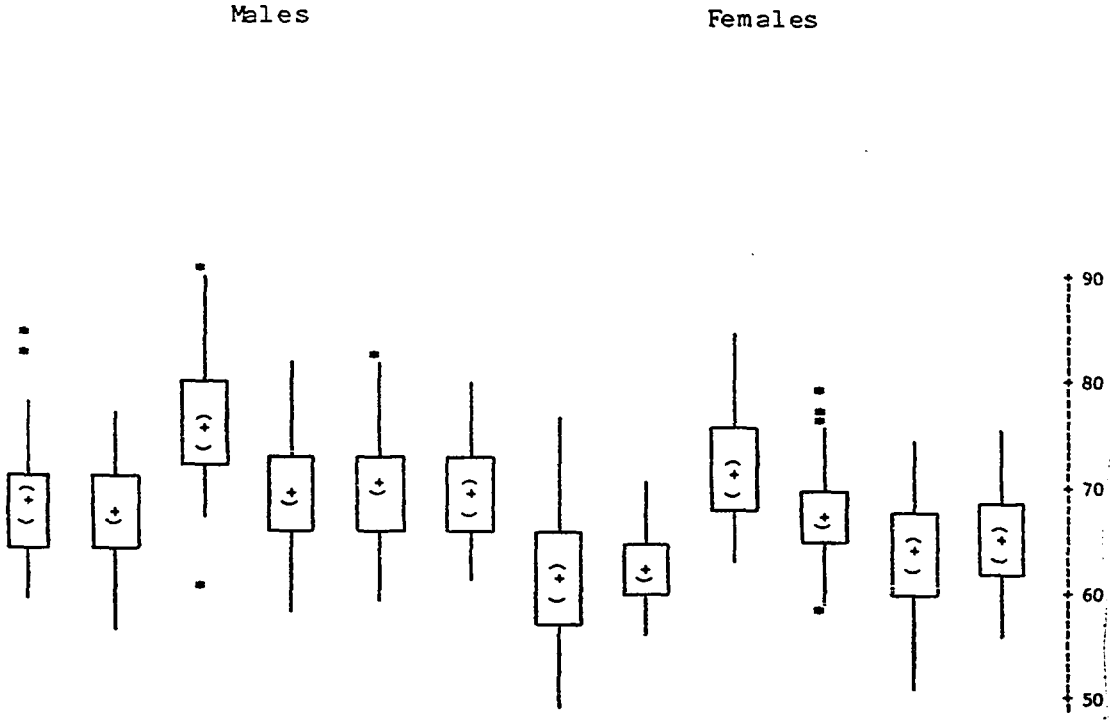




Exhibit 3.11 Boxplot for total facial height

Exhibit 3.12 Boxplot for upper facial height



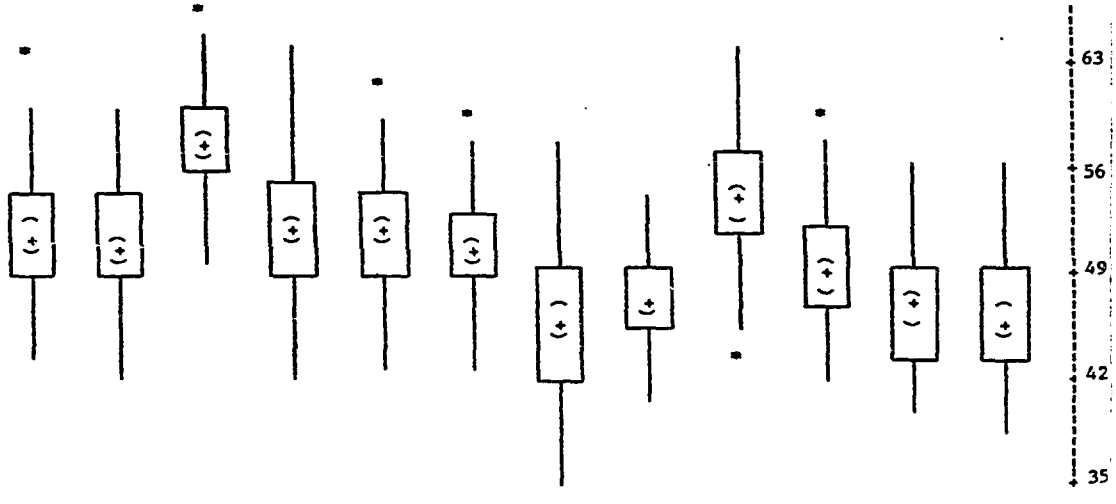
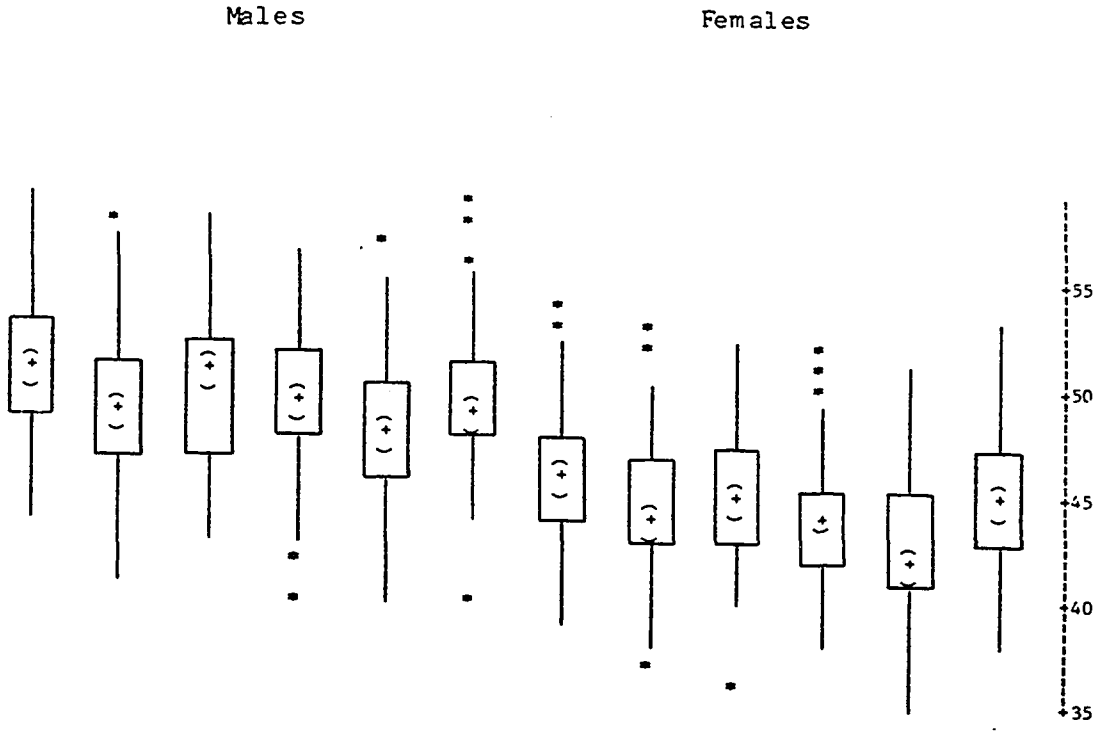




Exhibit 3.13 Boxplot for nose length

Exhibit 3.14 Boxplot for nose breadth



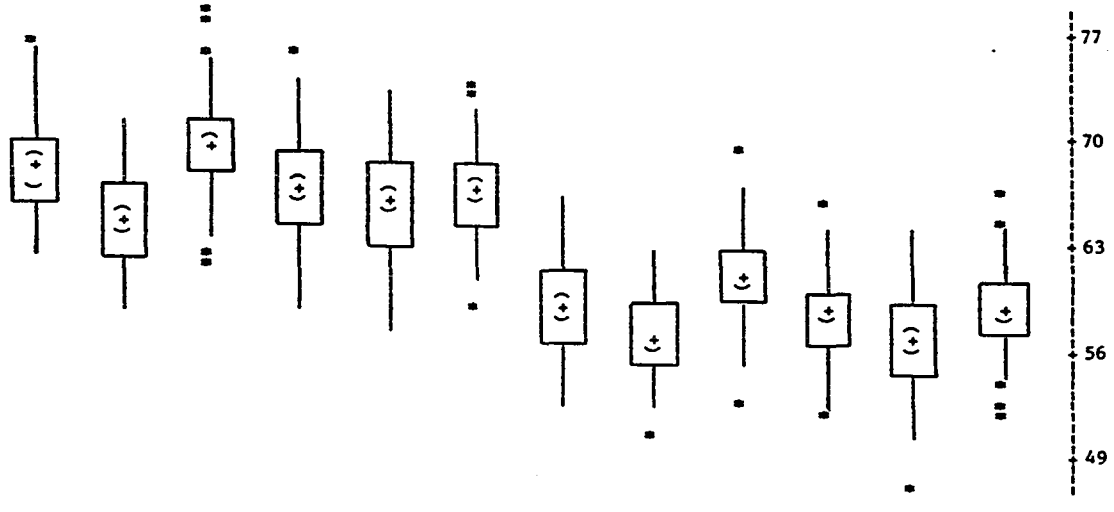
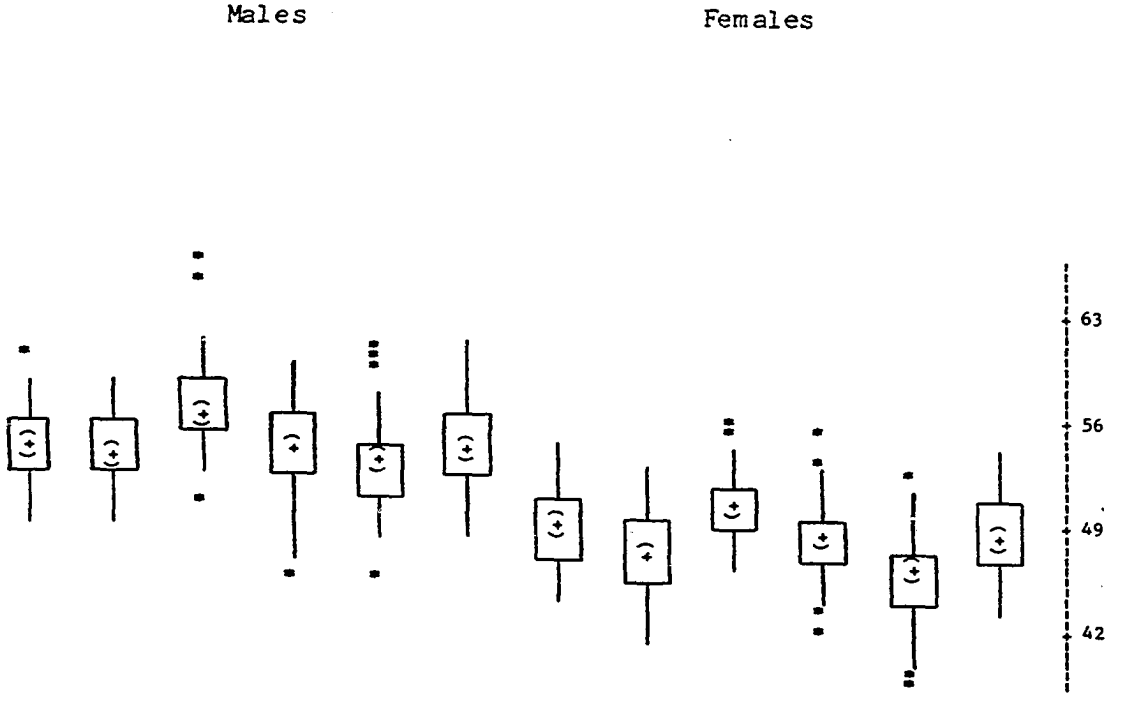




Exhibit 3.15 Boxplot for bicondylar humerus

Exhibit 3.16 Boxplot for wrist breadth



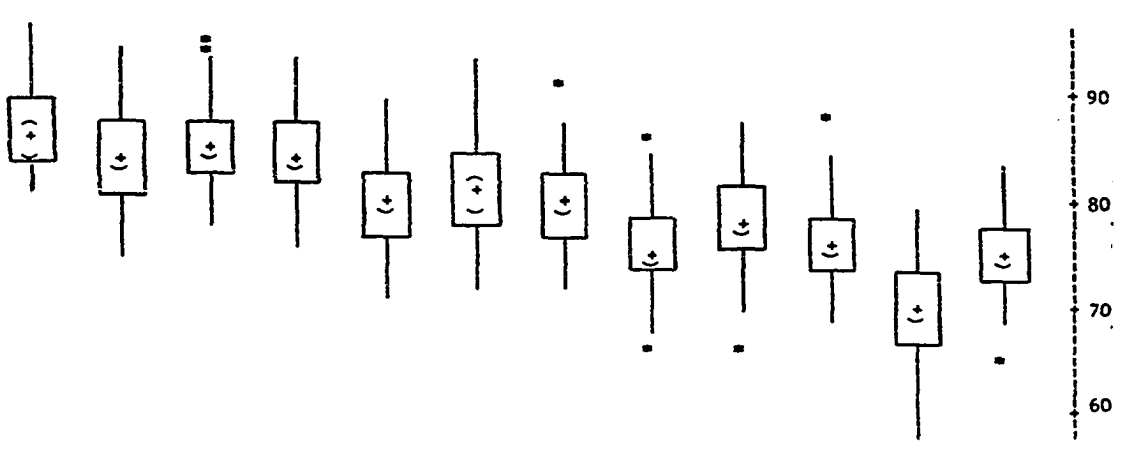
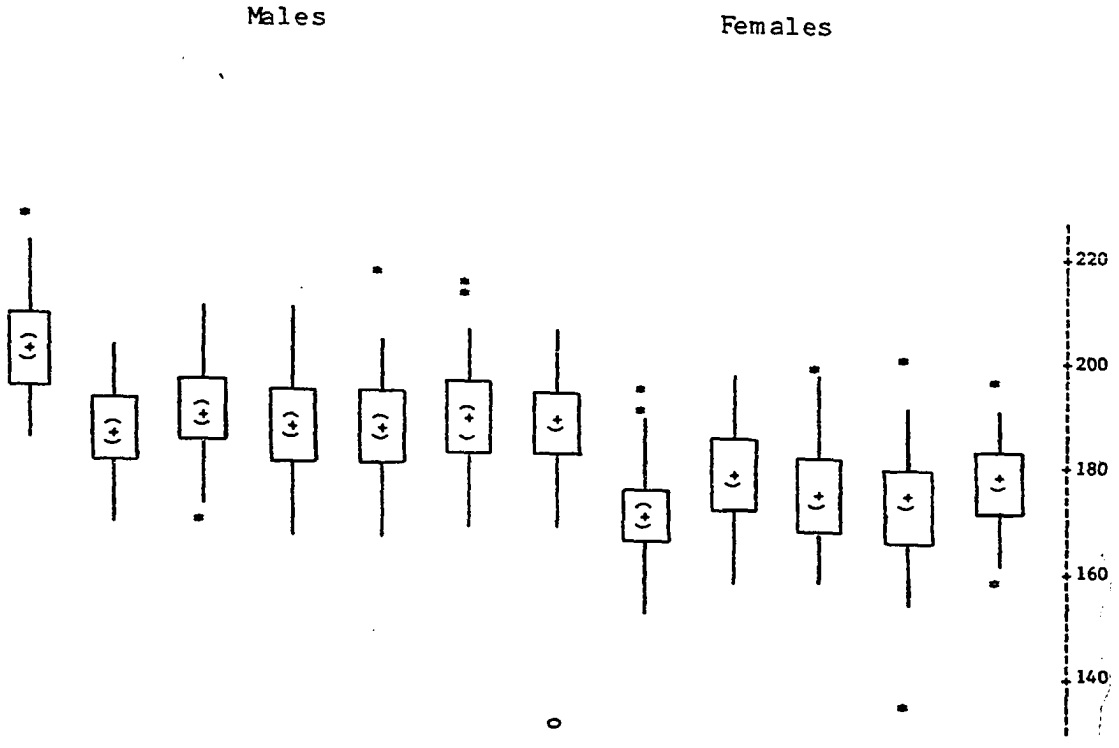




Exhibit 3.17 Boxplot for hand breadth

Exhibit 3.18 Boxplot for hand length



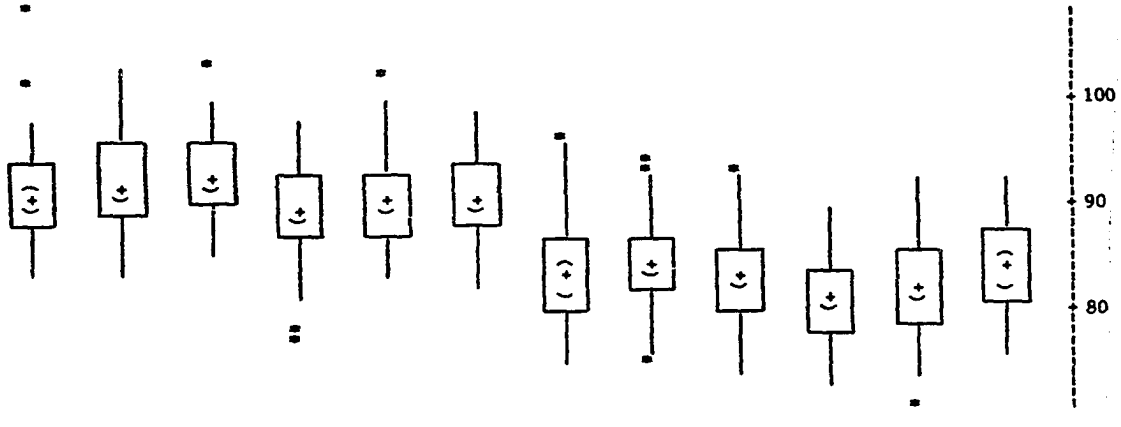
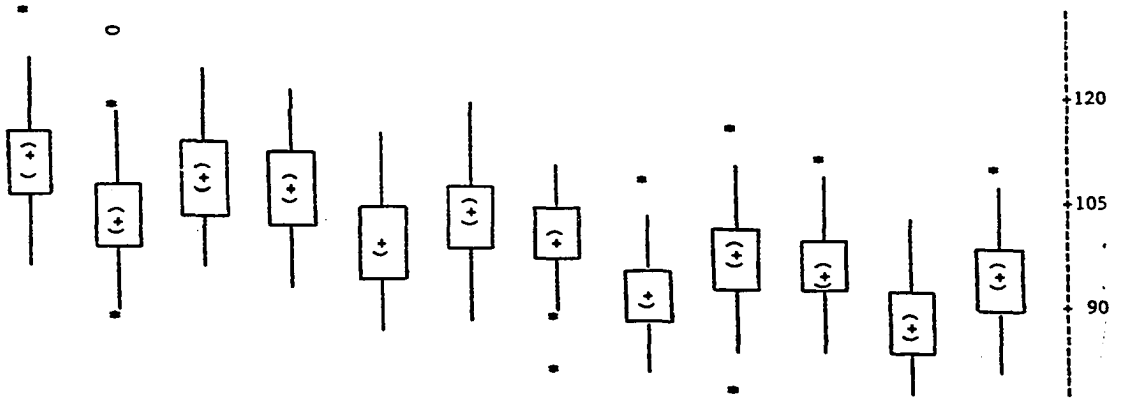




Exhibit 3.19 Boxplot for bicondylar femur

Exhibit 3.20 Boxplot for foot breadth





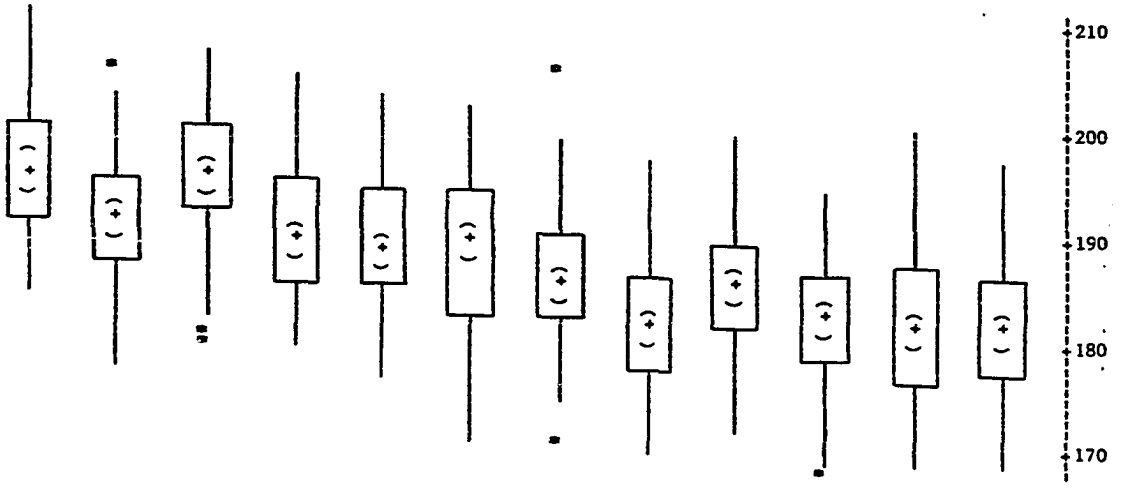
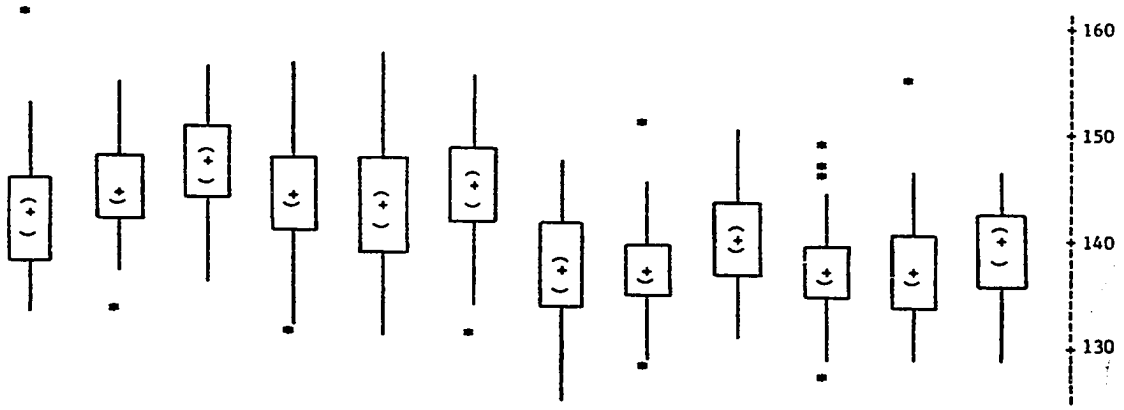



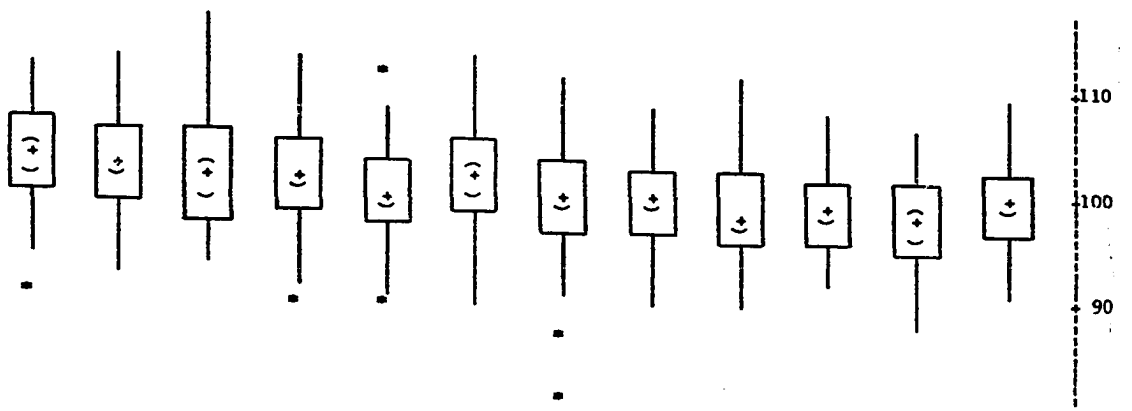

Exhibit 3.21 Boxplot for head length

Exhibit 3.22 Boxplot for head breadth

Males Females




Reef Kwaio Lau Baegu Nago Aita Reef Kwaio Lau Baegu Nago Aita



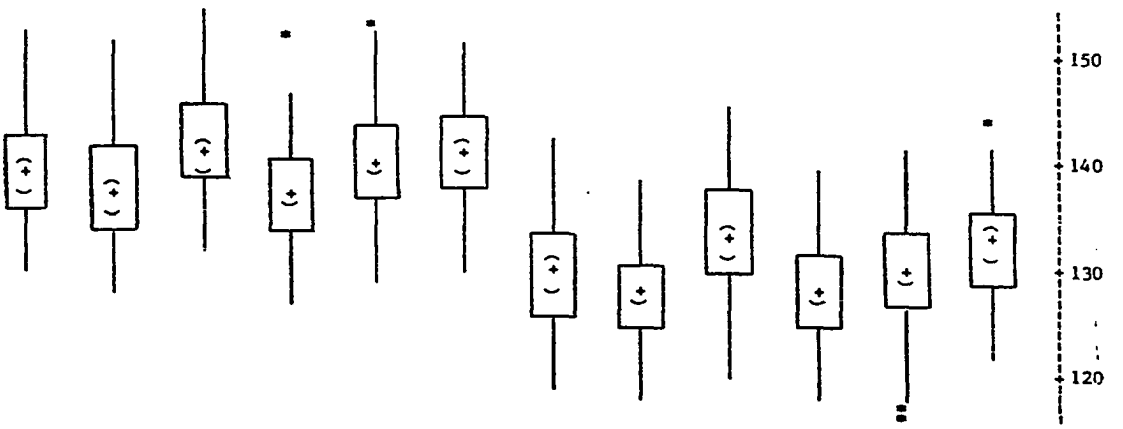

Reef Kwaio Lau Baegu Nago Aita Reef Kwaio Lau Baegu Nago Aita

Exhibit 3.23 Boxplot for minimum frontal diameter

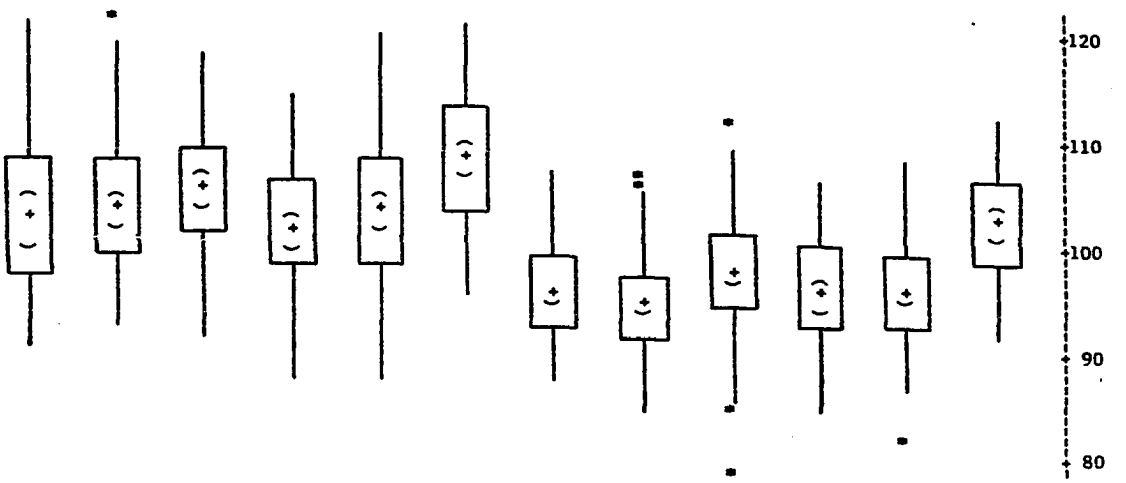
Exhibit 3.24 Boxplot for bizygomatic diameter



Males Females



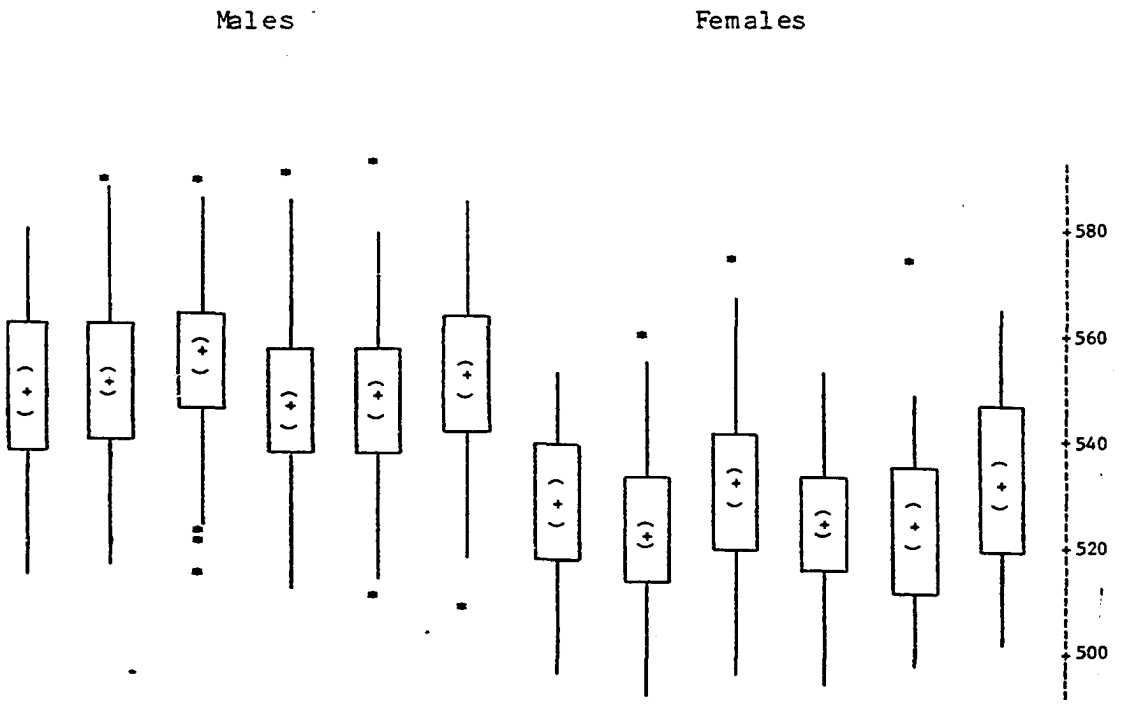

Reef Kwaio Lau Baegu Nago Aita Reef Kwaio Lau Baegu Nago Aita




Reef Kwaio Lau Baegu Nago Aita Reef Kwaio Lau Baegu Nago Aita

Exhibit 3.25 Boxplot for bigonial diameter

Exhibit 3.26 Boxplot for head circumference



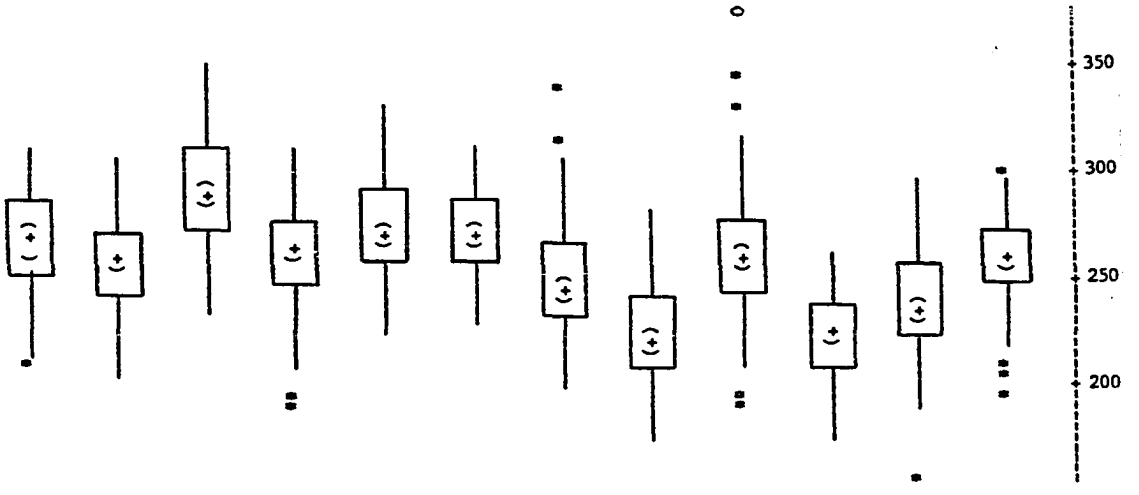
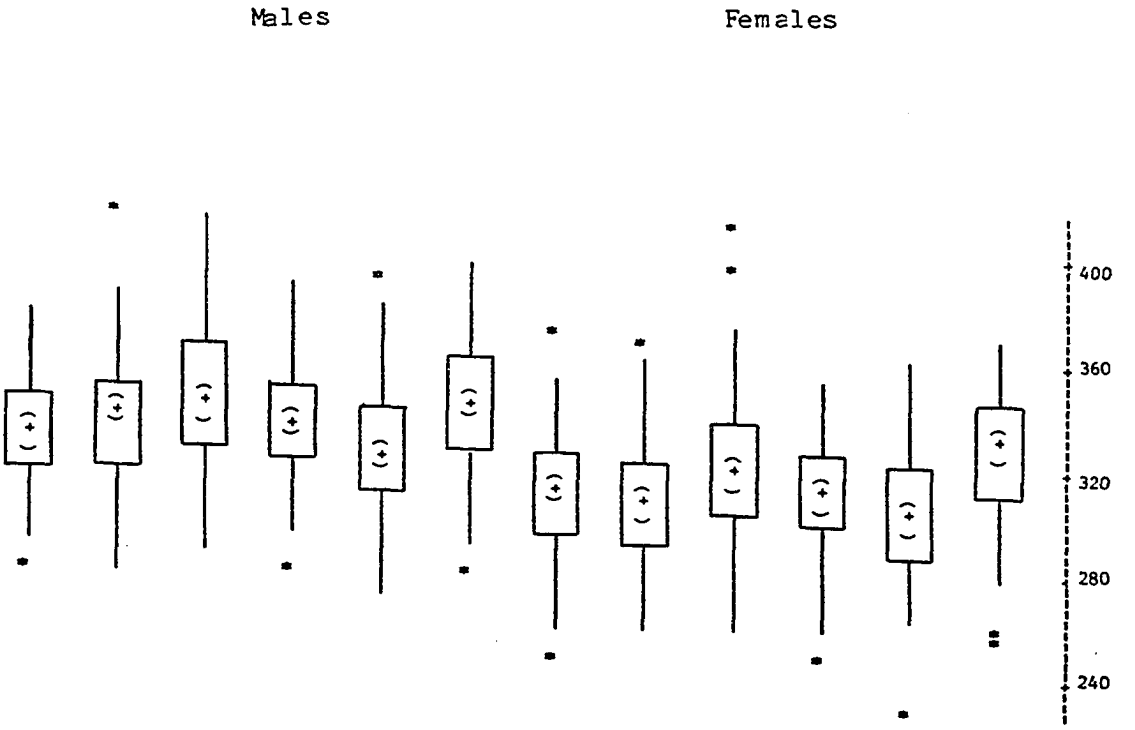




Exhibit 3.27 Boxplot for upper arm circumference

Exhibit 3.28 Boxplot for calf circumference



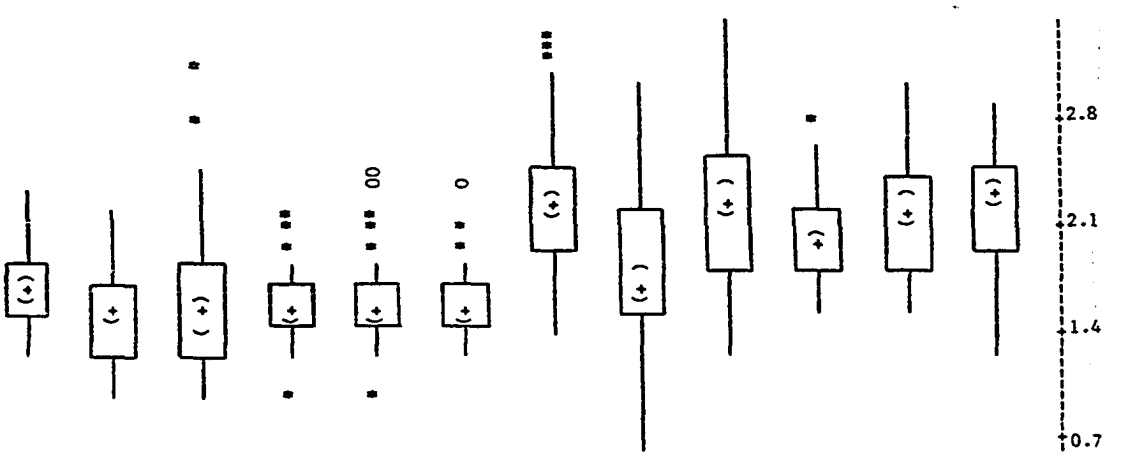
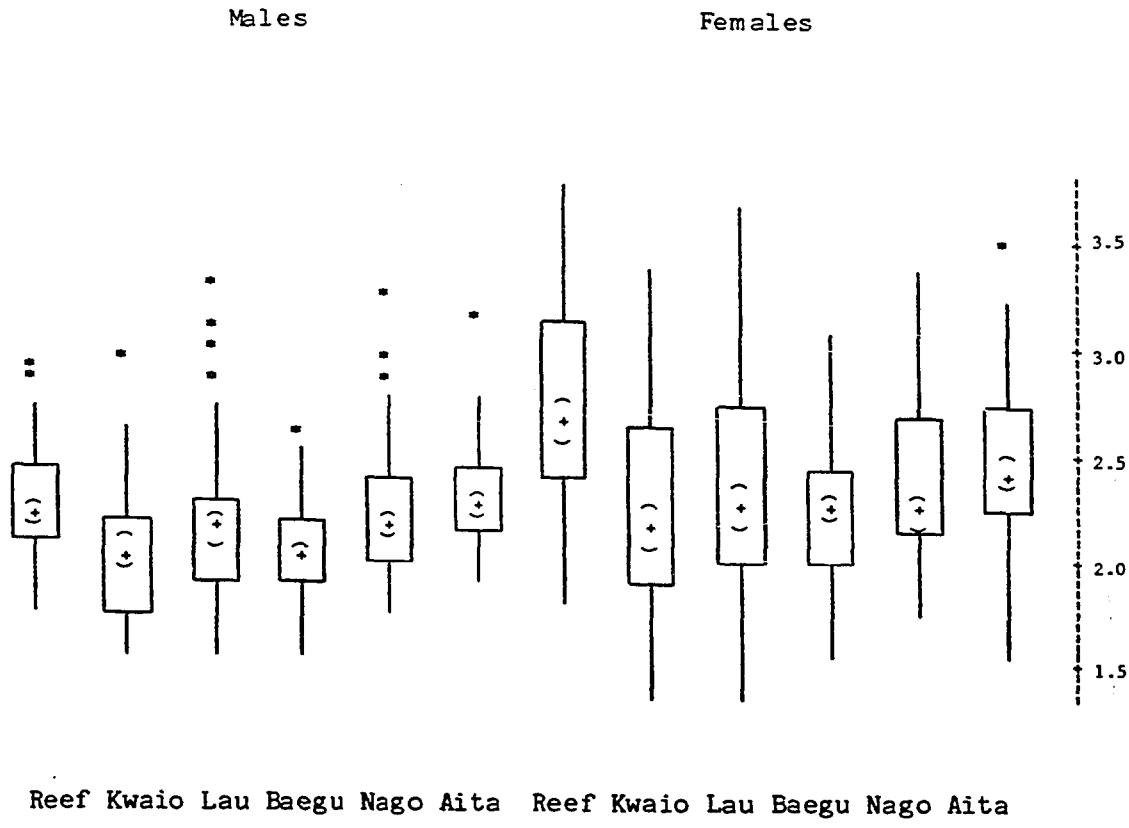




Exhibit 3.29 Boxplot for triceps skinfold

Exhibit 3.30 Boxplot for subscapular skinfold





tendency to skewing toward larger values.

Differences in sitting height are apparent in exhibit 3.5. There is an obvious difference between the sexes, with males tending toward larger sitting heights. The pattern of population differences within each sex is different. In general there appears to be much greater variation in male median values than in female median values.

Biacromial diameter is shown in exhibit 3.7. There is once again an obvious component of sexual dimorphism. Other differences are apparent between the populations. Unlike the pattern for sitting height, there appears to be greater population variation in medians for females rather than males. The sex by population interaction may be seen by taking the between-population pattern for one sex as a standard, and comparing the other sex with it. If we take the males as a reference group then the major differences are the low median for Kwaio females, and the high median for Aita females.

The pattern for bicristal diameter is shown in exhibit 3.8. There is a less obvious component of sexual dimorphism, and less obvious between-population variation in males. There are extremes of H-spread with Reefs males at the low end and Reefs females at the high end. That males and females of the same population are at the extremes of H-spread further emphasizes that there are no clear patterns of between-sex or between-population variation. The interaction effect is

emphasized in the higher median for Lau females (relative to the between-population pattern for males).

The variation in medians for chest breadth is shown in exhibit 3.9. There is some variation in H-spread but this is not clearly based on between-sex or between-population differences. There are some differences in medians between the sexes, and between the populations. However, the most striking pattern is the interaction of the two main effects. Conspicuous differences in between-population variation for males and females are evident. The Nagovisi female median is distinctly low, and the male Lau median is distinctly high.

Differences in upper facial height are shown in ex 3.11. Both the Kwaio and Baegu females have narrow H-spreads, and Reefs females have the largest H-spread. The variation in H-spread for females is greater than that for males. There is an overall pattern of sexual dimorphism (males having larger values), but the most conspicuous pattern is greater upper facial height for both males and females from Lau. The interaction effect seems to stem from the larger median for Baegu females which is missing in the males. The pattern for nose length (shown in exhibit 3.12) is similar to that for upper facial height. This is not suprising as nose length is a component of upper facial height, and the two variables are in a parts and wholes relationship.

Hand breadth is shown in exhibit 3.16. The common pattern of sexual dimorphism persists, with males having larger median

values than the corresponding female group. Nagovisi females have conspicuously lower values for hand breadth than do the other female groups.

There is an obvious difference between males and females for bicondylar femur (exhibit 3.18). Between population variation appears to be much less important in females, with no two populations proving significantly different in pairwise comparisons of medians at the .05 level. There is, however, a significant difference between the Lau males and the Nagovisi males.

Variation in upper arm circumference is shown in ex 3.26. There is some variation in H-spread. Aita females have the narrowest H-spread, and Lau males have the widest. There appear to be greater between-population differences for females than for males.

The natural log of triceps skinfold is shown in exhibit 3.28. Even after a log transform the values for Baegu, Nagovisi and Aita males are badly skewed. These three groups also have much lower H-spreads. There is an obvious component of sexual dimorphism, both in H-spread and median. Females exceed males in both variability and median. Note that higher median values for females is the opposite of the pattern for other variables. There is also significant between population variation in medians for females, but not for males. A similar result is found for the log of subscapular skinfold (exhibit 3.29). Although there

are significant between population differences for males, there is greater variation between populations for females.

In discussing the boxplots of individual variables which are significant in the sex by population multivariate interaction, we have also had occasion to comment on the general pattern of between population or between sex variation for these same variables. It is now time to turn to canonical discriminant analysis to examine further the differences between populations. As there is a significant sex by population interaction, a discriminant analysis between populations is carried out separately for each sex.

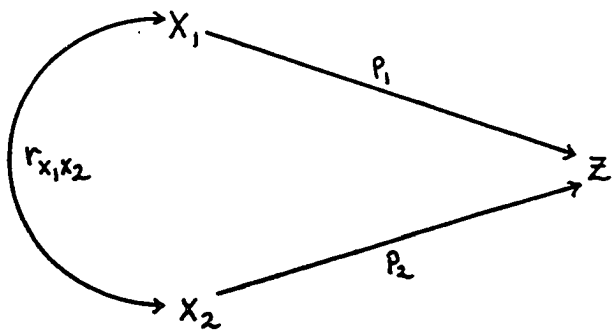
### 3.2.3 Female Between Population Discriminant Analysis

Canonical discriminant analysis is a fairly common data analysis tool in the kit used by physical anthropologists, and as such it requires little introduction. However, there has been some recent discussion concerning the appropriate method for relating the original variables measured to the derived canoncial variates. There are two methods for identifying which original variables are important in differentiating between groups. Traditionally, the relative importance of different variables has been estimated by the standardized discriminant function coefficient for each variable (Nie, et al. 1975; Bock 1975: 248). Howells (1973) and Friedlaender (1975) have more recently

recommended the use of discriminant loadings. These are defined as the correlation between each original variable and the score on the composite discriminant axis (Cooley and Lohnes 1971:248). In fact these two alternatives are complementary and each provides essential information concerning the nature of group differences. The relationship between discriminant loadings and standardized coefficients may be most easily visualized by a path diagram and its associated equations. For the sake of brevity the two variable case is illustrated in exhibit 3.31.

Equation 1 (in exhibit 3.31) represents the complete determination of a discriminant score (z) by a weighted combination of the original variables. The path coefficients ($p_1$ and $p_2$) are identical to the standardized coefficients. Discriminant loadings are represented by the correlations in equations 2 and 3 of exhibit 3.31. The standardized coefficients represent the unique contribution of each original variable to the discriminant score (Friedlaender 1975:150). Discriminant loadings represent the contribution of an original variable taking into account both its direct effect and its indirect effect through correlation with other variables. The use of a path diagram also emphsizes that the correlations between the original variables ($r_{x_1 x_2}$ in the sample case illustrated here) are left unanalyzed.

It is usually neccessary to examine both discriminant loadings and standardized coefficients, supplemented by examination of the group means on the original variables.




$$z = P_1 X_1 + P_2 X_2 \quad (1)$$

$$r_{x_1 z} = P_1 + r_{x_1 x_2} P_2 \quad (2)$$

$$r_{x_2 z} = P_2 + r_{x_1 x_2} P_1 \quad (3)$$

Exhibit 3.31 Path Diagram Illustrating Discriminant Loadings

Standardized discriminant function coefficients interpreted in isolation can be misleading because they may emphasize some variables as variance supressors. Supressor variables do not differ in value between groups, but their covariance with other variables in the discriminant function causes reduction of the within group variance and thus greater discriminatory power. An examinaiton of group means for all variables in a discriminant function will identify supressor variables. Supressor variables are also likely to have low discriminant loadings.

Standardized coefficients may include supressor variables which do not differ between groups, and they may also leave out variables for which the groups are different. Given two (or more) highly correlated variables, only one will be entered into the discriminant function. The others are redundant, containing no more unique information for discriminating between groups. If the goal of discriminant analysis is to find all the ways in which the groups are different (versus classification only) then it is important to include the redundant variables in the description of group differences. These redundant variables may be identified in the discriminant loadings where their indirect contribution to the canonical variate will be seen. Note that the interpretation of discriminant loadings in isolation suffers from the same problem that the standardized coefficients display with supressor variables. Variables with high discriminant loadings need not always represent those with univariate group differences (Friedlaender 1975:150). They may have high loadings through their covariance with other variables for which the

groups are different. The final arbitrator in interpreting group differences is an examination of the group means or medians for the variables concerned.

In the analysis which follows we will examine both the standardized discriminant function coefficients and the discriminant loadings, supplemented by a return to the boxplots of exhibits 3.4 to 3.30. Based on the univariate F tests all 27 variables show significant between population and between sex variation ($p<0.01$) so our interest is concentrated on the particular way in which the variables contribute to the discriminant functions contrasting particular groups.

The standardized discriminant function coefficients and the discriminant loadings for between population variation based on females are given in exhibit 3.32. There five discriminant functions, all are orthogonal to one another. These five functions all represent significant dimensions of between population variation ($p<0.01$). Plots of the group mean vectors (centroids) in the discriminant space are given in exhibits 3.33 to 3.35. Each plot represents a pair of axes plotted against one another. The approximate 99% confidence circle for each group mean is shown on the plot (computed as in Seal 1964:137).

In exhibit 3.33 the first discriminant function separates the Lau females from the rest of the groups, with the Reefs females at the other extreme. Examining the standardized coefficients in exhibit 3.32 we see that upper facial height

MULTIVARIATE TESTS OF SIGNIFICANCE (S= 5, M= 10 1/2, N= 252)

| TEST | VALUE | APPROX. F | HYP.DF | ERROR DF | PROB |
|---|---|---|---|---|---|
| PILLAIS | 2.60282 | 20.50920 | 135.00 | 2550.00 | <0.01 |
| HOTELLINGS | 6.18074 | 23.09308 | 135.00 | 2522.00 | <0.01 |
| WILKS | .02129 | 21.90528 | 135.00 | 2500.74 | <0.01 |
| ROYS | .67092 | | | | |

EIGENVALUES AND CANONICAL CORRELATIONS

| ROOT | EIGENVALUE | PCT. | CUM. PCT. | CAN. COR. |
|---|---|---|---|---|
| 1 | 2.03880 | 32.986 | 32.986 | .81910 |
| 2 | 1.74672 | 28.260 | 61.247 | .79745 |
| 3 | 1.18631 | 19.193 | 80.440 | .73662 |
| 4 | .61976 | 10.027 | 90.468 | .61857 |
| 5 | .58915 | 9.531 | 100.000 | .60888 |

Standardized Discriminant Function Coefficients

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| WEIGHT | 0.255 | 0.412 | -0.768 | -0.350 | 0.106 |
| SITHT | -0.180 | 0.091 | 0.390 | -0.398 | -0.041 |
| STATURE | -0.195 | -0.216 | -0.328 | 0.381 | 0.223 |
| BIACROM | 0.283 | -0.124 | -0.071 | 0.087 | -0.105 |
| BICRIST | 0.096 | 0.075 | 0.413 | -0.109 | 0.231 |
| CHESTB | 0.307 | -0.462 | 0.475 | -0.327 | -0.316 |
| FOOTL | 0.063 | -0.096 | -0.287 | -0.175 | 0.650 |
| TFACHT | -0.424 | -0.074 | -0.238 | -0.169 | 0.083 |
| UFACHT | 0.694 | 0.321 | 0.002 | 0.575 | -0.003 |
| NOSEL | 0.263 | -0.140 | 0.243 | -0.492 | 0.166 |
| NOSEB | 0.015 | -0.241 | -0.033 | -0.040 | -0.219 |
| BICHUM | 0.303 | 0.187 | -0.055 | 0.128 | 0.261 |
| WRISTB | 0.329 | 0.080 | 0.170 | 0.162 | -0.174 |
| HANDB | -0.064 | -0.508 | 0.620 | 0.028 | -0.192 |
| HANDL | -0.272 | -0.306 | -0.294 | 0.256 | -0.329 |
| BICFEM | -0.448 | 0.176 | 0.038 | -0.620 | -0.474 |
| FOOTB | 0.111 | -0.346 | -0.049 | 0.507 | -0.114 |
| HEADL | 0.113 | -0.678 | 0.021 | -0.592 | 0.456 |
| HEADB | 0.220 | -0.060 | -0.002 | -0.146 | 0.117 |
| MFRONT | -0.239 | -0.073 | 0.250 | -0.031 | -0.103 |
| BIZYGO | 0.094 | 0.097 | -0.394 | -0.267 | 0.211 |
| BIGON | 0.009 | 0.119 | -0.068 | 0.359 | -0.462 |
| HEADCR | -0.176 | 0.872 | 0.037 | 0.702 | -0.518 |
| UPARM | 0.139 | -0.070 | -0.840 | -0.861 | -0.637 |
| CALFC | -0.258 | 0.519 | 0.867 | 0.743 | 0.038 |
| TRISKN | 0.464 | 0.047 | -0.021 | 0.386 | 0.304 |
| SUBSKN | -0.551 | -0.548 | -0.033 | 0.339 | 0.467 |

Exhibit 3.32 Female Discriminant Analysis

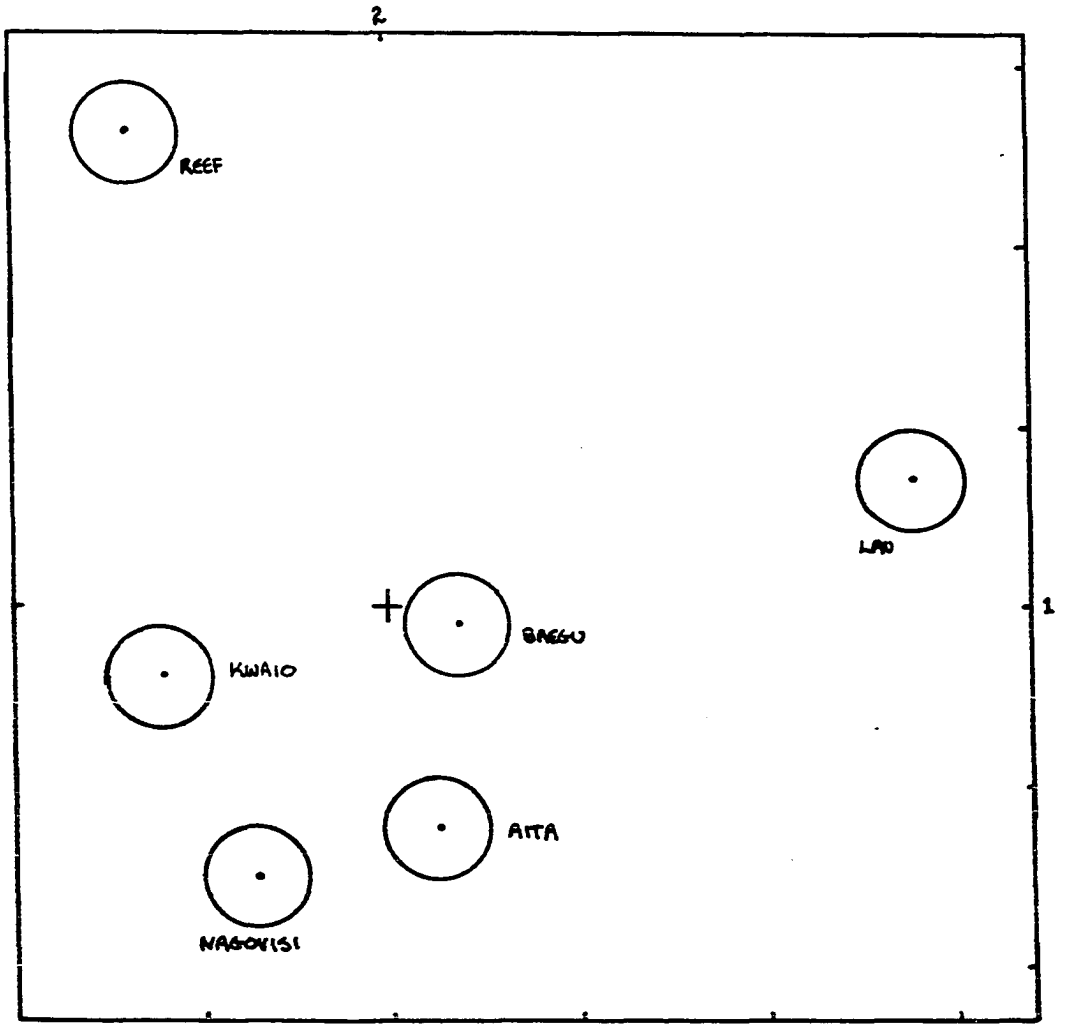
Discriminant Loadings (correlations between canonical variates and original variates)

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| WEIGHT | 0.217 | -0.155 | -0.219 | -0.044 | -0.250 |
| SITHT | 0.011 | -0.099 | 0.000 | -0.104 | -0.108 |
| STATURE | 0.047 | -0.259 | -0.187 | 0.048 | -0.010 |
| BIACROM | 0.293 | -0.291 | -0.204 | 0.014 | -0.273 |
| BICRIST | 0.259 | -0.123 | 0.108 | -0.162 | -0.027 |
| CHESTB | 0.303 | -0.288 | -0.046 | -0.162 | -0.312 |
| FOOTL | 0.134 | -0.336 | -0.147 | 0.088 | 0.028 |
| TFACHT | 0.312 | -0.008 | -0.022 | -0.070 | 0.018 |
| UFACHT | 0.540 | 0.127 | 0.063 | 0.055 | 0.106 |
| NOSEL | 0.510 | 0.051 | 0.158 | -0.173 | 0.161 |
| NOSEB | 0.059 | -0.217 | 0.006 | -0.047 | -0.315 |
| BICHUM | 0.365 | -0.115 | -0.059 | -0.018 | -0.166 |
| WRISTB | 0.327 | -0.200 | 0.070 | 0.023 | -0.305 |
| HANDB | 0.206 | -0.507 | 0.212 | 0.089 | -0.348 |
| HANDL | 0.070 | -0.391 | -0.259 | 0.158 | -0.175 |
| BICFEM | -0.052 | -0.041 | 0.014 | -0.246 | -0.362 |
| FOOTB | 0.241 | -0.411 | 0.081 | 0.270 | -0.240 |
| HEADL | 0.093 | -0.229 | -0.034 | -0.107 | -0.038 |
| HEADB | 0.208 | 0.035 | -0.043 | -0.080 | -0.172 |
| MFRONT | -0.043 | -0.075 | 0.024 | -0.014 | -0.156 |
| BIZYGO | 0.226 | 0.016 | -0.250 | -0.105 | -0.280 |
| BIGON | 0.093 | 0.098 | -0.187 | 0.209 | -0.498 |
| HEADCR | 0.128 | -0.043 | -0.098 | 0.007 | -0.251 |
| UPARM | 0.258 | -0.127 | -0.384 | -0.144 | -0.382 |
| CALFC | 0.147 | 0.017 | -0.027 | 0.097 | -0.303 |
| TRISKN | 0.122 | -0.090 | -0.323 | 0.058 | -0.050 |
| SUBSKN | -0.022 | -0.210 | -0.280 | 0.007 | -0.087 |

DIMENSION REDUCTION ANALYSIS

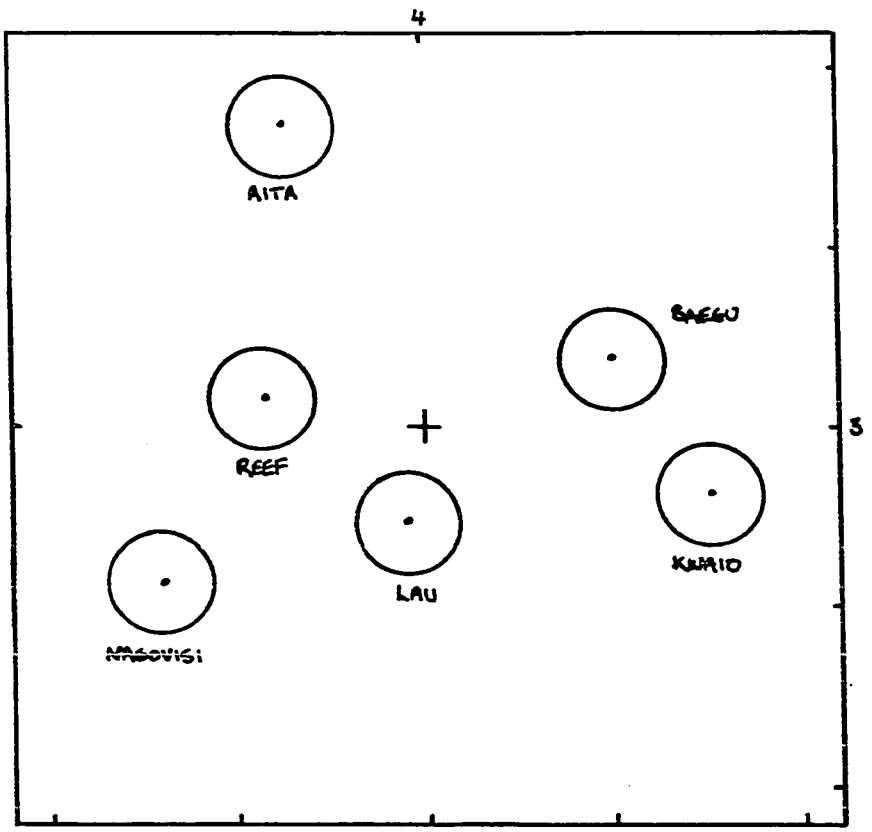
| ROOTS | LAMBDA | F | HYP.DF | ERR.DF | PROB |
|---|---|---|---|---|---|
| 1 TO 5 | .02129 | 21.905 | 135 | 2500 | <0.01 |
| 2 TO 5 | .06469 | 19.227 | 104 | 2013 | <0.01 |
| 3 TO 5 | .17769 | 15.817 | 75 | 1517 | <0.01 |
| 4 TO 5 | .38850 | 12.780 | 48 | 1015 | <0.01 |
| 5 TO 5 | .62927 | 13.012 | 23 | 508 | <0.01 |

Exhibit 3.32 Female Discriminant Analysis



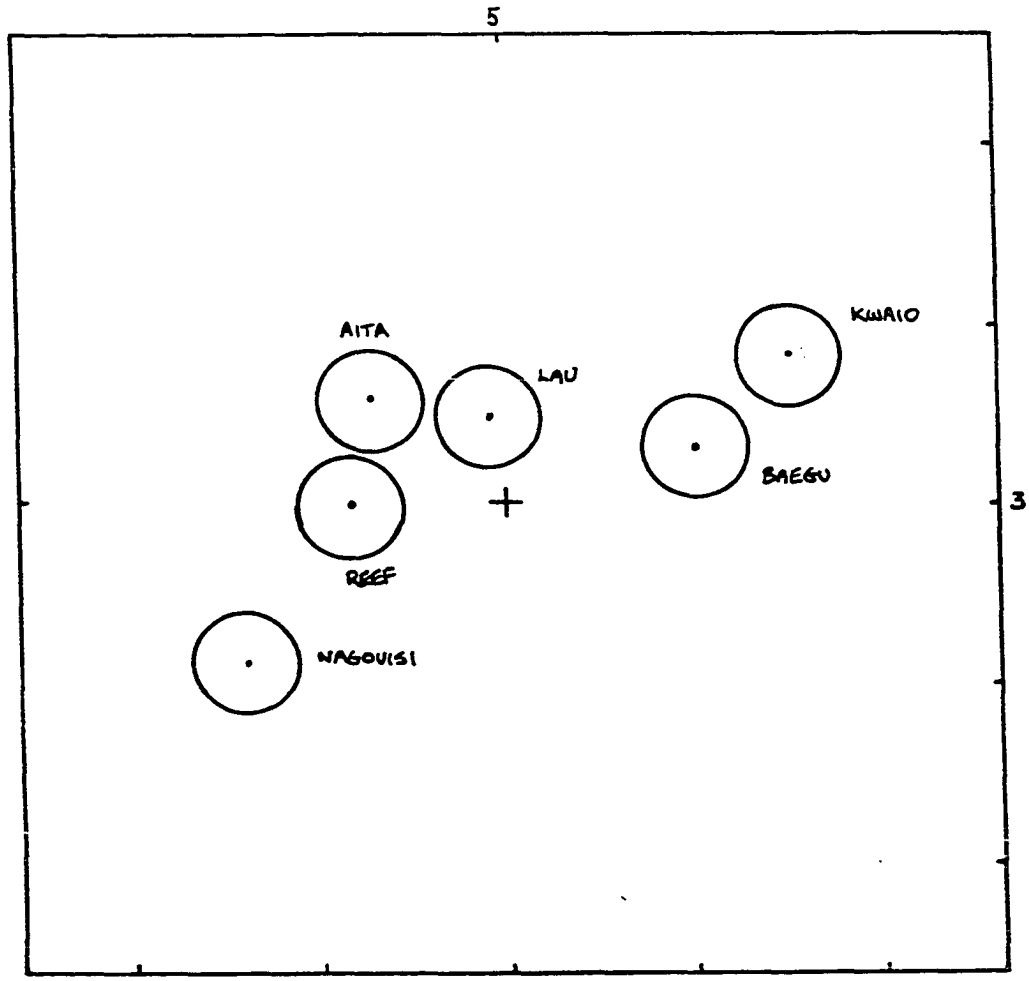

Circles are approximate 99% confidence limits for group means.

Exhibit 3.33 Canonical Group Means (Females) Functions 1 and 2




Circles are approximate 99% confidence limits for group means.

Exhibit 3.34 Canonical Group Means (Females) Functions 3 and 4




Circles are approximate 99% confidence limits for group means.

Exhibit 3.35 Canonical Group Means (Females) Functions 3 and 5

makes the largest direct contribution to this contrast, and that subscapular skinfold is next important in magnitude (although opposite in sign). There are 6 other variables making a substantial contribution to this discriminant function using an arbitrary cutoff value of .3. Those with positive coefficients are weight, bicondylar humerus, wrist breadth, and triceps skinfold. Negative coefficients are observable for total facial height and bicondylar femur. When the boxplots for these variables are examined it is clear that this contrast is more complex than it first appears.

Firstly, variables which are traditionally positively correlated (the two skinfolds; total facial height and upper facial height) take on opposite signs for discriminant function coefficients. This is because the coefficients include only the unique contribution of each variable. Looking at the boxplots for total facial height and upper facial height (exhibits 3.11 and 3.12), it is apparent that the Lau females have relatively large values for both. Lau females stand out clearly in total facial height, and both Lau and Baegu females have larger upper facial height than the other female groups. The proportion of variance in total facial height which is entering the discriminant function is that not shared with upper facial height, and it is acting as a contrast of these two measurements. Looking at the discriminant loadings in exhibit 3.32 we note that the set of three facial height measurements (upper facial height, total facial height, nose length) are all positively correlated with the first discriminant function. Nose length does not

appear in the discriminant function coefficients because of its intercorrelation with upper facial height and total facial height.

Turning to the boxplots for the two skinfold measurements (exhibits 3.29 and 3.30) we see that the Lau females are among the 4 larger groups for triceps skinfold, but that they fall below the Reefs females in subscapular skinfold values. Thus the negative coefficient for subscapular skinfold places the Reefs females at the negative end of the function. The negative coefficient also picks out the fact that the Lau females have smaller subscapular skinfold values than expected, given their values for the other measurements.

Returning to the discriminant function coefficients in exhibit 3.32 we note that both bicondylar humerus and wrist breadth enter the discriminant funciton. Examination of the boxplots for these two variables (exhibits 3.15 and 3.16) shows that the Lau females are distinguished by larger values for these variables. Weight also appears in the discriminant function coefficients, but its interpretation in the discriminant function is confounded by the observation that both the Reefs and Lau females (who lie at opposite extremes on this function) have the largest values for weight. Weight may be a composite variable which includes one or more independent components of physique, and one such component is being included in the discriminant function. It may also be that weight is acting as a standardizing variable in the discriminant function (in concert

with the other variables in the set) by absorbing differences in the other variables which are due to differences in body weight. Finally, bicondylar femur appears in the equation with a negative coefficient. There are no clear differences between groups in the boxplot for bicondylar femur (exhibit 3.19) so this must represent a supressor variable.

The second discriminant function also appears in exhibit 3.33, and this fuction contrasts the Reefs females with the other 5 groups, although the Lau remain intermediate. From the coefficients in exhibit 3.32 the most important variables are head circumference and head length (with opposite signs). Examining the boxplots for head circumference and head length (exhibits 3.26 and 3.21) we see that the Reefs and Lau females have longer heads, and are among the largest groups for head circumference. The contrast in signs between head circumference and head length may indicate that differences in shape are also present. In fact, from the boxplots it appears that this is a profile difference between (1) the Nagovisi and Aita females with larger head circumference and shorter heads, and (2) the Reefs and Lau females with larger head circumference and long heads. This contrast by head shape echoes the first discriminant function derived by Friedlaender (1975:151) which separates males from different villages within Bougainville.

The breadth of extremities (hand breadth, foot breadth) is also a factor in this second function. An examination of the discriminant loadings (exhibit 3.32) shows that hand length and

foot length are also correlated with this function, although they are not present in the function itself. Examination of the relevant boxplots for extremities (exhibits 3.10, 3.17, 3.18 and 3.20) shows that Reefs and Lau females tend to have the largest hands and feet. Subscapular skinfold is also important in this function and it serves to further separate the Reefs females from the Lau females. Although the Reefs and Lau females are generally similar in size, there are other ways in which they differ. Returning to the boxplots for facial height (exhibits 3.11, 3.12 and 3.13) we note that the Reefs females have relatively smaller facial height measures than we would expect given their general robustness. Continuing with the discriminant function coefficients (exhibit 3.32) we see that weight is once again included in this function in a way which contrasts (in sign) with its appearance in the first discriminant function. This may, in part, be due to the contrast between Aita females and the Reefs and Lau females, as the Aita are relatively heavy but otherwise distinct from the Reefs and Lau females. Calf circumference also appears in this second discriminant funciton with a negative sign. Examining we see that the boxplot for calf circumference (exhibit 3.28) the Aita have the largest values for calf circumference so they would again be contrasted with the Reefs and Lau females. Finally we note that chest breadth has a substantial positive coefficient. Examining the boxplots for chest breadth (exhibit 3.9) it is apparent that both Lau and Reefs females have broader chests than the other groups.

The third and fourth discriminant functions are shown in

exhibit 3.34. The third function contrasts the inland Malaitan females (Kwaio and Baegu) with the other groups. The most important variables are upper arm circumference, calf circumference, and weight. Kwaio and Baegu females weigh less than the Reefs, Lau and Aita females. Similar patterns hold true for upper arm circumference and calf circumference. Although the Nagovisi females also weigh less and have smaller upper arm circumference and calf circumference, they are distinct from the Kwaio and Baegu females in other ways. Bicristal diameter and chest breadth both enter the discriminant function and these serve to distinguish the Nagovisi from the inland Malaitan females. The Nagovisi have significantly lower values for bicristal diameter and chest breadth than do the Kwaio or Baegu (see exhibits 3.8 and 3.9). Bizygomatic diameter appears to enter the equation for the same reason, distinguishing the larger Nagovisi from the smaller Kwaio and Baegu females (exhibit 3.24). Similarly, hand breadth further separates the Nagovisi, as they have narrower hands (exhibit 3.17). Although sitting height and stature are entered in the discriminant function these appear to be acting as supressor variables. Judging from the boxplots for sitting height and stature (exhibits 3.5 and 3.6) the only significant finding is that the Reefs females are taller than the rest.

The fourth discriminant function contrasts the Aita with the other groups. Head circumference and head length are major contributors to this function, with their signs reversed from the corresponding coefficients for discriminant function 2.

Re-examining the boxplots for both variables (exhibits 3.26 and 3.21) we remember that the Aita are distinct in having a large head circumference combined with a short head. This is picked up as a strong profile difference because these two variables are positively correlated within each group. Another contrast is hand length and foot breadth against foot length. The Aita females have relatively shorter feet (exhibit 3.18) given their longer hands and broader feet (exhibits 3.18 and 3.20). A third contrast pair is upper facial height and nose length (exhibits 3.12 and 3.13). Once again the Aita females have shorter noses in combination with medium values for upper facial height. Continuing with the discriminant function coefficients, the Aita are distinguished from the other groups in having the largest calf circumference and bigonial diameter (see exhibits 3.28 and 3.25). Bizygomatic diameter is also identified by the fourth discriminant function although the Aita share with the Lau and Nagovisi females larger values for this variable.

The fifth (and last!) discriminant function contrasts the Nagovisi with the other groups (see exhibit 3.35). These coefficients are not easily interpretable, as most of the significant ones (upper arm circumference, bicondylar femur, sitting height, stature, foot length, upper facial height, calf circumference, triceps skinfold, subscapular skinfold) cannot be related to any obvious distinction in the boxplots. This implies that the contrasts are in the interrelation of sets of variables rather than the individual variables themselves. Chest breadth does appear in the discriminant function and is interpretable in

its associated boxplot (exhibit 3.9). The Nagovisi females have narrower chests than other groups.

Summarizing then, females from the Reefs, Lau and Aita groups are larger in most measurements than are the other 3 groups. Rhoads (1977:156) has already commented that Aita males "contradict the image of the stunted highlander." It appears that this observation also holds true for females, although the Reefs females are actually the tallest group. The Aita females may be characterized as having broad but relatively short heads. In contrast, the Lau females have long and broad heads while the Reefs females have long and narrow heads. The Lau females have the largest values for total facial height and nose length, while the Reefs females have shorter noses and facial heights.

The Reefs and Lau females both have relatively larger hands and feet. In contrast, the Aita females have relatively short feet. Both the Reefs and Lau females may be distinguished from the Aita in having broader chests. The Reefs and Lau females are, in turn, distinct from one another in other ways. Although all three of the robust female groups have larger skinfold values, the Reefs females stand out in having the largest subscapular skinfold values. The Lau have the largest bicondylar humerus values.

Turning to the more gracile female groups (Baegu, Kwaio, Nagovisi) we note that the Baegu are distinct in having large upper facial height and long noses. We observe however that the

Baegu do not have similarly large values for total facial height. Nagovisi females are distinct from the Kwaio and Baegu in having generally broader but shorter heads, and larger bizygomatic diameter. Nagovisi females also have the smallest values for chest breadth and bicristal diameter, and the narrowest heads.

### 3.2.4 Male Between Population Discriminant Analysis

The result of a discriminant analysis of between population variation for males is presented in exhibit 3.36. There are once again five discriminant functions which represent significant ($p<0.01$) dimensions of between population variation. Based on the univariate F tests all 27 variables show significant between population variation, as they did in the case of females. Plots of the five functions are given in exhibits 3.37 to 3.39.

In exhibit 3.37 the first discriminant function separates the Lau and Reefs males at one extreme, from the Kwaio at the other. Judging by the standardized coefficients for the first discriminant function (exhibit 3.36) the variables making the greatest direct contribution to this function are head circumference and head length (with opposite signs). Examining the boxplots for these variables (exhibits 3.26 and 3.21), it is clear that the Reefs and Lau males have the largest values for head length. The pattern for head circumference is more complex. On the basis of pairwise comparisons of medians, both groups have

MULTIVARIATE TESTS OF SIGNIFICANCE (S= 5, M= 10 1/2, N= 253 1/2)

| TEST NAME | VALUE | APPROX. F | HYP.DF | ERR.DF | PROB |
|---|---|---|---|---|---|
| PILLAIS | 2.24772 | 15.516 | 135.00 | 2565.00 | <0.01 |
| HOTELLINGS | 4.91587 | 18.476 | 135.00 | 2537.00 | <0.01 |
| WILKS | .04035 | 17.090 | 135.00 | 2515.53 | <0.01 |
| ROYS | .63116 | | | | |

EIGENVALUES AND CANONICAL CORRELATIONS

| ROOT | EIGENVALUE | PCT. | CUM. PCT. | CAN.COR. |
|---|---|---|---|---|
| 1 | 1.71121 | 34.809 | 34.809 | .79446 |
| 2 | 1.36166 | 27.699 | 62.509 | .75932 |
| 3 | 1.16272 | 23.652 | 86.161 | .73323 |
| 4 | .41950 | 8.533 | 94.695 | .54363 |
| 5 | .26078 | 5.304 | 100.000 | .45480 |

Standardized Discriminant Function Coefficients

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| WEIGHT | 0.544 | -0.437 | 0.045 | -0.018 | -0.109 |
| SITHT | -0.574 | -0.350 | 0.361 | 0.123 | -0.313 |
| STATURE | 0.115 | 0.391 | -0.272 | -0.297 | 0.376 |
| BIACROM | 0.168 | -0.097 | -0.025 | 0.232 | -0.425 |
| BICRIST | -0.074 | 0.193 | 0.098 | -0.161 | 0.132 |
| CHESTB | 0.133 | -0.071 | 0.368 | 0.044 | -0.245 |
| FOOTL | 0.038 | 0.017 | 0.121 | 0.085 | 0.780 |
| TFACHT | -0.304 | 0.050 | -0.457 | 0.273 | 0.053 |
| UFACHT | 0.493 | -0.407 | 0.255 | -0.580 | 0.228 |
| NOSEL | 0.081 | 0.110 | 0.433 | 0.388 | -0.219 |
| NOSEB | -0.001 | 0.106 | 0.027 | -0.200 | -0.120 |
| BICHUM | 0.275 | 0.030 | 0.087 | -0.449 | -0.155 |
| WRISTB | 0.206 | -0.374 | 0.299 | -0.456 | 0.098 |
| HANDB | -0.375 | 0.607 | 0.443 | 0.132 | -0.011 |
| HANDL | 0.142 | 0.297 | -0.739 | 0.137 | -0.739 |
| BICFEM | -0.415 | -0.142 | -0.121 | 0.970 | -0.034 |
| FOOTB | 0.239 | 0.310 | -0.015 | -0.363 | -0.026 |
| HEADL | 0.884 | 0.746 | 0.183 | 0.772 | -0.076 |
| HEADB | 0.164 | 0.107 | 0.315 | 0.034 | -0.075 |
| MFRONT | 0.009 | 0.291 | 0.133 | -0.111 | -0.074 |
| BIZYGO | 0.303 | -0.211 | -0.352 | 0.063 | 0.069 |
| BIGON | -0.156 | -0.117 | -0.057 | -0.065 | -0.399 |
| HEADCR | -0.940 | -0.801 | -0.306 | -0.479 | 0.075 |
| UPARM | 0.619 | -0.259 | -0.240 | 0.523 | 0.515 |
| CALFC | -0.769 | 0.227 | 0.161 | -0.538 | -0.218 |
| TRISKN | 0.005 | 0.109 | 0.071 | 0.346 | 0.206 |
| SUBSKN | -0.080 | 0.047 | -0.389 | -0.448 | -0.259 |

Exhibit 3.36 Male Discriminant Analysis

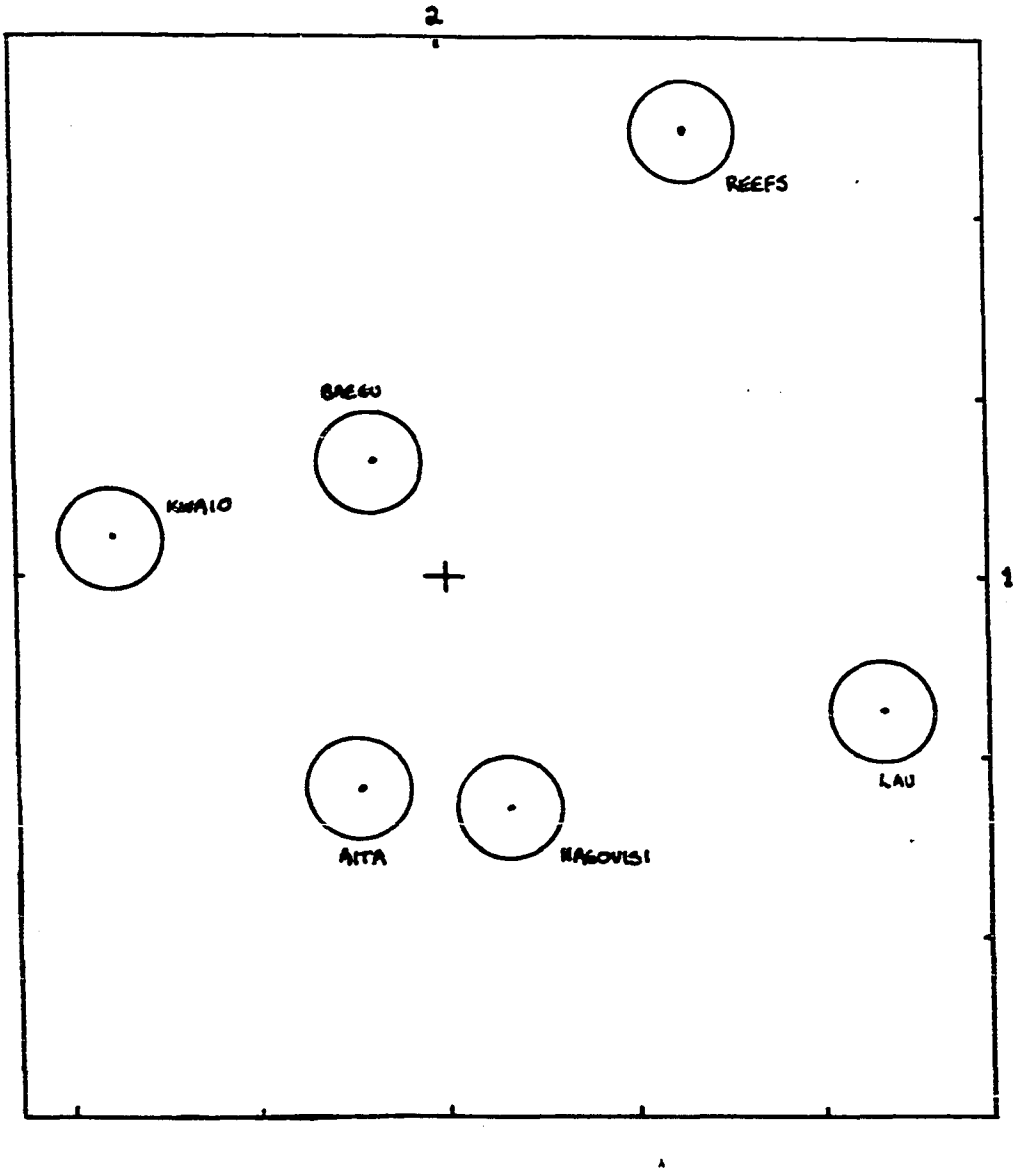
Discriminant Loadings (correlations between canonical variates and original variates)

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| WEIGHT | 0.276 | -0.041 | 0.090 | -0.056 | -0.349 |
| SITHT | -0.056 | -0.026 | 0.259 | 0.063 | -0.314 |
| STATURE | 0.144 | 0.216 | 0.040 | -0.007 | -0.185 |
| BIACROM | 0.289 | -0.002 | 0.141 | 0.152 | -0.476 |
| BICRIST | 0.206 | 0.112 | 0.107 | -0.043 | -0.161 |
| CHESTB | 0.267 | -0.079 | 0.314 | 0.037 | -0.489 |
| FOOTL | 0.214 | 0.262 | 0.079 | -0.018 | -0.008 |
| TFACHT | 0.208 | -0.091 | 0.086 | 0.073 | -0.080 |
| UFACHT | 0.360 | -0.202 | 0.226 | -0.051 | -0.007 |
| NOSEL | 0.290 | -0.105 | 0.362 | 0.128 | -0.086 |
| NOSEB | 0.115 | 0.114 | 0.030 | -0.122 | -0.266 |
| BICHUM | 0.330 | 0.042 | 0.183 | -0.150 | -0.301 |
| WRISTB | 0.237 | -0.013 | 0.291 | -0.081 | -0.254 |
| HANDB | 0.095 | 0.425 | 0.334 | -0.029 | -0.298 |
| HANDL | 0.250 | 0.310 | -0.214 | -0.029 | -0.406 |
| BICFEM | 0.029 | -0.024 | 0.123 | 0.324 | -0.340 |
| FOOTB | 0.219 | 0.346 | 0.217 | -0.204 | -0.268 |
| HEADL | 0.226 | 0.205 | 0.140 | 0.289 | -0.203 |
| HEADB | 0.045 | -0.135 | 0.163 | -0.004 | -0.235 |
| MFRONT | 0.004 | 0.147 | 0.066 | -0.012 | -0.183 |
| BIZYGO | 0.227 | -0.164 | -0.078 | 0.028 | -0.308 |
| BIGON | 0.015 | -0.166 | -0.034 | -0.075 | -0.518 |
| HEADCR | 0.050 | -0.041 | 0.092 | 0.093 | -0.249 |
| UPARM | 0.352 | -0.193 | 0.031 | 0.023 | -0.157 |
| CALFC | 0.033 | -0.035 | 0.161 | -0.126 | -0.298 |
| TRISKN | 0.137 | 0.023 | -0.136 | 0.087 | -0.062 |
| SUBSKN | 0.145 | -0.039 | -0.304 | -0.096 | -0.254 |

DIMENSION REDUCTION ANALYSIS

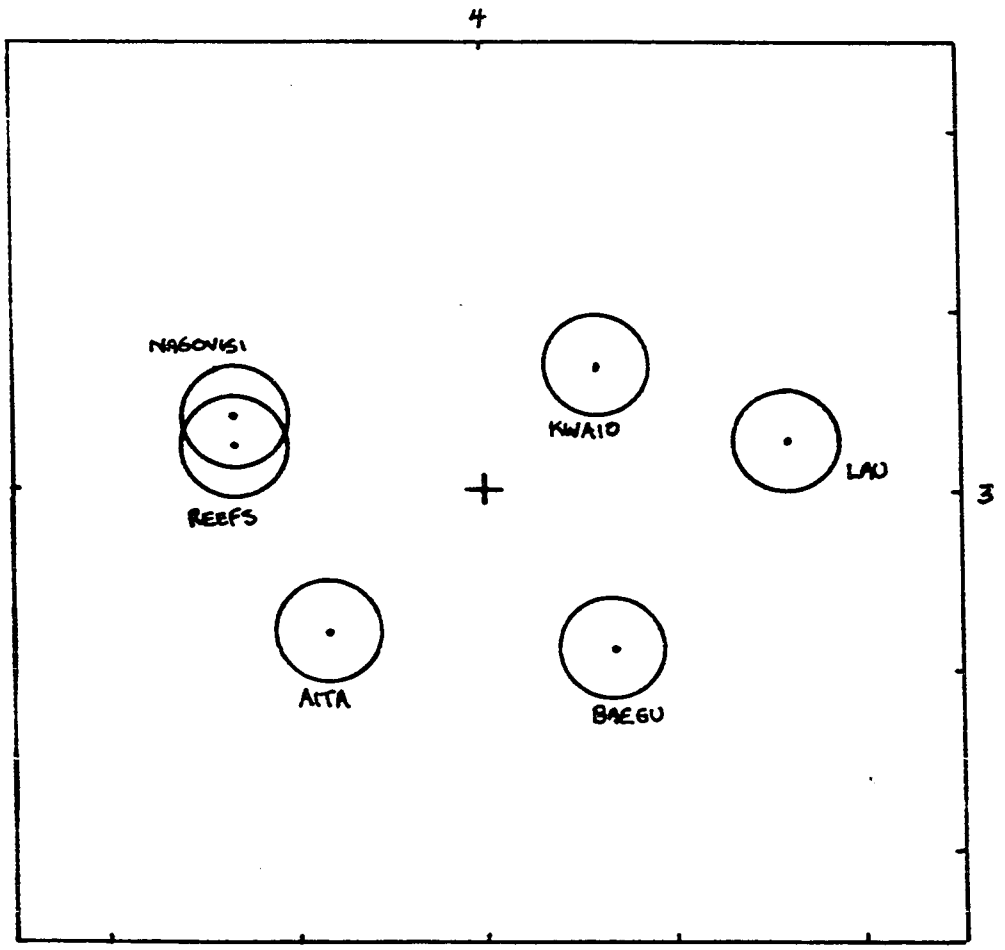
| ROOTS | LAMBDA | F | HYP.DF | ERR.DF | PROB |
|---|---|---|---|---|---|
| 1 TO 5 | .04035 | 17.090 | 135 | 2515 | <0.01 |
| 2 TO 5 | .10940 | 14.529 | 104 | 2025 | <0.01 |
| 3 TO 5 | .25836 | 11.645 | 78 | 1526 | <0.01 |
| 4 TO 5 | .55876 | 7.185 | 48 | 1021 | <0.01 |
| 5 TO 5 | .79316 | 5.793 | 23 | 511 | <0.01 |

Exhibit 3.36 Male Discriminant Analysis



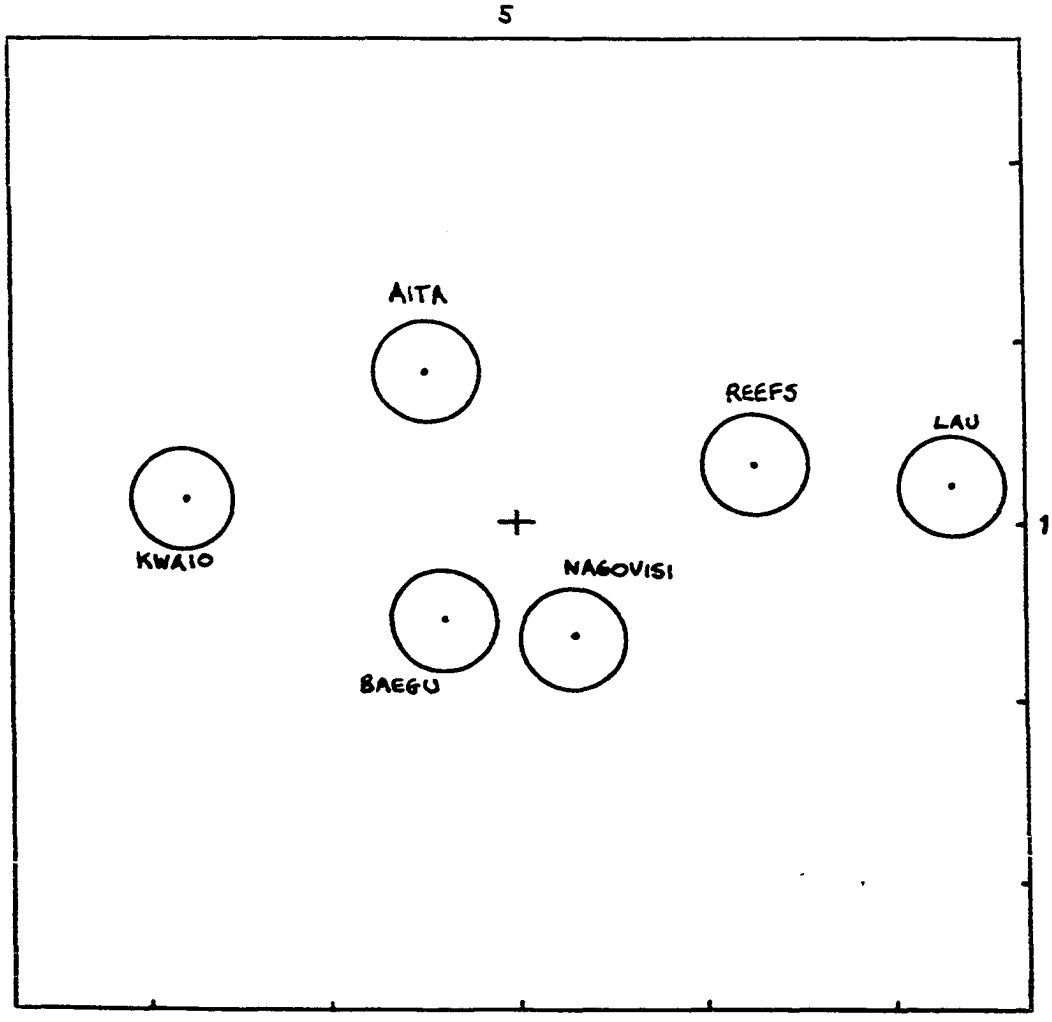

Circles are approximate 99% confidence limits for group means.

Exhibit 3.37 Canonical Group Means (Males) Functions 1 and 2




Circles are approximate 99% confidence limits for group means.

Exhibit 3.38 Canonical Group Means (Males) Functions 3 and 4




Circles are approximate 99% confidence limits for group means.

Exhibit 3.39 Canonical Group Means (Males) Functions 1 and 5

large head circumference values (along with the Aita and Kwaio males). However, the Lau median is significantly ($p<.05$) larger than the medians for the two smallest groups (Nagovisi, Baegu) but the Reefs median is not.

The next most important coefficients are calf circumference and upper arm circumference (exhibit 3.36). The boxplot for upper arm circumference (exhibit 3.27) shows that the Lau males have the largest values. For calf circumference (exhibit 3.28) the pattern is less clear, and the only finding is that Nagovisi males are smaller than all the others. Since the Lau and Kwaio males have the same values for calf circumference, but are at opposite extremes on the discriminant function, it seems likely that this variable is acting as a supressor. Weight and sitting height also enter the discriminant function equation with opposite signs. In absolute terms the more robust groups (Lau, Reefs, Aita) weigh more (exhibit 3.4). However, in the context of the discriminant function coefficients weight appears to be acting as a supressor, in the same fashion as calf circumference. Sitting height (exhibit 3.5) seems to be picking out a contrast between the Kwaio males (with a relatively and absolutely larger sitting height) and the Reefs males (with a relatively smaller sitting height). Note that this relative difference in sitting height was not apparent in female between group variation. Consequently sitting height was one of the variables with a sex by population interaction.

Facial height measurements (total facial height, upper

facial height) also enter into the discriminant function equation with opposite signs. Looking at the boxplots for these variables (exhibits 3.11 and 3.12) it is clear that the Lau males have the highest values for both of these variables. Finally, hand breadth and bicondylar femur enter the equation. An examination of the boxplots for bicondylar femur and hand breadth (exhibits 3.19 and 3.17) shows that both the Lau and the Kwaio males (opposites on the discriminant function) have roughly the same value for these variables, so the variables may be acting as supressors. The skinfold measurements are absent from this first discriminant function. This is in marked contrast to their position in female between population variation.

The second discriminant function (also shown in exhibit 3.37) separates the Reefs males from the Lau, Aita and Nagovisi at the other extreme. The inland Malaitan males (Kwaio and Baegu) fall in an intermediate position. The most important discriminating variables in this funciton are once again head circumference and head length. Weight and sitting height are entered in this function as well. All of these variables appear to play the same role that they did in discriminant function 1. Stature has also been added to the list of variables. Examining the boxplots for stature (exhibit 3.6) it appears that the Reefs and Lau males are the tallest, yet they are at opposite extremes on this second function. However, stature is a valid contrast between the Reefs males (tallest) and the Nagovisi (shortest). This apparently contradictory role for stature is rather peculiar, yet it is not the only variable which exhibits this

pattern. Hand breadth, wrist breadth and foot breadth (exhibits 3.17, 3.16 and 3.20) also appear in this function and follow the same pattern as stature. These four variables seem to be acting to make distincitons in relative proportions between the Reefs males and other groups. The Reefs males have the largest extremities (hand breadth, foot breadth, hand length, foot length; see exhibits 3.17, 3.20, 3.18, 3.10). In addition the Reefs males and the Baegu males have relatively broader extremities (hand breadth, foot breadth) than do the others, given the other variables in the discriminant function. The ratio of stature to sitting height is also greater in Reefs males than it is in the other groups.

Finally, upper facial height appears in the function with a negative coefficient. Reexamining the boxplot for upper facial height (exhibit 3.12) it is clear that the Lau males have the largest values for upper facial height. The negative coefficient is picking out a contrast between the Reefs and other groups. The Reefs males have a relatively smaller upper facial height for thier size. This contrast echoes the pattern for females.

The third discriminant function is shown in exhibit 3.38. The contrast on this axis is between the Malaita populations (Lau, Kwaio, Baegu) and the other three groups. There is no reason for complacency in this contrast, however, as it places the Bougainville populations (Nagovisi, Aita) together with the Reef Islanders! The variable with the largest coefficient for this function is hand length (exhibit 3.36). This is followed in

importance by total facial height, nose length, and hand breadth. Hand length and hand breadth are operating in opposite directions, producing a contrast in hand shape between the groups. The three Malaitan groups have relatively shorter and broader hands than do the others. This relatively broader hand has already been seen for the Baegu in discriminant function 2. The contrast of total facial height and nose length highlights the relatively longer noses in the Lau males, given their total facial height (and the other variables in the set). The Lau males also have the broadest wrists and chests, both absolutely (exhibits 3.16 and 3.9), and relative to the other variables. Although sitting height and bizygomatic diameter also enter the discriminant function, examination of the boxplots (exhibits 3.5 and 3.24) shows that these may be acting as supressors. Finally, subscapular skinfold enters the discriminant function with a negative coefficient. In the boxplot (exhibit 3.30) it is clear that the three Malaitan groups have lower subscapular skinfold values.

The fourth discriminant function is also shown in exhibit 3.38. This function separates the Aita and Baegu males from the others. The variable with the highest coefficient is bicondylar femur, followed by head length. The positive signs for both these coefficients suggest that Aita and Baegu males have relatively narrower knees and shorter heads, given the other variables in the discriminant function. The remainder of the variables in this function (upper facial height, nose length, wrist breadth, foot breadth, head circumference, upper arm

circumference, calf circumference, subscapular skinfold) have all been present in earlier functions, with the exception of bicondylar humerus and triceps skinfold. None of these varaiables which have appeared earlier have any obvious new meaning in this function. They all appear to be forming some arbitrary contrast, and we note that only head length and bicondylar femur have any reasonable correlation with the canonical variate. Examining the boxplots for triceps skinfold (exhibit 3.29) there is no obvious pattern of variation between groups. The inference is that triceps skinfold is also acting as a supressor. The boxplot for bicondylar humerus (exhibit 3.15) shows a contrast between the Lau and Reefs males at one end, and the smaller Kwaio males at the other. Yet these 3 groups are not differentiated on the fourth discriminant function. Clearly there is little interpretable pattern present in this function. Although it is statistically significant it is not meaningful. The interpretation of the final discriminant function will also be abandoned, as it accounts for an even smaller proportion of the original variance, and is even more likely to contain nothing but statistical noise.

### 3.2.5 Comparing Male and Female Discriminant Functions

Summarizing the results of the between population variation for males, it is obvious that a robust trio of groups (Reefs, Lau, Aita) may be identified. As in the female pattern, the Reefs males have relatively smaller facial heights. The patterns of cranial variation are essentially the same for males and females. However, there are some differences in the patterns for males and females for other variables.

The relatively lower sitting height for the Reefs males is more immediately apparent than it was for females. Other differences are to be found in upper facial height and nose length. The Baegu females stand out in having unusually large values for these two variables. The same pattern is not obvious for Baegu males. Triceps, biacromial diameter, and bicristal diameter also appear to be much more variable between populations in females than in males. The variables which showed a significant population by sex interaction tend to be the same ones which show differing patterns.

Judging the similarity of the discriminant functions derived for males and females is a difficult task if tackled one variable at a time. Clearly it is in the nature of a multivariate technique that it is the relationship between the weightings (coefficients) of the different variables which is crucial. It is neccessary to have a comparative technique which handles the

set of coefficients as a single pattern.

One method for comparing two discriminant analysis solutions is to use the pairwise distances between groups obtained for each of the two solutions, and compute a correlation coefficient between the corresponding distances. This correlation is called a cophenetic correlation (Sneath and Sokal 1973). Unfortunately, this method may be misleading because the distances used to calculate the correlation coefficient are not independent (Gower 1971, 1975). This is a serious problem when there are two tight clusters of groups, and the clusters are separated by much larger distances. Additionally, the cophenetic correlation does not offer an easy means of identifying the original variables which give rise to the poor fit. Gower (1971) has described an alogrithm for comparing two matrices (called Procrustes rotation) which allows one to be rotated, reflected, translated and scaled to maximum congruence with the other. Thus it is possible to make a more direct comparison of the matrices of discriminant function coefficients obtained from two different analyses. The residual sum of squared distances after the fitting procedure is a measure of "badness of fit" called Gower's R squared. Values of Gower's R squared greater than 1 are considered to be a poor fit.

As a concrete example of the potential success of rotation, consider the plots of the first two discriminant functions for each sex (exhibits 3.33 and 3.37). Imagine that one plot were placed on top of the other, and allowed to rotate and slide until

the Reefs and Lau centroids were on top of one another. The rest of the centroids would be brought closely into alignment. Since the particular axes on which these plots are produced are the result of an arbitrary mathematical criterion, it seems reasonable to move the plots around until the points line up. It is the relationship of the points and not the reference axes which are of primary importance. By comparing the positions of the two sets of reference axes once the points have been aligned, it is possible to see the rotation and translation required to do the job.

When more than two matrices are involved in a comparison it is possible to rotate them to maximum congruence in a pairwise fashion. This process results in a matrix of R squared values which is in the form of a distance matrix. This method has been used successfully by Friedlaender (1975) and Rhoads (1977).

Following a Procrustes rotation of the male discriminant function coefficient matrix onto the female matrix the R squared value is 0.44. This suggests that the patterns of between group variation for males and females are fairly similar.

The process of Procrustes rotation is not a panacea with which to comapre the results of different multivariate analyses. Although it is quite a general technique, there are still situations which it handles poorly. The solution for maximum congruence is based on the given order of columns in each matrix. Permutations of columns may give better fits. Fortunately, if

two multivariate patterns are not too different, the derived variates will tend to have the same ordering. There is no guarantee of this however.

Most multivariate techniques such as principal components analysis (PCA) or discriminant analysis rely on the criterion of maximum variance explained in each derived variate to obtain a unique solution. Thus the first principal component will account for the largest possible amount of variance in the data set being analyzed. Likewise, the first discriminant function maximizes the ratio of between to within group variance. Any rotation of the solution (such as the popular rotations of Factor Analysis) destroys the variance maximizing properties. Consequently, when the male discriminant function coefficient matrix is rotated, the new discriminanat function is no longer the one which maximally discriminates between groups. The general similarity of the male and female matrices after rotation suggests that differences in the patterns are primarily one of degree rather than kind. However, the ordering (relative weighting) of these variables in a discriminant function may be somewhat different from one sex to another. The weighted sum of variables which maximally discriminates in one sex may be adequate in the other sex, but not quite maximal. Procrustes rotation removes the restriction of maximum variance.

The distribution of the residuals after a rotational fit is displayed in exhibit 3.40. There are larger residuals (>.02) representing (in decreasing order): subscapular skinfold, upper

Residuals after rotational fit of two solutions

| | |
|---|---|
| WEIGHT | 0.036 |
| SITHT | 0.025 |
| STATURE | 0.009 |
| BIACROM | 0.013 |
| BICRIST | 0.011 |
| CHESTB | 0.017 |
| FOOTL | 0.015 |
| TFACHT | 0.004 |
| UFACHT | 0.008 |
| NOSEL | 0.006 |
| NOSEB | 0.009 |
| BICHUM | 0.015 |
| WRISTB | 0.014 |
| HANDB | 0.021 |
| HANDL | 0.018 |
| BICFEM | 0.005 |
| FOOTB | 0.009 |
| HEADL | 0.019 |
| HEADB | 0.003 |
| MFRONT | 0.009 |
| BIZYGO | 0.011 |
| BIGON | 0.005 |
| HEADCR | 0.010 |
| UPARM | 0.048 |
| CALFC | 0.009 |
| TRISKN | 0.039 |
| SUBSKN | 0.051 |

Histogram of residuals

| MIDDLE OF INTERVAL | NUMBER OF OBSERVATIONS | |
|---|---|---|
| 0.005 | 5 | ***** |
| 0.010 | 9 | ********* |
| 0.015 | 5 | ***** |
| 0.020 | 3 | *** |
| 0.025 | 1 | * |
| 0.030 | 0 | |
| 0.035 | 1 | * |
| 0.040 | 1 | * |
| 0.045 | 0 | |
| 0.050 | 2 | ** |

Exhibit 3.40 Residuals from rotational fit, two sexes

arm circumference, triceps skinfold, weight, sitting height, and hand breadth. This, then, is a list of the variables for which the pattern of male versus females between population variation is different.

There are other variables which showed a significant sex by population interaction, but which do not have large residuals in the rotational fit. These are: biacromial diameter, bicrystal diameter, chest breadth, upper facial height, nose length, and bicondylar femur. It is these variables which have the same pattern of male and female between population variation, but which have different levels of variation in the two sexes. Good examples of varibles with differing variation levels are bicristal diameter and upper facial height. Both of these measures are more variable between populations for females than they are for males. Consequently they are relatively more important in the discriminant function based on females. Nonetheless, the pattern of between population variation is similar for both sexes.

### 3.2.6 Sexual Dimorphism

Differences between the sexes for some of the variables measured have been commented on earlier. Let us now turn to a more detailed consideration of sexual dimorphism using discriminant analysis. The interaction between sex and

population has already been discussed. Because of this interaction, six separate analyses of sexual dimorphism were performed, one for each population. The result of the multivariate test for sexual dimorphism was significant ($p<0.01$) in every population, which is hardly suprising. The univariate F tests for each variable (for each group) were also significant ($p<0.01$) except for bicristal diameter in the Kwaio and Lau groups. A cursory examination of the boxplots (exhibits 3.4 to 3.30) shows that males exceed females from the same population on all measurements except the skinfolds. The pattern is reversed in the two skinfold measurements (exhibits 3.29 and 3.30). Clearly males and females are generally different in size, and our attention should be directed to differences in shape (or relative differences in size). The standardized discriminant function coefficients shown in exhibit 3.41 are useful in this situation because they help us to isolate the additional (unique) contribution of each variable given that the other variables are already accounted for. Examining these coefficients, we note that a subset of the variables appears in almost all (5 out of 6) of the functions, and has consistent signs across the six populations. Variables with positive coefficients are: biacromial diameter, total facial height and bicondylar humerus. These are contrasted with two variables with substantial ($<0.3$) negative coefficients: bicristal diameter and triceps skinfold.

The positive coefficients for biacromial diameter, total facial height, and bicondylar humerus are picking out the relatively larger values which males have for these measurements.

Standardized Discriminant Function Coefficients

| | Reef | Kwaio | Lau | Baegu | Nagov | Aita |
|---|---|---|---|---|---|---|
| WEIGHT | -0.594 | -0.507 | 0.135 | -0.042 | 0.066 | 0.191 |
| SITHT | -0.062 | 0.111 | 0.329 | 0.064 | -0.011 | 0.486 |
| STATURE | 0.098 | 0.161 | -0.185 | 0.220 | 0.052 | -0.306 |
| BIACROM | 0.511 | 0.509 | 0.433 | 0.205 | 0.628 | 0.433 |
| BICRIST | -0.018 | -0.605 | -0.456 | -0.388 | -0.544 | -0.668 |
| CHESTB | -0.084 | 0.209 | -0.025 | 0.121 | -0.137 | 0.331 |
| FOOTL | -0.238 | 0.310 | 0.226 | 0.294 | -0.064 | 0.002 |
| TFACHT | 0.342 | 0.358 | 0.178 | 0.354 | 0.415 | 0.417 |
| UFACHT | -0.140 | -0.142 | -0.058 | -0.282 | -0.042 | -0.285 |
| NOSEL | -0.103 | -0.064 | -0.061 | 0.090 | -0.032 | 0.059 |
| NOSEB | 0.039 | 0.184 | 0.073 | 0.278 | 0.260 | -0.075 |
| BICHUM | 0.533 | 0.326 | 0.467 | 0.363 | 0.210 | 0.623 |
| WRISTB | 0.154 | -0.041 | 0.068 | 0.082 | 0.108 | 0.226 |
| HANDB | -0.186 | -0.152 | -0.253 | 0.094 | 0.057 | -0.525 |
| HANDL | 0.086 | -0.146 | -0.508 | -0.371 | -0.381 | -0.043 |
| BICFEM | 0.171 | 0.343 | 0.314 | 0.024 | 0.418 | -0.111 |
| FOOTB | 0.124 | 0.060 | 0.173 | 0.072 | 0.199 | 0.259 |
| HEADL | 0.285 | -0.137 | 0.411 | 0.039 | 0.239 | -0.390 |
| HEADB | 0.133 | 0.073 | 0.274 | -0.112 | 0.065 | -0.074 |
| MFRONT | -0.172 | -0.031 | -0.166 | -0.075 | -0.C96 | -0.152 |
| BIZYGO | 0.204 | 0.040 | 0.273 | 0.112 | 0.192 | 0.347 |
| BIGON | 0.129 | 0.086 | 0.066 | 0.059 | -0.077 | -0.052 |
| HEADCR | -0.219 | 0.109 | -0.314 | 0.189 | -0.131 | 0.439 |
| UPARM | 0.072 | 0.528 | 0.485 | 0.347 | 0.439 | 0.350 |
| CALFC | 0.405 | -0.123 | -0.393 | -0.357 | -0.577 | -0.627 |
| TRISKN | -0.483 | -0.427 | -0.998 | -0.525 | -0.661 | -0.988 |
| SUBSKN | -0.126 | -0.062 | 0.365 | 0.012 | 0.142 | 0.524 |

Exhibit 3.41 Sexual Dimorphism Discriminant Analysis

Discriminant Loadings (correlations between canonical variates and the original variates)

| | Reef | Kwaio | Lau | Baegu | Nagov | Aita |
|---|---|---|---|---|---|---|
| WEIGHT | 0.210 | 0.281 | 0.172 | 0.334 | 0.238 | 0.183 |
| SITHT | 0.288 | 0.424 | 0.338 | 0.448 | 0.302 | 0.348 |
| STATURE | 0.430 | 0.394 | 0.304 | 0.433 | 0.324 | 0.330 |
| BIACROM | 0.421 | 0.586 | 0.440 | 0.477 | 0.516 | 0.420 |
| BICRIST | 0.110 | 0.009 | -0.025 | 0.062 | 0.087 | 0.079 |
| CHESTB | 0.132 | 0.330 | 0.211 | 0.352 | 0.292 | 0.263 |
| FOOTL | 0.377 | 0.370 | 0.287 | 0.384 | 0.291 | 0.259 |
| TFACHT | 0.394 | 0.339 | 0.220 | 0.264 | 0.340 | 0.328 |
| UFACHT | 0.246 | 0.218 | 0.126 | 0.080 | 0.235 | 0.175 |
| NOSEL | 0.241 | 0.235 | 0.149 | 0.113 | 0.222 | 0.202 |
| NOSEB | 0.321 | 0.229 | 0.246 | 0.345 | 0.311 | 0.232 |
| BICHUM | 0.640 | 0.575 | 0.439 | 0.495 | 0.468 | 0.441 |
| WRISTB | 0.481 | 0.453 | 0.417 | 0.423 | 0.449 | 0.345 |
| HANDB | 0.369 | 0.378 | 0.308 | 0.415 | 0.419 | 0.259 |
| HANDL | 0.282 | 0.307 | 0.197 | 0.252 | 0.248 | 0.222 |
| BICFEM | 0.354 | 0.329 | 0.402 | 0.427 | 0.338 | 0.272 |
| FOOTB | 0.396 | 0.329 | 0.293 | 0.351 | 0.345 | 0.221 |
| HEADL | 0.354 | 0.267 | 0.270 | 0.251 | 0.234 | 0.167 |
| HEADB | 0.219 | 0.323 | 0.213 | 0.245 | 0.206 | 0.224 |
| MFRONT | 0.167 | 0.134 | 0.126 | 0.168 | 0.097 | 0.079 |
| BIZYGO | 0.409 | 0.376 | 0.295 | 0.343 | 0.350 | 0.317 |
| BIGON | 0.258 | 0.301 | 0.218 | 0.219 | 0.229 | 0.175 |
| HEADCR | 0.300 | 0.350 | 0.231 | 0.291 | 0.281 | 0.180 |
| UPARM | 0.145 | 0.264 | 0.171 | 0.326 | 0.273 | 0.133 |
| CALFC | 0.217 | 0.224 | 0.142 | 0.210 | 0.171 | 0.101 |
| TRISKN | -0.286 | -0.141 | -0.223 | -0.332 | -0.276 | -0.339 |
| SUBSKN | -0.247 | -0.082 | -0.094 | -0.117 | -0.100 | -0.078 |

Exhibit 3.41 Sexual Dimorphism Discriminant Analysis

In contast, the negative coefficients for bicristal diameter and triceps skinfold highlight these two variables for which femalesare relativey larger. Note that females also have absolutely larger triceps skinfold values. It is common to find that females have relatively wider hips and greater subcoutaneous fat deposits in most populations.

Although these general observations are common to all six populations, there are other variations in coefficients which are apparent in exhibit 3.41. The coefficients for calf circumference are important in five out of six populations, but the coefficient for the Reef Islanders has an the sign reversed relative to the other populations. The negative coefficients for the other five populations once again suggest that females have relatively larger values for calf circumference. However, there is a profile difference in the Reef Islanders where males have relatively larger calf circumferences.

Although there are other differences when the discriminant coefficient vector for one group is compared directly with another, there are no other broadly consistent patterns. Additionally, when the discriminant function coefficient vectors are rotated to maximum congruence there is a reasonable fit of each against the others, except for the Reefs vector. The matrix of residual distances (Gower's R squared) is shown in exhibit 3.42.

If the residuals for each pairwise comparison (shown in

| | | | | | |
|---|---|---|---|---|---|
| Kwaio | 0.93 | | | | |
| Lau | 1.13 | 0.75 | | | |
| Baegu | 1.39 | 0.46 | 0.61 | | |
| Nagovisi | 1.16 | 0.60 | 0.31 | 0.46 | |
| Aita | 1.50 | 0.81 | 0.60 | 0.63 | 0.76 |
| | Reefs | Kwaio | Lau | Baegu | Nagovisi |

(Residual distances between groups after rotation)

Exhibit 3.42 R-square matrix for sexual dimorphism

Residuals after rotation for each pairwise comparison

| | 2-1 | 3-1 | 3-2 | 4-1 | 4-2 |
|---|---|---|---|---|---|
| WEIGHT | 0.006 | 0.266 | 0.194 | 0.159 | 0.104 |
| SITHT | 0.015 | 0.055 | 0.013 | 0.009 | 0.001 |
| STATURE | 0.002 | 0.028 | 0.043 | 0.011 | 0.004 |
| BIACROM | 0.000 | 0.017 | 0.012 | 0.044 | 0.037 |
| BICRIST | 0.173 | 0.054 | 0.033 | 0.094 | 0.012 |
| CHESTB | 0.043 | 0.003 | 0.024 | 0.025 | 0.002 |
| FOOTL | 0.153 | 0.093 | 0.007 | 0.170 | 0.000 |
| TFACHT | 0.000 | 0.021 | 0.021 | 0.001 | 0.001 |
| UFACHT | 0.000 | 0.006 | 0.006 | 0.017 | 0.017 |
| NOSEL | 0.001 | 0.002 | 0.000 | 0.022 | 0.014 |
| NOSEB | 0.010 | 0.000 | 0.007 | 0.038 | 0.009 |
| BICHUM | 0.027 | 0.016 | 0.001 | 0.009 | 0.004 |
| WRISTB | 0.021 | 0.005 | 0.006 | 0.002 | 0.009 |
| HANDB | 0.001 | 0.000 | 0.001 | 0.044 | 0.034 |
| HANDL | 0.028 | 0.115 | 0.029 | 0.136 | 0.040 |
| BICFEM | 0.013 | 0.003 | 0.004 | 0.012 | 0.050 |
| FOOTB | 0.003 | 0.000 | 0.004 | 0.001 | 0.000 |
| HEADL | 0.094 | 0.001 | 0.110 | 0.032 | 0.016 |
| HEADB | 0.002 | 0.004 | 0.012 | 0.037 | 0.021 |
| MFRONT | 0.010 | 0.002 | 0.004 | 0.004 | 0.002 |
| BIZYGO | 0.015 | 0.000 | 0.017 | 0.004 | 0.004 |
| BIGON | 0.001 | 0.003 | 0.000 | 0.002 | 0.000 |
| HEADCR | 0.055 | 0.000 | 0.059 | 0.098 | 0.006 |
| UPARM | 0.101 | 0.049 | 0.009 | 0.052 | 0.008 |
| CALFC | 0.149 | 0.258 | 0.015 | 0.350 | 0.043 |
| TRISKN | 0.003 | 0.037 | 0.059 | 0.006 | 0.017 |
| SUBSKN | 0.002 | 0.090 | 0.064 | 0.010 | 0.003 |

Comparison keys: 1 Reefs
2 Kwaio
3 Lau
4 Baegu
5 Nagovisi
6 Aita

Exhibit 3.43 Residuals for Sexual Dimorphism Vectors

| | 4-3 | 5-1 | 5-2 | 5-3 | 5-4 |
|---|---|---|---|---|---|
| WEIGHT | 0.014 | 0.234 | 0.166 | 0.001 | 0.007 |
| SITHT | 0.019 | 0.002 | 0.006 | 0.036 | 0.003 |
| STATURE | 0.075 | 0.001 | 0.005 | 0.018 | 0.019 |
| BIACROM | 0.007 | 0.001 | 0.002 | 0.025 | 0.058 |
| BICRIST | 0.005 | 0.106 | 0.008 | 0.009 | 0.000 |
| CHESTB | 0.011 | 0.000 | 0.051 | 0.005 | 0.031 |
| FOOTL | 0.011 | 0.020 | 0.063 | 0.027 | 0.074 |
| TFACHT | 0.033 | 0.000 | 0.000 | 0.027 | 0.000 |
| UFACHT | 0.043 | 0.007 | 0.007 | 0.000 | 0.045 |
| NOSEL | 0.010 | 0.004 | 0.001 | 0.000 | 0.007 |
| NOSEB | 0.032 | 0.020 | 0.002 | 0.016 | 0.003 |
| BICHUM | 0.001 | 0.063 | 0.008 | 0.016 | 0.024 |
| WRISTB | 0.000 | 0.001 | 0.011 | 0.001 | 0.000 |
| HANDB | 0.043 | 0.032 | 0.023 | 0.031 | 0.001 |
| HANDL | 0.001 | 0.090 | 0.017 | 0.002 | 0.005 |
| BICFEM | 0.026 | 0.021 | 0.001 | 0.009 | 0.065 |
| FOOTB | 0.002 | 0.002 | 0.009 | 0.001 | 0.006 |
| HEADL | 0.042 | 0.003 | 0.066 | 0.006 | 0.017 |
| HEADB | 0.064 | 0.003 | 0.000 | 0.012 | 0.020 |
| MFRONT | 0.000 | 0.005 | 0.001 | 0.001 | 0.000 |
| BIZYGO | 0.005 | 0.000 | 0.010 | 0.001 | 0.002 |
| BIGON | 0.000 | 0.019 | 0.010 | 0.007 | 0.008 |
| HEADCR | 0.102 | 0.007 | 0.023 | 0.008 | 0.053 |
| UPARM | 0.000 | 0.054 | 0.007 | 0.000 | 0.000 |
| CALFC | 0.007 | 0.433 | 0.074 | 0.022 | 0.004 |
| TRISKN | 0.013 | 0.004 | 0.012 | 0.017 | 0.000 |
| SUBSKN | 0.041 | 0.036 | 0.020 | 0.012 | 0.008 |

Comparison keys: 1 Reefs
2 Kwaio
3 Lau
4 Baegu
5 Nagovisi
6 Aita

Exhibit 3.43 Residuals for Sexual Dimorphism Vectors

| | 6-1 | 6-2 | 6-3 | 6-4 | 6-5 |
|---|---|---|---|---|---|
| WEIGHT | 0.295 | 0.218 | 0.001 | 0.021 | 0.004 |
| SITHT | 0.086 | 0.029 | 0.004 | 0.039 | 0.062 |
| STATURE | 0.040 | 0.058 | 0.001 | 0.093 | 0.028 |
| BIACROM | 0.023 | 0.018 | 0.001 | 0.003 | 0.033 |
| BICRIST | 0.083 | 0.016 | 0.003 | 0.000 | 0.001 |
| CHESTB | 0.055 | 0.001 | 0.033 | 0.006 | 0.065 |
| FOOTL | 0.037 | 0.040 | 0.013 | 0.048 | 0.003 |
| TFACHT | 0.001 | 0.001 | 0.012 | 0.005 | 0.003 |
| UFACHT | 0.000 | 0.000 | 0.009 | 0.013 | 0.010 |
| NOSEL | 0.014 | 0.008 | 0.005 | 0.001 | 0.003 |
| NOSEB | 0.002 | 0.022 | 0.004 | 0.059 | 0.036 |
| BICHUM | 0.006 | 0.007 | 0.002 | 0.000 | 0.030 |
| WRISTB | 0.000 | 0.024 | 0.006 | 0.004 | 0.002 |
| HANDB | 0.009 | 0.015 | 0.010 | 0.094 | 0.076 |
| HANDL | 0.005 | 0.010 | 0.074 | 0.091 | 0.054 |
| BICFEM | 0.026 | 0.076 | 0.047 | 0.003 | 0.095 |
| FOOTB | 0.002 | 0.010 | 0.001 | 0.007 | 0.000 |
| HEADL | 0.142 | 0.005 | 0.161 | 0.039 | 0.107 |
| HEADB | 0.014 | 0.005 | 0.031 | 0.006 | 0.004 |
| MFRONT | 0.005 | 0.001 | 0.001 | 0.000 | 0.000 |
| BIZYGO | 0.001 | 0.024 | 0.001 | 0.009 | 0.003 |
| BIGON | 0.011 | 0.004 | 0.003 | 0.003 | 0.001 |
| HEADCR | 0.149 | 0.023 | 0.154 | 0.005 | 0.092 |
| UPARM | 0.017 | 0.035 | 0.008 | 0.010 | 0.010 |
| CALFC | 0.334 | 0.037 | 0.005 | 0.000 | 0.006 |
| TRISKN | 0.010 | 0.022 | 0.009 | 0.000 | 0.002 |
| SUBSKN | 0.128 | 0.097 | 0.003 | 0.067 | 0.029 |

Histogram of residuals

EACH * REPRESENTS 10 OBSERVATIONS

| MIDDLE OF INTERVAL | NUMBER OF OBSERVATIONS | |
|---|---|---|
| 0.00 | 281 | ****************************** |
| 0.05 | 80 | ******** |
| 0.10 | 23 | *** |
| 0.15 | 12 | ** |
| 0.20 | 2 | * |
| 0.25 | 3 | * |
| 0.30 | 1 | * |
| 0.35 | 2 | * |
| 0.40 | 0 | |
| 0.45 | 1 | * |

Exhibit 3.43 Residuals for Sexual Dimorphism Vectors

exhibit 3.43) are examined by plotting a histogram, a few unusually large values are apparent in each of the comparisons with large R-squared values. Taking a cutoff value of 0.2 as denoting a large residual, these are concentrated in the Reefs comparisons. The variables which tend to have large residuals across all comparisons are weight and calf circumference.

Calf circumference has already been identified as having a different relationship to sexual dimorphism in the Reefs population, and this is re-emphasized by the analysis of the residuals. Weight also shows a large residual in some comparisons, including the Aita vs Kwaio pairwise comparison. The Kwaio join with the Reef Islanders in having a variant pattern of relative weight difference between the sexes. This is shown in the larger residuals and also in the standardized coefficients (exhibit 3.41). Kwaio and Reefs females are relatively heavier than males from these same groups.

## 3.3 The Structure of Within Group Covariation

### 3.3.1 Describing Covariance Structures

In this section we turn from a consideration of the differences between groups, to that of the covariation of variables in a single population. The basic data structure of interest is a variance-covariance matrix, or a correlation matrix. The multivariate techniques we will rely on to describe these data matrices are principal components analysis (PCA) and cluster analysis. PCA and cluster analysis represent fundamentally different views of a set of variables and their covariation. PCA transforms the original variables into a new set of uncorelated ones (components) which reproduce the original correlations. Often we will discard the last few components, and accept a solution in a lower dimensional space. As in discriminant analysis, interest centers on the coefficients or correlations which relate the original variables to the newly created components. A given variable may be important in several of the components. Although a rotation of the inital solution maximizes the loadings of variables on just one component, it is still possible for one variable to be split in importance across several components.

In contrast, cluster analysis is a relatively discrete process. A given variable may be assigned to one cluster or another, but not both. The clustering algorithm used here is centroid clustering (Sneath and Sokal 1973) which has the additional danger that when there are no definite clusters in the data, two similar variables may be somewhat arbitrarily assigned

to different clusters. This all-or-nothing feature of cluster analysis makes for a much simpler picture than PCA, but it is questionable whether or not anthropometric variables must work in such a fashion. It is not unreasonable for one variable, such as weight, to be related to general size on the one hand, and a body bulk component on the other. Although PCA could indicate such a pattern, cluster analysis would force weight into one cluster or the other (although these separate clusters could themselves be merged at a lower level of similarity). Cluster analysis sacrifices the haziness of reality for the decisive solution of a single tree. In fact the two techniques complement one another in offering different viewpoints of the same data matrix.

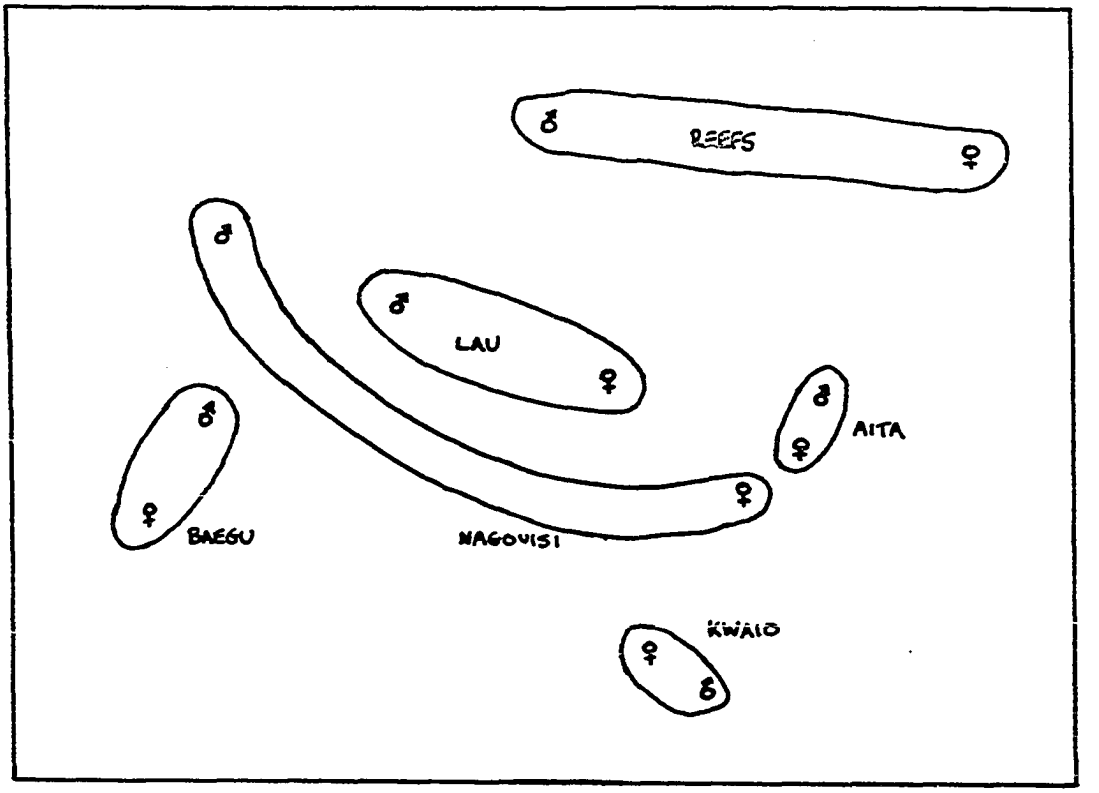
Given the six populations studied and the two sexes in each, there are 12 different correlation matrices which can be produced. The first task is to examine the question: "is the correlation structure of the 27 variables the same for all 12 groups?" Although the 12 groups have already been shown to be different via discriminant analysis, it is quite possible for them to have the same correlation structure for the variables. In fact, the translation of generalized (multivariate) F tests into probability statements relies on the groups having similar variance covariance matrices. The differences identified by discriminant analysis lie in the mean vectors, not in the correlation structure itself. Friedlaender (1975:145) suggests that there is a high level of similarity between the correlation matrices of different populations. This proposition can be examined by using Procrustes rotation to compare the latent

vectors derived from each of the 12 correlation matrices. Without going into the details of each PCA solution, the matrix of R-squared values following the rotational fitting procedure is given in exhibit 3.44. These PCA solutions are based on keeping 10 of the possible 27 components. Generally a 10-component solution contains all vectors with eigenvalues greater than 0.9 and accounts for 85% of the original variance. This distance matrix is displayed in reduced dimensionality in exhibit 3.45. The display is based on a multidimensional scaling solution for representing the distance matrix in 3 dimensions. The first noticeable aspect of this display is that the Reef Islanders and Nagovisi show much less similarity between males and females than do the other groups. This echoes the results of the discriminant analysis of sexual dimorphism in the previous section where both of these two groups had the most distinctive patterns of sexual dimorphism. Note that the location of the Nagovisi females places them closer to the Aita, Lau and Kwaio females than it does to the Nagovisi males. Although the 2 Nagovisi patterns may be relatively farther apart, they still match closely with the neighboring patterns. Given the generally low levels of Gower's R-squared in the rotational fits we will accept that the matrices represent different samplings of one underlying common correlation matrix. In what follows then, the best estimate of this one correlation matrix is estimated by pooling across all the groups.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Reefs F | 0.43 | | | | | | | |
| Kwaio M | 0.36 | 0.52 | | | | | | |
| Kwaio F | 0.46 | 0.62 | 0.22 | | | | | |
| Lau M | 0.28 | 0.51 | 0.45 | 0.46 | | | | |
| Lau F | 0.28 | 0.40 | 0.26 | 0.35 | 0.24 | | | |
| Baegu M | 0.39 | 0.65 | 0.54 | 0.46 | 0.18 | 0.43 | | |
| Baegu F | 0.50 | 0.70 | 0.57 | 0.60 | 0.30 | 0.41 | 0.25 | |
| Nagov M | 0.31 | 0.57 | 0.52 | 0.55 | 0.28 | 0.39 | 0.32 | 0.28 |
| Nagov F | 0.35 | 0.42 | 0.27 | 0.40 | 0.37 | 0.14 | 0.54 | 0.48 |
| Aita M | 0.30 | 0.41 | 0.26 | 0.39 | 0.29 | 0.15 | 0.44 | 0.45 |
| Aita F | 0.32 | 0.43 | 0.27 | 0.34 | 0.28 | 0.17 | 0.44 | 0.46 |
| | M F | | M F | | M F | | M F | |
| | Reefs | | Kwaio | | Lau | | Baegu | |

| | | | |
|---|---|---|---|
| Nagov F | 0.48 | | |
| Aita M | 0.41 | 0.13 | |
| Aita F | 0.41 | 0.21 | 0.11 |
| | M | F | M |
| | Nagovisi | | Aita |

Exhibit 3.44 R-squared matrix for 12 PCA solutions




The first 10 principal components of R for each group are rotated to maximum congruence, and the resulting matrix of residual distances is formed. The matrix of residual distances is displayed in reduced dimensionality using multidimensional scaling. The first two dimensions of a multidimensional scaling solution in three dimensions (MU = 0.96) are shown.

Exhibit 3.45 Display of Distances for 12 PCA Solutions

### 3.3.2 Principal Components Analysis

The pooled within-group correlation matrix is presented in exhibit 3.46. This matrix was analyzed using PCA followed by Varimax rotation of the first 10 latent vectors. The number of vectors to be rotated was decided by examining the effect of increasing or decreasing the number on the resulting components. Although 10 componenets is slightly generous by the criterion of "eigenvalues greater than 1", it avoids forcing together some variables which are otherwise quite distinct (in higher order analyses). The eigenvalues and the proportion of trace accounted for by each eigenvalue are shown in exhibit 3.47. The rotated latent vectors are presented in exhibit 3.48.

Loadings with an absolute value greater than 0.3 are singled out as making a significant contribution to the new component score. The variables with significant loadings on the first component are extremity breadths (hand breadth,foot breadth) and limb circumferences (upper arm circumference,calf circumference). The second component includes facial height variables (total facial height, upper facial height, nose length). Linearity is represented in the third component (sitting height,stature, foot length,hand length). Head length and head circumference make up the fourth function. These two measures of head size were also closely associated in the discriminant function analysis. The next (fifth) component represents lateral craniofacial size (head breadth, minimum frontal diameter, bizygomatic diameter),

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 1.0000 | | | | | |
| SITHT | 0.5424 | 1.0000 | | | | |
| STAT | 0.5561 | 0.7518 | 1.0000 | | | |
| BIACROM | 0.5492 | 0.4271 | 0.4962 | 1.0000 | | |
| BICRIST | 0.5793 | 0.3942 | 0.4642 | 0.3984 | 1.0000 | |
| CHESTB | 0.7318 | 0.3704 | 0.3781 | 0.5835 | 0.4614 | 1.0000 |
| FOOTL | 0.5126 | 0.4861 | 0.6527 | 0.4604 | 0.4547 | 0.3659 |
| TFACHT | 0.2395 | 0.2522 | 0.2458 | 0.1824 | 0.2105 | 0.2223 |
| UFACHT | 0.1404 | 0.1895 | 0.1896 | 0.0834 | 0.1739 | 0.1071 |
| NOSEL | 0.0386 | 0.0920 | 0.1134 | 0.0373 | 0.1454 | 0.0328 |
| NOSEB | 0.2126 | 0.1359 | 0.1485 | 0.1443 | 0.2028 | 0.1223 |
| BICHUM | 0.4240 | 0.3367 | 0.4053 | 0.3119 | 0.3914 | 0.2817 |
| WRISTB | 0.4117 | 0.3694 | 0.4002 | 0.3380 | 0.3625 | 0.2825 |
| HANDB | 0.4836 | 0.3833 | 0.4204 | 0.3610 | 0.3108 | 0.3457 |
| HANDL | 0.4611 | 0.4370 | 0.6247 | 0.4157 | 0.3842 | 0.3274 |
| BICFEM | 0.5480 | 0.3874 | 0.4344 | 0.3618 | 0.4746 | 0.3836 |
| FOOTB | 0.4997 | 0.3247 | 0.3485 | 0.3385 | 0.3633 | 0.3635 |
| HEADL | 0.3367 | 0.3430 | 0.3296 | 0.2158 | 0.2470 | 0.2556 |
| HEADB | 0.2832 | 0.2188 | 0.2026 | 0.1480 | 0.2209 | 0.2367 |
| MFRONT | 0.3337 | 0.2408 | 0.2117 | 0.1484 | 0.2092 | 0.1901 |
| BIZYGO | 0.4187 | 0.2918 | 0.2885 | 0.2977 | 0.3731 | 0.2999 |
| BIGON | 0.2789 | 0.2191 | 0.1955 | 0.1667 | 0.1872 | 0.1951 |
| HEADCR | 0.4634 | 0.3674 | 0.3495 | 0.2806 | 0.3136 | 0.3650 |
| UPARM | 0.7727 | 0.3133 | 0.2396 | 0.4004 | 0.3402 | 0.5530 |
| CALFC | 0.8282 | 0.3892 | 0.3474 | 0.4366 | 0.4032 | 0.5976 |
| TRISKN | 0.5333 | 0.1491 | 0.1130 | 0.1926 | 0.2883 | 0.3787 |
| SUBSKN | 0.5796 | 0.1133 | 0.0477 | 0.2203 | 0.3004 | 0.4402 |

| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
|---|---|---|---|---|---|---|

| | | | | | | |
|---|---|---|---|---|---|---|
| FOOTL | 1.0000 | | | | | |
| TFACHT | 0.2553 | 1.0000 | | | | |
| UFACHT | 0.2169 | 0.7763 | 1.0000 | | | |
| NOSEL | 0.2010 | 0.6169 | 0.7510 | 1.0000 | | |
| NOSEB | 0.1816 | 0.0655 | 0.0524 | 0.0933 | 1.0000 | |
| BICHUM | 0.4220 | 0.1808 | 0.1283 | 0.1709 | 0.2129 | 1.0000 |
| WRISTB | 0.4630 | 0.2244 | 0.1363 | 0.1701 | 0.1935 | 0.5460 |
| HANDB | 0.4946 | 0.2321 | 0.1496 | 0.1129 | 0.2149 | 0.4784 |
| HANDL | 0.7201 | 0.2475 | 0.2111 | 0.1853 | 0.1808 | 0.4146 |
| BICFEM | 0.4481 | 0.1975 | 0.1305 | 0.1414 | 0.2426 | 0.5217 |
| FOOTB | 0.4849 | 0.2211 | 0.1696 | 0.1337 | 0.2242 | 0.3403 |
| HEADL | 0.3266 | 0.2720 | 0.2121 | 0.1561 | 0.2008 | 0.1754 |
| HEADB | 0.1704 | 0.2147 | 0.1380 | 0.1187 | 0.1924 | 0.1822 |
| MFRONT | 0.2101 | 0.1980 | 0.1097 | 0.0251 | 0.1706 | 0.1802 |
| BIZYGO | 0.3007 | 0.2230 | 0.1678 | 0.1473 | 0.2790 | 0.3594 |
| BIGON | 0.1669 | 0.1061 | 0.0979 | 0.0550 | 0.1882 | 0.2427 |
| HEADCR | 0.3690 | 0.3002 | 0.2291 | 0.1625 | 0.2646 | 0.2276 |
| UPARM | 0.2692 | 0.1321 | 0.0443 | -0.0439 | 0.1495 | 0.3381 |
| CALFC | 0.4306 | 0.1927 | 0.1042 | 0.0328 | 0.1662 | 0.3248 |
| TRISKN | 0.1103 | 0.0341 | -0.0531 | -0.1043 | 0.0799 | 0.1842 |
| SUBSKN | 0.0805 | 0.0289 | -0.0465 | -0.0984 | 0.1122 | 0.1349 |

| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |
|---|---|---|---|---|---|---|

Exhibit 3.46 Phenotypic Correlation Matrix

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 1.0000 | | | | | |
| HANDB | 0.5603 | 1.0000 | | | | |
| HANDL | 0.4672 | 0.4907 | 1.0000 | | | |
| BICFEM | 0.5452 | 0.4234 | 0.4167 | 1.0000 | | |
| FOOTB | 0.4174 | 0.5783 | 0.3835 | 0.4185 | 1.0000 | |
| HEADL | 0.2680 | 0.2943 | 0.2881 | 0.2630 | 0.2887 | 1.0000 |
| HEADB | 0.1596 | 0.2333 | 0.1732 | 0.2477 | 0.1985 | 0.3074 |
| MFRONT | 0.1984 | 0.2794 | 0.1552 | 0.2530 | 0.2399 | 0.3666 |
| BIZYGO | 0.3551 | 0.3525 | 0.3140 | 0.4181 | 0.3217 | 0.3076 |
| BIGON | 0.2210 | 0.2167 | 0.1896 | 0.2648 | 0.1924 | 0.1703 |
| HEADCR | 0.2917 | 0.3526 | 0.3373 | 0.3382 | 0.3250 | 0.8251 |
| UPARM | 0.3219 | 0.4088 | 0.2554 | 0.3528 | 0.3586 | 0.1960 |
| CALFC | 0.3454 | 0.4226 | 0.3576 | 0.4749 | 0.4929 | 0.2696 |
| TRISKN | 0.1298 | 0.1317 | 0.1091 | 0.2971 | 0.1246 | 0.1211 |
| SUBSKN | 0.1275 | 0.1374 | 0.0909 | 0.2890 | 0.1413 | 0.1141 |

| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
|---|---|---|---|---|---|---|
| HEADB | 1.0000 | | | | | |
| MFRONT | 0.3541 | 1.0000 | | | | |
| BIZYGO | 0.4899 | 0.4466 | 1.0000 | | | |
| BIGON | 0.2311 | 0.2091 | 0.4269 | 1.0000 | | |
| HEADCR | 0.5687 | 0.4848 | 0.4855 | 0.2442 | 1.0000 | |
| UPARM | 0.1929 | 0.2488 | 0.3104 | 0.2006 | 0.3283 | 1.0000 |
| CALFC | 0.2074 | 0.2520 | 0.3417 | 0.2102 | 0.3841 | 0.7329 |
| TRISKN | 0.1250 | 0.1996 | 0.2266 | 0.1117 | 0.2087 | 0.5297 |
| SUBSKN | 0.1156 | 0.1870 | 0.1969 | 0.1323 | 0.2223 | 0.5784 |

| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
|---|---|---|---|---|---|---|
| CALFC | 1.0000 | | | | | |
| TRISKN | 0.4101 | 1.0000 | | | | |
| SUBSKN | 0.4277 | 0.7413 | 1.0000 | | | |

| | CALFC | TRISKN | SUBSKN |
|---|---|---|---|

Exhibit 3.46 Phenotypic Correlation Matrix

Latent Roots

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 9.0885 | 2.7660 | 1.9745 | 1.7233 | 1.2907 | 1.0064 | 0.8943 | 0.8633 |
| 0.7473 | 0.6960 | 0.6539 | 0.6294 | 0.6066 | 0.5123 | 0.4831 | 0.4291 |
| 0.4129 | 0.3396 | 0.3241 | 0.3201 | 0.2614 | 0.2378 | 0.1966 | 0.1895 |
| 0.1716 | 0.1083 | 0.0731 | | | | | |

Percentage of Trace (Latent Roots 1 - 27)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 33.66 | 10.24 | 7.31 | 6.38 | 4.78 | 3.73 | 3.31 | 3.20 |
| 2.77 | 2.58 | 2.42 | 2.33 | 2.25 | 1.90 | 1.79 | 1.59 |
| 1.53 | 1.26 | 1.20 | 1.19 | 0.97 | 0.88 | 0.73 | 0.70 |
| 0.64 | 0.40 | 0.27 | | | | | |

Latent Vectors

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| WEIGHT | -0.2865 | 0.2005 | 0.0112 | 0.1411 | 0.0849 | 0.0057 |
| SITHT | -0.2137 | -0.0689 | -0.1621 | -0.0490 | 0.2973 | 0.2434 |
| STAT | -0.2254 | -0.1130 | -0.2730 | -0.0656 | 0.2905 | 0.2584 |
| BIACROM | -0.2045 | 0.0617 | -0.1743 | 0.0666 | 0.1950 | 0.1371 |
| BICRIST | -0.2138 | 0.0267 | -0.0636 | 0.0706 | -0.0104 | 0.2556 |
| CHESTB | -0.2225 | 0.1746 | 0.0145 | 0.1788 | 0.1696 | 0.0528 |
| FOOTL | -0.2306 | -0.1281 | -0.2662 | -0.0286 | 0.1247 | -0.0422 |
| TFACHT | -0.1344 | -0.3458 | 0.2058 | 0.3522 | 0.0142 | -0.0035 |
| UFACHT | -0.0991 | -0.4026 | 0.1982 | 0.3915 | -0.0229 | 0.0322 |
| NOSEL | -0.0740 | -0.4115 | 0.1486 | 0.3466 | -0.1475 | 0.0195 |
| NOSEB | -0.1085 | -0.0297 | 0.0808 | -0.1988 | -0.2635 | -0.0125 |
| BICHUM | -0.1966 | -0.0448 | -0.1783 | -0.0428 | -0.3646 | 0.0485 |
| WRISTB | -0.2064 | -0.0785 | -0.1911 | -0.0729 | -0.2975 | -0.1585 |
| HANDB | -0.2201 | -0.0552 | -0.1480 | -0.0949 | -0.1755 | -0.3745 |
| HANDL | -0.2156 | -0.1311 | -0.2629 | -0.0373 | 0.0747 | 0.0170 |
| BICFEM | -0.2276 | 0.0175 | -0.0835 | -0.0306 | -0.2532 | 0.0761 |
| FOOTB | -0.2069 | -0.0364 | -0.1011 | -0.0296 | -0.1210 | -0.4202 |
| HEADL | -0.1727 | -0.1308 | 0.2436 | -0.2296 | 0.3260 | -0.2563 |
| HEADB | -0.1420 | -0.0716 | 0.3233 | -0.2603 | 0.0178 | 0.1371 |
| MFRONT | -0.1480 | -0.0128 | 0.2905 | -0.2499 | 0.0311 | -0.0621 |
| BIZYGO | -0.1998 | -0.0405 | 0.2112 | -0.2269 | -0.2252 | 0.2453 |
| BIGON | -0.1255 | -0.0111 | 0.1090 | -0.1802 | -0.2771 | 0.4273 |
| HEADCR | -0.2138 | -0.0890 | 0.3298 | -0.2517 | 0.2545 | -0.1572 |
| UPARM | -0.2145 | 0.2849 | 0.0856 | 0.1800 | -0.0435 | -0.1667 |
| CALFC | -0.2401 | 0.1949 | 0.0165 | 0.1522 | 0.0313 | -0.1955 |
| TRISKN | -0.1381 | 0.3481 | 0.1950 | 0.1956 | -0.0529 | 0.0961 |
| SUBSKN | -0.1391 | 0.3696 | 0.2182 | 0.2256 | -0.0596 | 0.0467 |

Exhibit 3.47 Latent Roots and Vectors of Correlation Matrix

| | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|
| WEIGHT | 0.0791 | 0.0326 | 0.0324 | -0.0588 | -0.0456 | 0.0081 |
| SITHT | -0.0044 | -0.0958 | 0.2125 | -0.2114 | -0.4082 | -0.1201 |
| STAT | -0.0915 | -0.0447 | 0.0979 | -0.1773 | -0.0874 | -0.0923 |
| BIACROM | 0.2431 | 0.2024 | -0.2138 | 0.1782 | -0.1112 | -0.0515 |
| BICRIST | -0.2068 | 0.1237 | -0.3226 | -0.0081 | 0.0321 | 0.5499 |
| CHESTB | 0.2380 | 0.1593 | -0.2034 | 0.2204 | -0.0608 | 0.0458 |
| FOOTL | -0.1025 | 0.0325 | 0.0265 | -0.1010 | 0.4256 | 0.0211 |
| TFACHT | 0.0590 | -0.0592 | 0.0193 | -0.0747 | -0.0902 | -0.0638 |
| UFACHT | 0.0334 | 0.0035 | 0.0811 | -0.0698 | -0.0076 | 0.0008 |
| NOSEL | -0.0712 | 0.0724 | -0.0252 | 0.0570 | 0.0405 | -0.0099 |
| NOSEB | -0.2196 | 0.8191 | 0.1298 | -0.2321 | -0.1690 | -0.1836 |
| BICHUM | -0.1744 | -0.1859 | -0.0939 | 0.1569 | -0.2534 | -0.1780 |
| WRISTB | -0.1402 | -0.2180 | -0.0004 | 0.2378 | -0.1920 | -0.0546 |
| HANDB | 0.1493 | -0.1219 | 0.0417 | -0.0849 | 0.0174 | -0.1826 |
| HANDL | -0.1379 | -0.0014 | 0.0879 | -0.0270 | 0.5389 | -0.2225 |
| BICFEM | -0.2201 | -0.0893 | -0.1208 | 0.1285 | -0.1400 | 0.2253 |
| FOOTB | 0.2509 | 0.1088 | -0.0309 | -0.1597 | 0.1394 | 0.3578 |
| HEADL | -0.2376 | 0.0226 | 0.2364 | 0.3861 | -0.0857 | 0.1729 |
| HEADB | 0.1364 | -0.0481 | -0.4908 | 0.0306 | 0.1429 | -0.4056 |
| MFRONT | 0.0078 | -0.2783 | -0.0143 | -0.5909 | -0.1280 | 0.2231 |
| BIZYGO | 0.1532 | -0.0622 | -0.1742 | -0.0740 | 0.1406 | 0.0212 |
| BIGON | 0.4083 | -0.0177 | 0.5720 | 0.2231 | 0.1543 | 0.1563 |
| HEADCR | -0.1210 | 0.0189 | 0.0253 | 0.2614 | 0.0223 | -0.0178 |
| UPARM | 0.1630 | -0.0289 | 0.1013 | -0.0257 | -0.1117 | -0.2314 |
| CALFC | 0.2316 | 0.0577 | 0.0483 | -0.0269 | -0.0356 | 0.0191 |
| TRISKN | -0.3543 | -0.1378 | 0.1158 | -0.0826 | 0.1709 | -0.0987 |
| SUBSKN | -0.2647 | -0.0259 | 0.1134 | -0.0102 | 0.1584 | -0.0454 |

Exhibit 3.47 Latent Roots and Vectors of Correlation Matrix

| | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|
| WEIGHT | 0.1184 | 0.1361 | 0.0389 | -0.0240 | 0.0654 | 0.0186 |
| SITHT | 0.2777 | -0.1889 | -0.0661 | -0.1111 | -0.1365 | -0.0395 |
| STAT | 0.1183 | -0.0728 | -0.0129 | 0.0534 | -0.0368 | 0.0357 |
| BIACROM | -0.5634 | -0.1460 | -0.1538 | 0.1000 | -0.2433 | -0.3002 |
| BICRIST | 0.1486 | -0.0857 | 0.4453 | -0.2682 | 0.1722 | -0.0259 |
| CHESTB | -0.1690 | -0.0616 | 0.0292 | 0.1560 | 0.2976 | 0.3336 |
| FOOTL | -0.0440 | 0.1833 | -0.0124 | 0.0902 | 0.0242 | -0.2111 |
| TFACHT | -0.0957 | -0.1219 | -0.0554 | 0.0155 | 0.1411 | 0.2388 |
| UFACHT | 0.0081 | -0.0085 | 0.0153 | -0.0022 | -0.0092 | 0.0461 |
| NOSEL | 0.0219 | 0.0919 | -0.0062 | 0.0085 | -0.1355 | -0.3037 |
| NOSEB | -0.0489 | 0.0006 | -0.0207 | -0.0161 | 0.0885 | 0.0281 |
| BICHUM | -0.0408 | 0.2079 | 0.4685 | 0.4776 | -0.1959 | -0.0043 |
| WRISTB | -0.1535 | -0.1267 | -0.1811 | -0.5109 | 0.2531 | -0.3197 |
| HANDB | -0.0510 | -0.3966 | 0.1958 | -0.0368 | 0.1127 | 0.3609 |
| HANDL | -0.1241 | 0.1606 | -0.0125 | -0.0663 | 0.1239 | 0.1724 |
| BICFEM | 0.1449 | 0.1597 | -0.6327 | 0.2456 | 0.0946 | 0.2398 |
| FOOTB | 0.2532 | -0.3316 | -0.0855 | 0.2258 | -0.2809 | -0.1922 |
| HEADL | -0.0384 | 0.0084 | 0.0836 | 0.0165 | -0.1272 | 0.0637 |
| HEADB | 0.3610 | -0.1395 | -0.0539 | 0.1127 | 0.2161 | -0.2422 |
| MFRONT | -0.4188 | 0.1755 | 0.0107 | 0.1436 | 0.2388 | -0.1442 |
| BIZYGO | -0.1257 | 0.0820 | -0.0532 | -0.3879 | -0.5683 | 0.3366 |
| BIGON | 0.0244 | -0.0694 | 0.0582 | 0.1222 | 0.1949 | -0.1238 |
| HEADCR | 0.0206 | 0.0521 | 0.0418 | 0.0102 | -0.0244 | -0.0155 |
| UPARM | 0.0588 | 0.2413 | 0.1848 | -0.2029 | -0.0301 | -0.1409 |
| CALFC | 0.2275 | 0.4650 | -0.1051 | -0.1014 | -0.0246 | -0.0096 |
| TRISKN | -0.0249 | -0.2559 | -0.0542 | 0.1097 | -0.2195 | -0.0279 |
| SUBSKN | -0.0681 | -0.2620 | -0.0516 | 0.0230 | 0.0465 | -0.0913 |

Exhibit 3.47 Latent Roots and Vectors of Correlation Matrix

| | 19 | 20 | 21 | 22 | 23 | 24 |
|---|---|---|---|---|---|---|
| WEIGHT | 0.0100 | -0.0424 | 0.0314 | 0.0078 | 0.0522 | 0.2552 |
| SITHT | 0.0414 | -0.1558 | 0.0715 | -0.1232 | -0.3558 | -0.4116 |
| STAT | 0.0134 | -0.0311 | 0.0061 | 0.1278 | 0.4577 | 0.5508 |
| BIACROM | -0.2811 | 0.2226 | 0.0245 | 0.0655 | -0.1046 | 0.0137 |
| BICRIST | -0.1864 | 0.1576 | -0.0033 | 0.0783 | -0.0742 | -0.0722 |
| CHESTB | 0.3924 | -0.4515 | -0.0663 | 0.0210 | 0.0983 | -0.1608 |
| FOOTL | 0.0786 | 0.0033 | -0.4841 | -0.5136 | 0.0914 | -0.1809 |
| TFACHT | 0.2317 | 0.5180 | -0.0752 | -0.1079 | -0.1398 | 0.0488 |
| UFACHT | -0.0535 | 0.0705 | 0.0756 | -0.0262 | 0.2162 | -0.0664 |
| NOSEL | -0.2113 | -0.5667 | -0.0222 | 0.1493 | -0.0747 | 0.0494 |
| NOSEB | 0.0616 | 0.0304 | -0.0468 | 0.0161 | 0.0067 | -0.0068 |
| BICHUM | 0.1775 | 0.0584 | 0.0808 | -0.0707 | -0.1130 | 0.0400 |
| WRISTB | 0.3250 | -0.0242 | -0.0500 | 0.0571 | 0.0364 | 0.0919 |
| HANDB | -0.4962 | -0.1348 | -0.2214 | -0.0249 | -0.0755 | 0.0637 |
| HANDL | 0.0378 | 0.0373 | 0.4737 | 0.3323 | -0.1991 | -0.1533 |
| BICFEM | -0.2959 | 0.0532 | 0.0548 | -0.0332 | 0.1303 | -0.1587 |
| FOOTB | 0.2832 | 0.0452 | 0.2400 | 0.0831 | 0.0726 | -0.0339 |
| HEADL | -0.0189 | 0.0323 | -0.0003 | 0.0403 | 0.0131 | 0.0227 |
| HEADB | -0.0201 | 0.0789 | -0.0124 | 0.0343 | -0.0220 | 0.0116 |
| MFRONT | -0.0039 | -0.1115 | 0.0556 | 0.0910 | -0.0270 | -0.0208 |
| BIZYGO | 0.1299 | -0.0965 | -0.0094 | -0.1485 | 0.0520 | 0.0447 |
| BIGON | -0.0495 | 0.0451 | -0.0550 | 0.0432 | -0.0111 | -0.0045 |
| HEADCR | -0.0453 | 0.0056 | 0.0246 | -0.0417 | 0.0118 | -0.0213 |
| UPARM | -0.1708 | 0.1391 | 0.1706 | -0.0213 | 0.4919 | -0.3775 |
| CALFC | -0.0222 | 0.0732 | -0.1999 | 0.1215 | -0.4497 | 0.2991 |
| TRISKN | 0.1064 | 0.0602 | -0.4260 | 0.4648 | 0.0110 | -0.1460 |
| SUBSKN | -0.0571 | -0.1074 | 0.3741 | -0.5134 | -0.1563 | 0.2609 |

Exhibit 3.47 Latent Roots and Vectors of Correlation Matrix

| | 25 | 26 | 27 |
|---|---|---|---|
| WEIGHT | -0.0326 | -0.0538 | -0.8500 |
| SITHT | -0.0265 | 0.0038 | -0.0214 |
| STAT | 0.1000 | 0.0586 | 0.2648 |
| BIACROM | -0.0589 | -0.0094 | -0.0214 |
| BICRIST | 0.0239 | 0.0223 | 0.0768 |
| CHESTB | -0.0105 | -0.0165 | 0.1502 |
| FOOTL | 0.0052 | -0.0495 | -0.0218 |
| TFACHT | 0.4492 | 0.0543 | -0.0215 |
| UFACHT | -0.7396 | -0.0695 | 0.0409 |
| NOSEL | 0.3577 | 0.0197 | -0.0165 |
| NOSEB | -0.0161 | -0.0178 | 0.0085 |
| BICHUM | -0.0639 | 0.0135 | 0.0128 |
| WRISTB | -0.1027 | 0.0117 | -0.0088 |
| HANDB | -0.0203 | 0.0031 | 0.0009 |
| HANDL | 0.0094 | -0.0269 | -0.0138 |
| BICFEM | 0.0445 | 0.0017 | -0.0014 |
| FOOTB | 0.0352 | 0.0426 | 0.0203 |
| HEADL | 0.0637 | -0.5767 | 0.0217 |
| HEADB | -0.0320 | -0.2340 | 0.0207 |
| MFRONT | -0.0026 | -0.0477 | 0.0363 |
| BIZYGO | 0.0233 | -0.0502 | -0.0037 |
| BIGON | 0.0318 | 0.0139 | 0.0184 |
| HEADCR | -0.0705 | 0.7636 | -0.0320 |
| UPARM | 0.2343 | -0.0317 | 0.1511 |
| CALFC | -0.1389 | -0.0113 | 0.3439 |
| TRISKN | -0.0539 | 0.0317 | -0.0030 |
| SUBSKN | -0.0119 | -0.0385 | 0.1718 |

Exhibit 3.47 Latent Roots and Vectors of Correlation Matrix

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| WEIGHT | -0.1826 | -0.0098 | -0.1222 | 0.0110 | -0.0334 | 0.0451 |
| SITHT | 0.0426 | 0.0005 | -0.5283 | 0.0067 | -0.0386 | 0.1348 |
| STAT | 0.1034 | 0.0210 | -0.5732 | 0.0262 | -0.0252 | 0.0339 |
| BIACROM | -0.0209 | 0.0425 | -0.1143 | 0.0243 | -0.0400 | 0.0283 |
| BICRIST | 0.2041 | -0.0400 | -0.1399 | 0.0964 | -0.1877 | -0.1911 |
| CHESTB | -0.0778 | -0.0152 | 0.0479 | -0.0412 | -0.0455 | 0.0575 |
| FOOTL | -0.1003 | -0.0159 | -0.3701 | -0.0266 | 0.0634 | -0.0924 |
| TFACHT | -0.0550 | -0.5485 | -0.0321 | -0.0116 | -0.0477 | 0.0576 |
| UFACHT | -0.0086 | -0.6097 | -0.0330 | 0.0106 | 0.0122 | 0.0593 |
| NOSEL | 0.0626 | -0.5664 | 0.0615 | -0.0021 | 0.0344 | -0.1156 |
| NOSEB | -0.0411 | 0.0155 | -0.0094 | -0.0196 | -0.0097 | 0.0600 |
| BICHUM | 0.0038 | 0.0003 | -0.0185 | 0.0698 | -0.0479 | -0.5457 |
| WRISTB | -0.1373 | 0.0116 | -0.0026 | -0.0859 | 0.0696 | -0.5314 |
| HANDB | -0.4868 | 0.0205 | -0.0435 | -0.0145 | -0.0025 | -0.1841 |
| HANDL | -0.0327 | -0.0152 | -0.3547 | -0.0426 | 0.0934 | -0.1571 |
| BICFEM | 0.0476 | 0.0066 | -0.0325 | 0.0045 | -0.0873 | -0.4372 |
| FOOTB | -0.5545 | -0.0195 | 0.0120 | 0.0263 | -0.0125 | -0.0115 |
| HEADL | 0.0175 | -0.0015 | -0.0506 | -0.7567 | 0.1249 | -0.0117 |
| HEADB | 0.0790 | 0.0065 | 0.1431 | -0.1285 | -0.6135 | -0.0238 |
| MFRONT | -0.2273 | 0.0114 | -0.1794 | 0.0161 | -0.5003 | 0.2038 |
| BIZYGO | 0.0069 | -0.0119 | 0.0398 | 0.0532 | -0.5066 | -0.1219 |
| BIGON | 0.0234 | -0.0066 | -0.0113 | -0.0013 | -0.0638 | -0.0386 |
| HEADCR | 0.0007 | -0.0028 | 0.0077 | -0.6148 | -0.1380 | 0.0148 |
| UPARM | -0.3342 | 0.0028 | 0.0798 | 0.0161 | 0.0334 | 0.0410 |
| CALFC | -0.3726 | -0.0141 | 0.0170 | -0.0015 | 0.0318 | 0.0821 |
| TRISKN | 0.0976 | 0.0100 | -0.0047 | -0.0035 | 0.0086 | -0.0813 |
| SUBSKN | 0.0415 | -0.0005 | 0.0806 | -0.0286 | 0.0476 | -0.0426 |

Exhibit 3.48 Varimax Rotated Latent Vectors

| | 7 | 8 | 9 | 10 |
|---|---|---|---|---|
| WEIGHT | -0.2563 | -0.0051 | 0.0296 | 0.2078 |
| SITHT | -0.0598 | -0.0802 | 0.1226 | -0.0116 |
| STAT | 0.0093 | -0.0264 | 0.0134 | 0.0427 |
| BIACROM | 0.1055 | 0.0047 | 0.0006 | 0.5341 |
| BICRIST | -0.1168 | 0.1494 | -0.2015 | 0.2504 |
| CHESTB | -0.0733 | -0.0469 | -0.0071 | 0.5408 |
| FOOTL | 0.0631 | 0.0630 | -0.1082 | 0.0289 |
| TFACHT | -0.0266 | -0.0759 | -0.0080 | -0.0013 |
| UFACHT | -0.0105 | -0.0081 | 0.0346 | -0.0233 |
| NOSEL | 0.0458 | 0.0855 | -0.0269 | 0.0104 |
| NOSEB | -0.0186 | 0.9535 | 0.0240 | -0.0440 |
| BICHUM | -0.0148 | -0.0202 | 0.0275 | -0.0363 |
| WRISTB | 0.0462 | -0.0804 | 0.0250 | -0.0710 |
| HANDB | 0.1112 | -0.0385 | -0.0095 | -0.1105 |
| HANDL | 0.0450 | 0.0494 | -0.0261 | 0.0047 |
| BICFEM | -0.1066 | 0.0481 | -0.0279 | 0.0284 |
| FOOTB | 0.1387 | 0.1148 | -0.0768 | 0.0193 |
| HEADL | -0.0110 | 0.0023 | 0.0230 | -0.0327 |
| HEADB | 0.1223 | -0.0432 | -0.1144 | 0.1711 |
| MFRONT | -0.1531 | -0.0629 | -0.0893 | -0.4349 |
| BIZYGO | 0.0166 | 0.0550 | 0.1789 | 0.0184 |
| BIGON | 0.0093 | 0.0270 | 0.9253 | 0.0150 |
| HEADCR | -0.0167 | 0.0100 | -0.0163 | 0.0364 |
| UPARM | -0.2954 | -0.0603 | 0.0818 | 0.1271 |
| CALFC | -0.1603 | -0.0209 | 0.0413 | 0.2083 |
| TRISKN | -0.6041 | -0.0133 | -0.0395 | -0.1016 |
| SUBSKN | -0.5735 | 0.0426 | -0.0072 | 0.0029 |

Exhibit 3.48 Varimax Rotated Latent Vectors

although minimum frontal diameter also makes an independent contribution to the tenth component. Bigonial diameter remains separate from the head measurements, and contributes to component nine.

Measures of the transverse diameters of limbs (bicondylar humerus, wrist breadth, bicondylar femur) form the sixth component. The two skinfolds (triceps skinfold, subscapular skinfold). make up the seventh component. Two measurements are independent of the others. These are nose breadth (the eighth component) and bigonial diameter (the ninth component). Finally, biacromial diameter and chest breadth are contrasted with minimum frontal diameter on the tenth component. A further comment must be made concerning what is missing from this solution. Bicristal diameter and weight are not closely associated with any of the 10 components.

The general features of the solution can be described as follows:

(1) the craniofacial region includes several independent dimensions of variation,

(2) transverse limb diameters tend to go together,

(3) length and breadth of extremities include independent dimensions of variation,

(4) lengths of extremities are associated with a general linear component including height and sitting height,

(5) nose breadth, bicristal diameter, weight and bigonial diameter are not closely associated with any other variables.

These rotated vectors are similar to those reported by other workers (Burt 1944; Burt and Banks 1947 ; Thurstone 1946, 1947; Hammond 1942; Heath 1952; Howells 1951; Vandenberg 1968; Rhoads 1972). The traditional component of linearity is present. However, there is no obvious component of general size in the rotated solution, although it forms the primary component in the unrotated solution. The presence or absence of particular components in a solution is not only a matter of rotation, but is also influenced by the sample of measurements included. The set used in this study is lacking in limb lengths and there is therefore no limb length component. Also missing is a bulk and circumferential measurement component. Weight is not strongly associated with any particular component, and the two limb circumferences are unexpectedly linked to hand breadth and foot breadth. Measures of biacromial diameter and chest breadth are associated, but distinct from the limb circumferences. This may be due to including relatively fewer girth measurements in the set.

The craniofacial region is well represented in the set of measurements, and it displays a relative independence from the

rest of the body. The three independent components of craniofacial variation echo those reported by Howells (1951).

Comparability of components across studies is hampered by differences in the variable set used, and the analytical technique used. In general terms, however, the derived components are in line with expectations from previous studies.

### 3.3.3 Cluster Analysis

In addition to PCA, a centroid cluster analysis was performed on the phenotypic correlation matrix, as if it represented a matrix of similarities between mesurements. One complication in using the correlation matrix as if it were a similarity matrix is that the clustering algorithm requires that all similarities be in the range 0-100%. Thus the sample correlation matrix has been transformed by converting negative correlations to small (0.05) positive values. The effect of this transformation is serious only when there are significant negative values in the matrix. The phenotypic correlation matrix has a few negative elements, but these tend to be small (less than -0.1) and few in number. Care was taken to determine if the transformation has any notable effect on the results. The form of the similarity matrix or derived tree was not significantly affected.

The dendrogram resulting from the cluster procedure is shown in exhibit 3.49. In this tree there are some measurements which are highly similar (weight, calf circumference, and upper arm circumference; head length and head circumference; sitting height and stature; total facial height and upper facial height) and other sets of measurements which are related but at a lower level of similarity. One such set might be called "bulk", and is made up of the set containing: weight, calf circumference, upper arm circumference, chest breadth, and bicristal diameter. Note that this less cohesive cluster contains the closely related trio of weight, calf circumference and upper arm circumference. In summarizing a dendrogram we will refer to closely related sets as secondary. In addition to those variables which form into clusters there are a number which are relatively independent. In the dendrogram the following measures are independents: nose breadth and bigonial diameter. The "facial height" set (total facial height, upper facial height, nose length) also acts as an independent. In addition to the sets "bulk", "skinfolds" and "facial height" which have already been introduced, there are a number of other clusters. A "linear" set appears at the secondary level, which is made up of two primary sets (stature, sitting height; foot length, hand length). A "limb breadth" set contains bicondylar humerus, wrist breadth and bicondylar femur. Hand breadth and foot breadth also join together in an "extremity breadth" cluster. There is a loose association as the "linear" and "limb breadth" and "extremity breadth" clusters join together. This grouping is contrasted with "bulk" and "skinfolds" on the one hand, and the head measurements on the

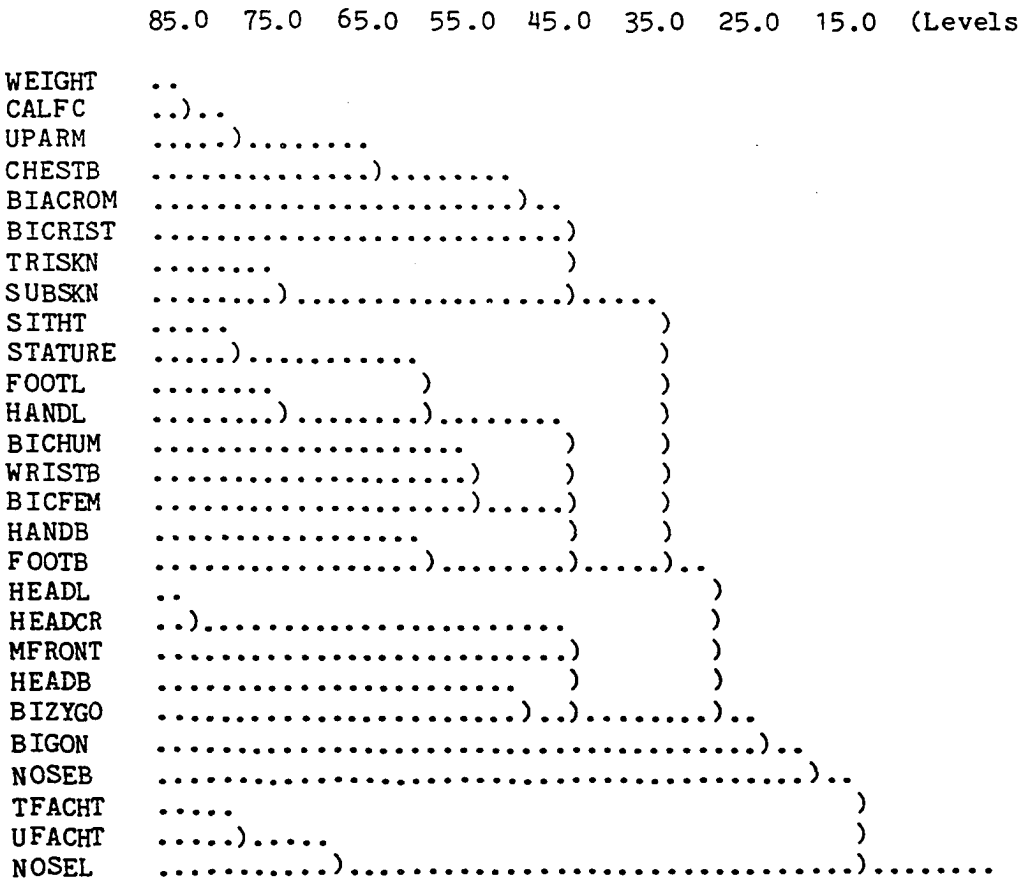



Exhibit 3.49 Cluster analysis of phenotypic correlations

other. The "bulk/skinfolds" group and the rest of the body measures join together before any of the head measures are incuded. There is also a loose association of "head size" which included head length, head circumference, minimum frontal diameter, head breadth and bizygomatic diameter.

Summarizing what these clusters suggest, we see firstly that body and head are independent entities. Further, measures of facial height are independent of the other craniofacial measures. Reading the secondary associations in the branch relating the body, it appears that there are five clusters: "bulk", "skinfolds", "linear", "extremity breadth" and "limb breadth". On the basis of tertiary associations the "bulk" and "skinfolds" clusters go together, as do the "linear" cluster and the two breadth clusters.

### 3.3.4 Comparison of PCA and Cluster Analysis

Comparing the PCA and cluster representations of the pooled within-group correlation matrix there are several differences and similarities to be noted. Firstly, there is a close correpondence between the components with just a few significant variables, and the low level clusters. The combination of sitting height, stature, hand length and foot length into a linear grouping is identical in the two solutions. Likewise the close association of (1) triceps skinfold and subscapular

skinfold, (2) total facial height, upper facial height, nose length, and (3) head length, head circumference is clear in both results. Transverse limb measurements (wrist breadth, bicondylar femur, bicondylar humerus) are clustered together in the dendrogram as they are on the sixth component. However, these three variables are related much more loosely in the dendrogram than is indicated by the PCA solution.

The two variables bigonial diameter and nose breadth play the same very independent role in both cluster diagrams. The variable bicristal diameter which is independent in the PCA solution remains fairly so in the dendrogram, although it eventually links with weight, calf circumference, upper arm circumference and chest breadth.

Component one of the PCA produced a somewhat peculiar combination of extremity breadths (hand breadth, foot breadth) and limb circumferences (upper arm circumference, calf circumference). This situation is changed in the dendrogram, with limb circumferences joining weight in a distinct "bulk/circumferences" cluster. Foot breadth and hand breadth remain most closely related to one another in the cluster solution, but they associate with the linear and transverve limb measurements rather than with limb circumferences. In this case the PCA solution has forced together two different pairs of variables which remain distinct in cluster analysis. The inclusion of weight with the limb circumferences makes the dendrogram a more satisfying picture because it displays the

previously missing component of bulk and circumference measures. There is no easy way to relate the tenth principal component to the dendrogram. The component includes biacromial diameter and chest breadth acting in concert, and both of these contrasted with minimum frontal diameter. Once again it appears the the PCA is mixing two different entities. In the dendrogram biacromial diameter and chest breadth are part of a bulk and circumferential cluster, although biacromial diameter is very loosly associated. In contrast, minimum frontal diameter is loosely associated with the head measurements.

In conclusion, the PCA and cluster solutions are generally similar. Where they differ in detail, the dendrogram provides a more easily interpretable picture. This simple picture must be interpreted with caution, however, as it forces a variable to be in one cluster rather than spread its influence in several dimensions.

# Chapter 4

## The Genetic Basis of Anthropometric Variation

### 4.1 Familial Correlations

The fitting of the path model developed in Chapter 2.4 requires observations on three types of correlations: parent-offspring, spouse-spouse, and sib-sib. These correlations were originally calculated separately for each of the six populations, and the subsequent heritability and genetic correlations were based on these values. Unfortunately, when correlations for each group were estimated separately, the resulting genetic correlations and heritability values contained many obviously bad estimates (negative heritabilities, or genetic correlations and heritabilities >1.0). Since the goal of this work was to examine genetic correlations, much time was spent examining different approaches to the problem which might lead to more reliable estimates. Finally, it became apparent that the most immediate solution was to pool together the corresponding correlation matrices for the six different groups. This approach

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 0.2137 | | | | | |
| SITHT | 0.1092 | 0.1507 | | | | |
| STAT | 0.1081 | 0.0905 | 0.1185 | | | |
| BIACROM | 0.1561 | 0.0829 | 0.0854 | 0.1457 | | |
| BICRIST | 0.1635 | 0.1179 | 0.1167 | 0.1454 | 0.2043 | |
| CHESTB | 0.2214 | 0.1185 | 0.1009 | 0.1775 | 0.1738 | 0.2816 |
| FOOTL | 0.1442 | 0.0915 | 0.1371 | 0.1104 | 0.1437 | 0.1342 |
| TFACHT | 0.1911 | 0.0929 | 0.1021 | 0.1360 | 0.1560 | 0.1988 |
| UFACHT | 0.2324 | 0.1166 | 0.1249 | 0.1779 | 0.2246 | 0.2562 |
| NOSEL | 0.2068 | 0.1288 | 0.1240 | 0.1622 | 0.2217 | 0.2361 |
| NOSEB | 0.0863 | 0.0454 | 0.0357 | 0.0749 | 0.0848 | 0.0967 |
| BICHUM | 0.1860 | 0.1191 | 0.1062 | 0.1371 | 0.1543 | 0.1875 |
| WRISTB | 0.1787 | 0.1150 | 0.0865 | 0.1375 | 0.1442 | 0.1949 |
| HANDB | 0.1717 | 0.1127 | 0.1139 | 0.1382 | 0.1507 | 0.1937 |
| HANDL | 0.1273 | 0.0541 | 0.1246 | 0.1065 | 0.1045 | 0.1134 |
| BICFEM | 0.1118 | 0.0934 | 0.0613 | 0.0724 | 0.0759 | 0.1016 |
| FOOTB | 0.1825 | 0.0883 | 0.1228 | 0.1394 | 0.1722 | 0.1898 |
| HEADL | 0.0875 | 0.0690 | 0.0731 | 0.0725 | 0.0698 | 0.1084 |
| HEADB | 0.1428 | 0.0622 | 0.0528 | 0.0876 | 0.0872 | 0.1466 |
| MFRONT | 0.0525 | 0.0191 | 0.0137 | 0.0117 | 0.0106 | 0.0436 |
| BIZYGO | 0.1616 | 0.0732 | 0.0553 | 0.1067 | 0.1019 | 0.1525 |
| BIGON | 0.1293 | 0.0707 | 0.0173 | 0.0650 | 0.0417 | 0.1030 |
| HEADCR | 0.0883 | 0.0656 | 0.0312 | 0.0523 | 0.0525 | 0.1004 |
| UPARM | 0.2203 | 0.0892 | 0.0808 | 0.1641 | 0.1419 | 0.2342 |
| CALFC | 0.1967 | 0.0978 | 0.0767 | 0.1181 | 0.1519 | 0.1963 |
| TRISKN | 0.0786 | -0.0044 | 0.0245 | 0.0496 | 0.0068 | 0.0574 |
| SUBSKN | 0.0557 | -0.0319 | 0.0198 | 0.0414 | -0.0131 | 0.0283 |
| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
| FOOTL | 0.2174 | | | | | |
| TFACHT | 0.1231 | 0.2723 | | | | |
| UFACHT | 0.1424 | 0.3202 | 0.4661 | | | |
| NOSEL | 0.1327 | 0.2805 | 0.4077 | 0.4193 | | |
| NOSEB | 0.0709 | 0.0703 | 0.1035 | 0.1232 | 0.2106 | |
| BICHUM | 0.1263 | 0.1417 | 0.1903 | 0.1958 | 0.0909 | 0.2069 |
| WRISTB | 0.1110 | 0.1554 | 0.2028 | 0.2210 | 0.1100 | 0.1819 |
| HANDB | 0.1520 | 0.1015 | 0.0964 | 0.1354 | 0.1460 | 0.1549 |
| HANDL | 0.1978 | 0.1058 | 0.0987 | 0.0752 | 0.0636 | 0.1012 |
| BICFEM | 0.0715 | 0.0849 | 0.0734 | 0.0862 | 0.0638 | 0.1035 |
| FOOTB | 0.1690 | 0.1185 | 0.1284 | 0.1468 | 0.1384 | 0.1566 |
| HEADL | 0.0969 | 0.1335 | 0.1429 | 0.1239 | 0.0577 | 0.0699 |
| HEADB | 0.0651 | 0.1305 | 0.1521 | 0.1355 | 0.0555 | 0.1037 |
| MFRONT | 0.0219 | 0.0761 | 0.0317 | 0.0213 | 0.0338 | 0.0285 |
| BIZYGO | 0.0648 | 0.1399 | 0.1794 | 0.1444 | 0.0577 | 0.1278 |
| BIGON | 0.0116 | 0.0942 | 0.1401 | 0.1107 | 0.0700 | 0.1196 |
| HEADCR | 0.0435 | 0.1353 | 0.1511 | 0.1253 | 0.0461 | 0.0652 |
| UPARM | 0.1189 | 0.2057 | 0.2409 | 0.2058 | 0.1085 | 0.1914 |
| CALFC | 0.1168 | 0.1660 | 0.1969 | 0.1962 | 0.0820 | 0.1683 |
| TRISKN | 0.0431 | 0.0626 | 0.0365 | -0.0097 | 0.0367 | 0.0288 |
| SUBSKN | 0.0468 | 0.0373 | -0.0008 | -0.0500 | 0.0344 | 0.0154 |
| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |

Exhibit 4.1 Parent Offspring correlations

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 0.2188 | | | | | |
| HANDB | 0.1749 | 0.3112 | | | | |
| HANDL | 0.0862 | 0.1568 | 0.2500 | | | |
| BICFEM | 0.1107 | 0.0772 | 0.0563 | 0.1502 | | |
| FOOTB | 0.1680 | 0.2702 | 0.1730 | 0.0726 | 0.2948 | |
| HEADL | 0.0801 | 0.1109 | 0.0909 | 0.0277 | 0.0988 | 0.2330 |
| HEADB | 0.1001 | 0.0676 | 0.0606 | 0.0678 | 0.0673 | 0.1116 |
| MFRONT | 0.0303 | 0.0723 | 0.0239 | 0.0516 | 0.0634 | 0.0709 |
| BIZYGO | 0.1123 | 0.0444 | 0.0547 | 0.0975 | 0.0734 | 0.0731 |
| BIGON | 0.1010 | 0.0411 | 0.0232 | 0.0858 | 0.0339 | 0.0259 |
| HEADCR | 0.0780 | 0.0535 | 0.0369 | 0.0470 | 0.0441 | 0.1575 |
| UPARM | 0.1915 | 0.1583 | 0.1119 | 0.1093 | 0.1699 | 0.0976 |
| CALFC | 0.1754 | 0.1590 | 0.0883 | 0.1130 | 0.1668 | 0.0685 |
| TRISKN | 0.0202 | 0.0451 | 0.0883 | 0.0320 | 0.0540 | 0.0044 |
| SUBSKN | 0.0102 | 0.0664 | 0.0983 | 0.0323 | 0.0733 | 0.0073 |
| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
| HEADB | 0.2333 | | | | | |
| MFRONT | 0.0812 | 0.2622 | | | | |
| BIZYGO | 0.1769 | 0.0835 | 0.2614 | | | |
| BIGON | 0.1291 | 0.0479 | 0.1591 | 0.2815 | | |
| HEADCR | 0.1870 | 0.0940 | 0.1316 | 0.1194 | 0.2153 | |
| UPARM | 0.1694 | 0.0645 | 0.1896 | 0.1682 | 0.1085 | 0.2752 |
| CALFC | 0.1372 | 0.0483 | 0.1435 | 0.1359 | 0.0967 | 0.2010 |
| TRISKN | 0.0691 | 0.0369 | 0.0653 | 0.0652 | 0.0238 | 0.0804 |
| SUBSKN | 0.0391 | 0.0581 | 0.0405 | 0.0508 | -0.0018 | 0.0696 |
| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
| CALFC | 0.2265 | | | | | |
| TRISKN | 0.0547 | 0.1950 | | | | |
| SUBSKN | 0.0298 | 0.1916 | 0.2300 | | | |
| | CALFC | TRISKN | SUBSKN | | | |

Exhibit 4.1 Parent Offspring correlations

treats differences in heritability between the populations as statistical noise. The return from this sacrifice is much greater precision in the heritability estimates, which made the calculation of genetic correlations practical. Only the pooled within-group correlation matrices are reported here (exhibits 4.1 - 4.3).

The correlation between parents and offspring (exhibit 4.1) has already been discussed in section 1.2.3. The approach taken here is the one criticized in that section. It consists of statistically controlling for age- and sex-related variation in children by linear regression (fitting terms for sex, age, and age squared). Accordingly, the parent-offspring correlations are not examined for patterns in time. The final matrix is based on averaging the off-diagonal elements of the parent-offspring cross correlation matrix so that the parent-offspring and offspring-parent correlation for a given trait are the same.

The correlation between sibs may be examined by using intraclass correlation (analysis of variance estimators) or by pairwise comparison of all sibs in each sibship. The difference between these techniques is discussed by Donner and Koval (1980) who also present a maximum likelihood estimator. They suggest that for low to moderate (<0.5) values of correlation the analysis of variance estimator is preferred, and that their maximum likelihood estimator is better for high correlations.

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 0.5668 | | | | | |
| SITHT | 0.5285 | 0.4927 | | | | |
| STAT | 0.5374 | 0.5019 | 0.5113 | | | |
| BIACROM | 0.5387 | 0.5025 | 0.5117 | 0.5127 | | |
| BICRIST | 0.5387 | 0.5023 | 0.5116 | 0.5122 | 0.5123 | |
| CHESTB | 0.5280 | 0.4909 | 0.5000 | 0.5010 | 0.5008 | 0.4899 |
| FOOTL | 0.5328 | 0.4970 | 0.5063 | 0.5069 | 0.5067 | 0.4952 |
| TFACHT | 0.5111 | 0.4752 | 0.4843 | 0.4851 | 0.4850 | 0.4736 |
| UFACHT | 0.5077 | 0.4717 | 0.4806 | 0.4815 | 0.4815 | 0.4702 |
| NOSEL | 0.5124 | 0.4769 | 0.4859 | 0.4867 | 0.4871 | 0.4755 |
| NOSEB | 0.5212 | 0.4852 | 0.4944 | 0.4951 | 0.4947 | 0.4835 |
| BICHUM | 0.5317 | 0.4954 | 0.5045 | 0.5054 | 0.5054 | 0.4939 |
| WRISTB | 0.5289 | 0.4925 | 0.5016 | 0.5025 | 0.5024 | 0.4911 |
| HANDB | 0.5306 | 0.4940 | 0.5032 | 0.5039 | 0.5037 | 0.4924 |
| HANDL | 0.5376 | 0.5012 | 0.5107 | 0.5113 | 0.5110 | 0.4996 |
| BICFEM | 0.5234 | 0.4871 | 0.4962 | 0.4968 | 0.4968 | 0.4854 |
| FOOTB | 0.5313 | 0.4955 | 0.5048 | 0.5053 | 0.5054 | 0.4938 |
| HEADL | 0.4885 | 0.4521 | 0.4614 | 0.4618 | 0.4617 | 0.4503 |
| HEADB | 0.4904 | 0.4538 | 0.4630 | 0.4636 | 0.4633 | 0.4521 |
| MFRONT | 0.4877 | 0.4516 | 0.4607 | 0.4611 | 0.4609 | 0.4497 |
| BIZYGO | 0.5114 | 0.4752 | 0.4844 | 0.4852 | 0.4848 | 0.4735 |
| BIGON | 0.5108 | 0.4748 | 0.4838 | 0.4845 | 0.4839 | 0.4729 |
| HEADCR | 0.4917 | 0.4554 | 0.4646 | 0.4651 | 0.4649 | 0.4536 |
| UPARM | 0.5361 | 0.4979 | 0.5068 | 0.5080 | 0.5078 | 0.4973 |
| CALFC | 0.5360 | 0.4995 | 0.5085 | 0.5092 | 0.5092 | 0.4980 |
| TRISKN | 0.3969 | 0.3592 | 0.3669 | 0.3669 | 0.3674 | 0.3611 |
| SUBSKN | 0.4857 | 0.4457 | 0.4542 | 0.4544 | 0.4559 | 0.4483 |
| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
| FOOTL | 0.5019 | | | | | |
| TFACHT | 0.4795 | 0.4587 | | | | |
| UFACHT | 0.4758 | 0.4558 | 0.4537 | | | |
| NOSEL | 0.4812 | 0.4614 | 0.4594 | 0.4660 | | |
| NOSEB | 0.4894 | 0.4676 | 0.4642 | 0.4694 | 0.4798 | |
| BICHUM | 0.4996 | 0.4782 | 0.4751 | 0.4807 | 0.4876 | 0.4993 |
| WRISTB | 0.4969 | 0.4756 | 0.4725 | 0.4783 | 0.4853 | 0.4960 |
| HANDB | 0.4987 | 0.4766 | 0.4730 | 0.4784 | 0.4867 | 0.4970 |
| HANDL | 0.5060 | 0.4835 | 0.4797 | 0.4848 | 0.4937 | 0.5037 |
| BICFEM | 0.4912 | 0.4695 | 0.4658 | 0.4712 | 0.4795 | 0.4899 |
| FOOTB | 0.5001 | 0.4781 | 0.4748 | 0.4801 | 0.4885 | 0.4982 |
| HEADL | 0.4564 | 0.4347 | 0.4314 | 0.4368 | 0.4444 | 0.4548 |
| HEADB | 0.4579 | 0.4365 | 0.4332 | 0.4384 | 0.4461 | 0.4565 |
| MFRONT | 0.4557 | 0.4343 | 0.4307 | 0.4360 | 0.4439 | 0.4543 |
| BIZYGO | 0.4793 | 0.4579 | 0.4545 | 0.4597 | 0.4677 | 0.4780 |
| BIGON | 0.4785 | 0.4571 | 0.4535 | 0.4584 | 0.4675 | 0.4774 |
| HEADCR | 0.4595 | 0.4380 | 0.4345 | 0.4398 | 0.4477 | 0.4580 |
| UPARM | 0.5017 | 0.4804 | 0.4769 | 0.4816 | 0.4903 | 0.5010 |
| CALFC | 0.5035 | 0.4817 | 0.4783 | 0.4833 | 0.4920 | 0.5022 |
| TRISKN | 0.3622 | 0.3438 | 0.3388 | 0.3425 | 0.3517 | 0.3622 |
| SUBSKN | 0.4490 | 0.4286 | 0.4217 | 0.4252 | 0.4383 | 0.4484 |
| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |

Exhibit 4.2 Sib-Sib Correlations

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 0.4936 | | | | | |
| HANDB | 0.4944 | 0.4965 | | | | |
| HANDL | 0.5010 | 0.5027 | 0.5107 | | | |
| BICFEM | 0.4873 | 0.4884 | 0.4955 | 0.4821 | | |
| FOOTB | 0.4957 | 0.4978 | 0.5042 | 0.4899 | 0.4997 | |
| HEADL | 0.4521 | 0.4533 | 0.4606 | 0.4465 | 0.4549 | 0.4118 |
| HEADB | 0.4537 | 0.4550 | 0.4622 | 0.4480 | 0.4566 | 0.4130 |
| MFRONT | 0.4515 | 0.4528 | 0.4598 | 0.4461 | 0.4544 | 0.4111 |
| BIZYGO | 0.4752 | 0.4763 | 0.4837 | 0.4696 | 0.4779 | 0.4345 |
| BIGON | 0.4744 | 0.4755 | 0.4831 | 0.4692 | 0.4770 | 0.4338 |
| HEADCR | 0.4553 | 0.4565 | 0.4638 | 0.4498 | 0.4581 | 0.4148 |
| UPARM | 0.4980 | 0.4991 | 0.5065 | 0.4926 | 0.5002 | 0.4575 |
| CALFC | 0.4993 | 0.5008 | 0.5080 | 0.4941 | 0.5023 | 0.4589 |
| TRISKN | 0.3588 | 0.3594 | 0.3681 | 0.3566 | 0.3600 | 0.3261 |
| SUBSKN | 0.4456 | 0.4472 | 0.4562 | 0.4433 | 0.4473 | 0.4106 |

| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
|---|---|---|---|---|---|---|
| HEADB | 0.4150 | | | | | |
| MFRONT | 0.4128 | 0.4116 | | | | |
| BIZYGO | 0.4364 | 0.4342 | 0.4583 | | | |
| BIGON | 0.4359 | 0.4339 | 0.4578 | 0.4587 | | |
| HEADCR | 0.4164 | 0.4145 | 0.4379 | 0.4375 | 0.4181 | |
| UPARM | 0.4595 | 0.4570 | 0.4810 | 0.4810 | 0.4610 | 0.5056 |
| CALFC | 0.4608 | 0.4585 | 0.4822 | 0.4822 | 0.4624 | 0.5056 |
| TRISKN | 0.3274 | 0.3261 | 0.3450 | 0.3451 | 0.3290 | 0.3701 |
| SUBSKN | 0.4115 | 0.4109 | 0.4298 | 0.4292 | 0.4136 | 0.4575 |

| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
|---|---|---|---|---|---|---|
| CALFC | 0.5072 | | | | | |
| TRISKN | 0.3668 | 0.2976 | | | | |
| SUBSKN | 0.4534 | 0.3763 | 0.4777 | | | |

| | CALFC | TRISKN | SUBSKN |
|---|---|---|---|

Exhibit 4.2 Sib-Sib Correlations

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 0.0184 | | | | | |
| SITHT | -0.0240 | 0.0390 | | | | |
| STAT | -0.0446 | -0.0232 | -0.0436 | | | |
| BIACROM | 0.0274 | 0.0119 | -0.0327 | -0.0315 | | |
| BICRIST | -0.0035 | -0.0099 | -0.0330 | 0.0273 | -0.0563 | |
| CHESTB | 0.0122 | -0.0129 | -0.0440 | -0.0195 | -0.0445 | -0.0340 |
| FOOTL | 0.0156 | 0.0219 | -0.0028 | -0.0137 | 0.0144 | 0.0027 |
| TFACHT | -0.0154 | -0.0200 | -0.0171 | -0.0040 | 0.0273 | -0.0011 |
| UFACHT | -0.0077 | 0.0072 | -0.0038 | 0.0188 | 0.0359 | 0.0460 |
| NOSEL | -0.0373 | -0.0352 | -0.0308 | -0.0251 | 0.0439 | -0.0144 |
| NOSEB | -0.0427 | -0.0037 | -0.0110 | -0.0557 | 0.0120 | -0.0681 |
| BICHUM | -0.0207 | -0.0277 | -0.0207 | -0.0370 | 0.0197 | -0.0493 |
| WRISTB | -0.0020 | -0.0125 | 0.0078 | -0.0330 | 0.0222 | -0.0492 |
| HANDB | -0.0752 | -0.0564 | -0.0588 | -0.0923 | -0.0357 | -0.0667 |
| HANDL | -0.0156 | -0.0346 | -0.0276 | -0.0007 | -0.0049 | 0.0001 |
| BICFEM | -0.0177 | -0.0777 | -0.0712 | -0.0215 | 0.0006 | -0.0342 |
| FOOTB | -0.0494 | 0.0019 | -0.0304 | -0.0766 | 0.0080 | -0.0435 |
| HEADL | -0.0825 | -0.0361 | -0.0521 | -0.0487 | -0.0552 | -0.0722 |
| HEADB | -0.0587 | -0.0636 | -0.0745 | -0.0923 | -0.0458 | -0.0755 |
| MFRONT | -0.0483 | -0.0405 | -0.0336 | -0.0801 | -0.0524 | -0.0687 |
| BIZYGO | -0.0231 | -0.0374 | -0.0018 | -0.0529 | 0.0233 | -0.0479 |
| BIGON | 0.0577 | -0.0067 | -0.0112 | 0.0168 | 0.0211 | 0.0266 |
| HEADCR | -0.0682 | -0.0398 | -0.0559 | -0.0640 | -0.0473 | -0.0611 |
| UPARM | 0.0736 | -0.0482 | -0.0320 | 0.0545 | 0.0251 | 0.0690 |
| CALFC | 0.0445 | -0.0266 | -0.0324 | 0.0569 | 0.0288 | 0.0665 |
| TRISKN | 0.0332 | -0.0519 | -0.0491 | 0.0521 | 0.0178 | 0.0326 |
| SUBSKN | 0.0319 | -0.0254 | -0.0201 | 0.0578 | -0.0040 | 0.0317 |
| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
| FOOTL | 0.0118 | | | | | |
| TFACHT | 0.0322 | 0.0479 | | | | |
| UFACHT | 0.0409 | 0.0678 | 0.1058 | | | |
| NOSEL | 0.0297 | 0.0703 | 0.0722 | 0.0814 | | |
| NOSEB | 0.0198 | 0.0375 | -0.0034 | 0.0253 | -0.0395 | |
| BICHUM | 0.0223 | 0.0575 | 0.0348 | 0.0268 | 0.0448 | 0.0247 |
| WRISTB | 0.0099 | 0.0028 | -0.0044 | 0.0144 | 0.0590 | 0.0135 |
| HANDB | -0.0517 | -0.0204 | -0.0326 | -0.0100 | -0.0368 | -0.0167 |
| HANDL | 0.0126 | 0.0474 | 0.0614 | 0.0323 | -0.0276 | 0.0114 |
| BICFEM | 0.0067 | -0.0208 | -0.0034 | -0.0147 | 0.0030 | 0.0181 |
| FOOTB | 0.0097 | 0.0143 | -0.0084 | 0.0344 | -0.0408 | 0.0057 |
| HEADL | 0.0263 | -0.0134 | 0.0294 | -0.0196 | -0.0398 | -0.0344 |
| HEADB | -0.0609 | -0.0023 | 0.0252 | 0.0195 | -0.0074 | -0.0204 |
| MFRONT | -0.0589 | 0.0128 | 0.0231 | 0.0195 | -0.0908 | -0.0215 |
| BIZYGO | -0.0007 | 0.0533 | 0.0433 | 0.0578 | -0.0201 | 0.0252 |
| BIGON | 0.0508 | 0.0011 | -0.0011 | 0.0431 | -0.0075 | 0.0400 |
| HEADCR | 0.0014 | 0.0150 | 0.0454 | 0.0005 | -0.0285 | -0.0547 |
| UPARM | 0.0348 | 0.0405 | 0.0100 | -0.0100 | -0.0072 | 0.0023 |
| CALFC | -0.0000 | 0.0307 | 0.0295 | -0.0155 | -0.0750 | -0.0417 |
| TRISKN | 0.0048 | 0.0067 | 0.0383 | 0.0227 | 0.0431 | 0.0278 |
| SUBSKN | 0.0158 | 0.0011 | 0.0041 | 0.0284 | -0.0274 | 0.0004 |
| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |

Exhibit 4.3 Spouse correlations

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 0.0288 | | | | | |
| HANDB | -0.0186 | -0.0759 | | | | |
| HANDL | 0.0220 | -0.0747 | 0.0397 | | | |
| BICFEM | 0.0285 | -0.0436 | 0.0276 | 0.0218 | | |
| FOOTB | 0.0043 | -0.0602 | -0.0122 | -0.0056 | -0.0098 | |
| HEADL | -0.0051 | -0.0243 | -0.0075 | -0.0572 | -0.0503 | -0.1714 |
| HEADB | -0.0169 | -0.0316 | -0.0394 | -0.0850 | -0.0530 | -0.1271 |
| MFRONT | -0.0240 | -0.0568 | -0.0759 | -0.0565 | -0.0606 | -0.0876 |
| BIZYGO | -0.0104 | -0.0155 | 0.0185 | 0.0080 | -0.0085 | -0.0521 |
| BIGON | 0.0612 | 0.0523 | 0.0845 | 0.0485 | -0.0014 | -0.0226 |
| HEADCR | -0.0134 | -0.0340 | -0.0103 | -0.0774 | -0.0789 | -0.1637 |
| UPARM | -0.0062 | -0.0246 | -0.0036 | -0.0028 | -0.0028 | -0.0459 |
| CALFC | -0.0401 | -0.0881 | -0.0345 | -0.0106 | -0.0485 | -0.0530 |
| TRISKN | -0.0105 | -0.0223 | 0.0262 | 0.0141 | -0.0052 | -0.0479 |
| SUBSKN | 0.0104 | -0.0301 | 0.0105 | -0.0097 | -0.0225 | -0.0846 |

| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
|---|---|---|---|---|---|---|
| HEADB | -0.1054 | | | | | |
| MFRONT | -0.1068 | -0.0240 | | | | |
| BIZYGO | -0.0668 | -0.0501 | -0.0007 | | | |
| BIGON | -0.0430 | -0.0291 | -0.0155 | -0.0344 | | |
| HEADCR | -0.1531 | -0.1106 | -0.0731 | -0.0212 | -0.1734 | |
| UPARM | -0.0313 | -0.0181 | -0.0215 | 0.0462 | -0.0302 | 0.1091 |
| CALFC | -0.0286 | -0.0331 | -0.0284 | 0.0463 | -0.0429 | 0.0930 |
| TRISKN | 0.0414 | -0.0226 | -0.0054 | 0.0651 | -0.0055 | 0.0769 |
| SUBSKN | 0.0014 | -0.0191 | -0.0262 | 0.1432 | -0.0504 | 0.0675 |

| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
|---|---|---|---|---|---|---|
| CALFC | 0.0709 | | | | | |
| TRISKN | 0.0264 | 0.0581 | | | | |
| SUBSKN | 0.0337 | 0.0450 | 0.0213 | | | |

| | CALFC | TRISKN | SUBSKN |
|---|---|---|---|

Exhibit 4.3 Spouse correlations

The pairwise correlation apparently declines in relative effectiveness as the population correlation increases. However, the pairwise correlation does have the practical advantage that it includes families with only one child measured. Because of the need to keep sample sizes as high as possible the pairwise correlation coefficient was calculated, based on the age- and sex-standardized values for children. The analysis of variance estimators were also obtained, but are not reported here. The pairwise correlations are used in the estimates of heritability.

The correlation between spouses is more straightforward, as it involves fully mature adults. It is based on the pairwise method described by Snedecor and Cochran (1967:295). Examining the spouse correlations (exhibit 4.3) we see that most are near zero, and there is a sprinkling of small positive and negative values.

One complication in model fitting concerns the independence of the three correlation matrices used as input to the path model fitting routine. Strictly speaking, the three matrices do not represent three independent pieces of information because they are based on the same measurements on the same individuals. This problem of "correlations between correlations" has been examined by Elsdon (1975). Elsdon provides estimates for variances and covariances of familial correlations when the number of children of each sex in each family is constant. Problems with estimating

correlations in different sized families are formidable, and Elsdon suggests that comparisons be limited to first and second borns. The rest of the observations on sibs would be unused. He suggests that pooled estimates be made on all families of a particular number of children (so long as there is more than one family in a group). Unfortunately, this solution once again sacrifices some of the data for the sake of the data analysis model. There is obviously much more work in familial correlation and age related changes which needs to be undertaken. This point will be taken up again in the final section (section 5.3). In the meantime the familial correlations are taken as given, and estimates of covariance between the corresponding elements of the correlation matrices are not available.

## 4.2 Heritability of Anthropometric Traits

The three correlation matrices (exhibits 4.1-4.3) are supplied as input to a GENSTAT macro (shown in Appendix 1) to solve the Li path model equations. The macro returns a matrix of heritability values (including cross trait heritabilities), a matrix of gamma (common household environment parameter) values, and the estimated genetic correlations between spouses. The heritability matrix (or gamma matrix) can be submitted to a further GENSTAT macro (also shown in Appendix 1) to calculate a genetic correlation matrix.

The three matrices resulting from the fitting of the path model are given in exhibits 4.5-4.7. But before we turn to an examination of these matrices we will concentrate on the individual trait heritability values which appear in exhibit 4.4. The first column of exhibit 4.4 presents the individual trait heritabilities, which are also to be found in the diagonal of the heritability matrix of exhibit 4.5. Included with the heritability estimates in exhibit 4.4 are the approximate lower and upper 95% confidence limits for the heritability. All of the variables all have non-zero heritabilities. Stature has the lowest heritability with the confidence limit running from 0.144 to 0.346. The highest value is obtained for upper facial height with a confidence limit extending from 0.809 to 0.872. Even on the large sample obtained by pooling over the six groups the heritability estimates have somewhat wide confidence limits.

Comparing the heritability estimates of exhibit 4.4 with other studies, the estimates for the Solomon Islanders look quite low. In particular, they are lower than the results reported by Howells (1966), Vandenberg (1962), Susanne (1977), Osborne and DeGeorge (1959) and Mueller and Titcomb (1977). Although head and face measurements tend to have higher heritabilities than body portions, the other patterns observed by these workers are not present. Contrary to expectations, linear measurements do not have significantly higher values than breadths or circumferences. There is also no suggestion that measures with a lower proportion of bone in them have lower heritabilities. In

Pooled within group and total sample heritability estimates with 95% confidence limits.

| | $h^2$ Within | Lower | Upper | $h^2$ Total | Lower | Upper |
|---|---|---|---|---|---|---|
| WEIGHT | 0.420 | 0.327 | 0.504 | 0.480 | 0.341 | 0.540 |
| SITHT | 0.290 | 0.188 | 0.386 | 0.584 | 0.430 | 0.609 |
| STATURE | 0.248 | 0.144 | 0.346 | 0.417 | 0.285 | 0.494 |
| BIACROM | 0.301 | 0.200 | 0.396 | 0.590 | 0.435 | 0.613 |
| BICRIST | 0.433 | 0.341 | 0.517 | 0.388 | 0.258 | 0.472 |
| CHESTB | 0.583 | 0.507 | 0.650 | 0.626 | 0.464 | 0.635 |
| FOOTL | 0.430 | 0.338 | 0.514 | 0.618 | 0.457 | 0.630 |
| TFACHT | 0.520 | 0.437 | 0.594 | 0.867 | 0.631 | 0.758 |
| UFACHT | 0.843 | 0.809 | 0.872 | 0.871 | 0.633 | 0.759 |
| NOSEL | 0.775 | 0.729 | 0.815 | 0.805 | 0.592 | 0.730 |
| NOSEB | 0.438 | 0.347 | 0.521 | 0.688 | 0.511 | 0.671 |
| BICHUM | 0.404 | 0.310 | 0.490 | 0.898 | 0.649 | 0.771 |
| WRISTB | 0.425 | 0.333 | 0.510 | 0.818 | 0.601 | 0.736 |
| HANDB | 0.673 | 0.610 | 0.728 | 0.779 | 0.575 | 0.718 |
| HANDL | 0.481 | 0.394 | 0.560 | 0.548 | 0.400 | 0.586 |
| BICFEM | 0.294 | 0.193 | 0.389 | 0.539 | 0.393 | 0.581 |
| FOOTB | 0.595 | 0.521 | 0.661 | 0.720 | 0.534 | 0.688 |
| HEADL | 0.562 | 0.484 | 0.632 | 0.656 | 0.487 | 0.653 |
| HEADB | 0.521 | 0.439 | 0.596 | 0.673 | 0.500 | 0.662 |
| MFRONT | 0.537 | 0.456 | 0.610 | 0.556 | 0.407 | 0.592 |
| BIZYGO | 0.523 | 0.440 | 0.597 | 0.845 | 0.617 | 0.748 |
| BIGON | 0.583 | 0.507 | 0.650 | 0.727 | 0.539 | 0.691 |
| HEADCR | 0.521 | 0.438 | 0.595 | 0.781 | 0.577 | 0.719 |
| UPARM | 0.496 | 0.411 | 0.573 | 0.554 | 0.405 | 0.590 |
| CALFC | 0.423 | 0.330 | 0.507 | 0.477 | 0.339 | 0.538 |
| TRISKN | 0.368 | 0.272 | 0.458 | 0.172 | 0.048 | 0.287 |
| SUBSKN | 0.450 | 0.360 | 0.532 | 0.112 | -0.012 | 0.232 |

Exhibit 4.4 Heritability Estimates

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 0.4197 | | | | | |
| SITHT | 0.2237 | 0.2901 | | | | |
| STAT | 0.2263 | 0.1854 | 0.2479 | | | |
| BIACROM | 0.3040 | 0.1638 | 0.1766 | 0.3008 | | |
| BICRIST | 0.3282 | 0.2382 | 0.2413 | 0.2830 | 0.4330 | |
| CHESTB | 0.4375 | 0.2400 | 0.2110 | 0.3621 | 0.3639 | 0.5830 |
| FOOTL | 0.2840 | 0.1790 | 0.2750 | 0.2239 | 0.2833 | 0.2676 |
| TFACHT | 0.3882 | 0.1896 | 0.2078 | 0.2731 | 0.3038 | 0.3980 |
| UFACHT | 0.4684 | 0.2316 | 0.2508 | 0.3492 | 0.4337 | 0.4899 |
| NOSEL | 0.4297 | 0.2670 | 0.2558 | 0.3327 | 0.4247 | 0.4790 |
| NOSEB | 0.1802 | 0.0912 | 0.0723 | 0.1587 | 0.1676 | 0.2075 |
| BICHUM | 0.3799 | 0.2450 | 0.2169 | 0.2848 | 0.3027 | 0.3945 |
| WRISTB | 0.3582 | 0.2330 | 0.1717 | 0.2843 | 0.2822 | 0.4100 |
| HANDB | 0.3714 | 0.2389 | 0.2421 | 0.3045 | 0.3126 | 0.4152 |
| HANDL | 0.2586 | 0.1121 | 0.2564 | 0.2131 | 0.2101 | 0.2268 |
| BICFEM | 0.2275 | 0.2026 | 0.1319 | 0.1480 | 0.1518 | 0.2104 |
| FOOTB | 0.3840 | 0.1762 | 0.2533 | 0.3019 | 0.3417 | 0.3969 |
| HEADL | 0.1906 | 0.1431 | 0.1541 | 0.1525 | 0.1478 | 0.2336 |
| HEADB | 0.3033 | 0.1328 | 0.1142 | 0.1931 | 0.1827 | 0.3172 |
| MFRONT | 0.1103 | 0.0398 | 0.0283 | 0.0254 | 0.0225 | 0.0936 |
| BIZYGO | 0.3309 | 0.1522 | 0.1107 | 0.2253 | 0.1991 | 0.3203 |
| BIGON | 0.2445 | 0.1423 | 0.0349 | 0.1279 | 0.0818 | 0.2006 |
| HEADCR | 0.1894 | 0.1367 | 0.0661 | 0.1119 | 0.1102 | 0.2138 |
| UPARM | 0.4105 | 0.1874 | 0.1669 | 0.3112 | 0.2769 | 0.4382 |
| CALFC | 0.3766 | 0.2010 | 0.1586 | 0.2236 | 0.2952 | 0.3681 |
| TRISKN | 0.1521 | -0.0094 | 0.0515 | 0.0943 | 0.0133 | 0.1112 |
| SUBSKN | 0.1079 | -0.0655 | 0.0404 | 0.0783 | -0.0263 | 0.0549 |
| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
| FOOTL | 0.4298 | | | | | |
| TFACHT | 0.2386 | 0.5198 | | | | |
| UFACHT | 0.2736 | 0.5997 | 0.8431 | | | |
| NOSEL | 0.2577 | 0.5242 | 0.7605 | 0.7754 | | |
| NOSEB | 0.1390 | 0.1355 | 0.2076 | 0.2402 | 0.4385 | |
| BICHUM | 0.2471 | 0.2679 | 0.3677 | 0.3813 | 0.1740 | 0.4037 |
| WRISTB | 0.2199 | 0.3100 | 0.4074 | 0.4357 | 0.2078 | 0.3590 |
| HANDB | 0.3207 | 0.2071 | 0.1993 | 0.2735 | 0.3031 | 0.3151 |
| HANDL | 0.3906 | 0.2020 | 0.1860 | 0.1456 | 0.1308 | 0.2001 |
| BICFEM | 0.1420 | 0.1734 | 0.1473 | 0.1749 | 0.1272 | 0.2033 |
| FOOTB | 0.3347 | 0.2337 | 0.2590 | 0.2839 | 0.2886 | 0.3114 |
| HEADL | 0.1888 | 0.2706 | 0.2776 | 0.2527 | 0.1202 | 0.1448 |
| HEADB | 0.1386 | 0.2616 | 0.2968 | 0.2658 | 0.1118 | 0.2117 |
| MFRONT | 0.0466 | 0.1503 | 0.0620 | 0.0417 | 0.0744 | 0.0582 |
| BIZYGO | 0.1296 | 0.2657 | 0.3440 | 0.2730 | 0.1178 | 0.2493 |
| BIGON | 0.0222 | 0.1882 | 0.2806 | 0.2122 | 0.1412 | 0.2299 |
| HEADCR | 0.0868 | 0.2666 | 0.2890 | 0.2504 | 0.0948 | 0.1380 |
| UPARM | 0.2298 | 0.3954 | 0.4770 | 0.4158 | 0.2187 | 0.3819 |
| CALFC | 0.2336 | 0.3221 | 0.3826 | 0.3987 | 0.1773 | 0.3512 |
| TRISKN | 0.0858 | 0.1244 | 0.0703 | -0.0190 | 0.0704 | 0.0560 |
| SUBSKN | 0.0921 | 0.0745 | -0.0017 | -0.0973 | 0.0708 | 0.0308 |
| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |

Exhibit 4.5 Heritability Matrix

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 0.4253 | | | | | |
| HANDB | 0.3565 | 0.6735 | | | | |
| HANDL | 0.1686 | 0.3389 | 0.4809 | | | |
| BICFEM | 0.2152 | 0.1613 | 0.1095 | 0.2940 | | |
| FOOTB | 0.3345 | 0.5750 | 0.3503 | 0.1460 | 0.5954 | |
| HEADL | 0.1610 | 0.2273 | 0.1833 | 0.0587 | 0.2081 | 0.5624 |
| HEADB | 0.2037 | 0.1397 | 0.1262 | 0.1482 | 0.1421 | 0.2556 |
| MFRONT | 0.0620 | 0.1533 | 0.0518 | 0.1094 | 0.1349 | 0.1553 |
| BIZYGO | 0.2269 | 0.0902 | 0.1074 | 0.1934 | 0.1480 | 0.1543 |
| BIGON | 0.1904 | 0.0780 | 0.0428 | 0.1637 | 0.0680 | 0.0531 |
| HEADCR | 0.1582 | 0.1107 | 0.0745 | 0.1020 | 0.0958 | 0.3768 |
| UPARM | 0.3854 | 0.3245 | 0.2247 | 0.2192 | 0.3407 | 0.2046 |
| CALFC | 0.3653 | 0.3488 | 0.1828 | 0.2284 | 0.3506 | 0.1446 |
| TRISKN | 0.0409 | 0.0923 | 0.1721 | 0.0632 | 0.1085 | 0.0092 |
| SUBSKN | 0.0202 | 0.1369 | 0.1946 | 0.0652 | 0.1499 | 0.0159 |
| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
| HEADB | 0.5215 | | | | | |
| MFRONT | 0.1818 | 0.5373 | | | | |
| BIZYGO | 0.3792 | 0.1758 | 0.5232 | | | |
| BIGON | 0.2698 | 0.0987 | 0.3231 | 0.5832 | | |
| HEADCR | 0.4417 | 0.2113 | 0.2840 | 0.2440 | 0.5210 | |
| UPARM | 0.3497 | 0.1313 | 0.3875 | 0.3216 | 0.2238 | 0.4962 |
| CALFC | 0.2824 | 0.0998 | 0.2955 | 0.2598 | 0.2021 | 0.3678 |
| TRISKN | 0.1327 | 0.0756 | 0.1314 | 0.1224 | 0.0480 | 0.1493 |
| SUBSKN | 0.0780 | 0.1185 | 0.0832 | 0.0889 | -0.0037 | 0.1305 |
| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
| CALFC | 0.4229 | | | | | |
| TRISKN | 0.1067 | 0.3685 | | | | |
| SUBSKN | 0.0576 | 0.3668 | 0.4504 | | | |
| | CALFC | TRISKN | SUBSKN | | | |

Exhibit 4.5 Heritability Matrix

fact, the skinfold measurements have as high a heritability as the linear or transverse measures do.

The large difference in heritability between the Solomons populations and others may reflect differences in both the genetic and environmental variation within samples. Another possible cause of these differences is the particular technique used to estimate heritability. One observation which is of particular importance is to watch what happens to the heritability estimates if they are based on the total correlations for the Solomons sample, rather than the pooled within-group correlations. The heritability values were recalculated ignoring population subdivision, and the results are presented in columns 4-6 of exhibit 4.4. These total heritability values have a more familiar look to them: the values are generally higher, and the values for the two skinfolds are now significantly lower than the rest. One difference between this result and others still remains, however. The linear measurements have lower heritabilities than the transverse measurements with a large component of bone (bicondylar humerus, wrist breadth). The measures of the head and face still have generally larger heritability values than body components.

The most important observation to be made from the pooled within-group versus total heritability results is that ignoring local subpopulations in a "national sample" produces inflated

heritability estimates, as predicted by Howells (1966). Although the Solomons may be an extreme case because of the highly diverse subpopulations found there, this point must be born in mind when examining the results of other "national" studies. It may also be that differing levels of genetic and environmental variation in the Solomons give rise to much lower heritability estimates. Nonetheless, the pooled within group solution is taken to be the "correct" one, and the pooled within group data is used in the following discussion of the matrix results from fitting the Li model.

The full matrix of heritability values is given in exhibit 4.5. The diagonal elements are identical to the single trait heritability estimates we have just reviewed, so attention is focused on the off-diagonal elements. The general impression is that cross trait heritability coefficients are in the same range as the diagonal values. There are a few negative values, but these are not significantly different from 0.0. The skinfold values have high cross trait heritability relative to one another, but low cross trait heritability relative to most other measurements.

The matrix of gamma values (common household environment) is shown in exhibit 4.6. All the values are positive, and generally in the range 0.25 to 0.45. Thus the sib-sib correlation is inflated by about 25-45% by the effect of common home

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 0.3553 | | | | | |
| SITHT | 0.4173 | 0.3460 | | | | |
| STAT | 0.4254 | 0.4097 | 0.3887 | | | |
| BIACROM | 0.3854 | 0.4204 | 0.4239 | 0.3638 | | |
| BICRIST | 0.3748 | 0.3834 | 0.3919 | 0.3696 | 0.3011 | |
| CHESTB | 0.3081 | 0.3712 | 0.3955 | 0.3212 | 0.3218 | 0.2042 |
| FOOTL | 0.3901 | 0.4071 | 0.3689 | 0.3953 | 0.3645 | 0.3613 |
| TFACHT | 0.3182 | 0.3808 | 0.3808 | 0.3487 | 0.3319 | 0.2747 |
| UFACHT | 0.2743 | 0.3557 | 0.3553 | 0.3058 | 0.2613 | 0.2197 |
| NOSEL | 0.3010 | 0.3447 | 0.3590 | 0.3218 | 0.2708 | 0.2376 |
| NOSEB | 0.4317 | 0.4397 | 0.4583 | 0.4164 | 0.4108 | 0.3812 |
| BICHUM | 0.3433 | 0.3737 | 0.3965 | 0.3645 | 0.3531 | 0.3005 |
| WRISTB | 0.3500 | 0.3764 | 0.4156 | 0.3616 | 0.3605 | 0.2902 |
| HANDB | 0.3501 | 0.3762 | 0.3839 | 0.3559 | 0.3492 | 0.2905 |
| HANDL | 0.4088 | 0.4453 | 0.3834 | 0.4047 | 0.4060 | 0.3862 |
| BICFEM | 0.4101 | 0.3874 | 0.4309 | 0.4230 | 0.4208 | 0.3809 |
| FOOTB | 0.3430 | 0.4073 | 0.3791 | 0.3578 | 0.3340 | 0.2987 |
| HEADL | 0.3947 | 0.3809 | 0.3849 | 0.3861 | 0.3884 | 0.3355 |
| HEADB | 0.3414 | 0.3879 | 0.4064 | 0.3687 | 0.3727 | 0.2973 |
| MFRONT | 0.4329 | 0.4317 | 0.4466 | 0.4484 | 0.4497 | 0.4032 |
| BIZYGO | 0.3473 | 0.3996 | 0.4290 | 0.3739 | 0.3848 | 0.3158 |
| BIGON | 0.3868 | 0.4037 | 0.4664 | 0.4204 | 0.4429 | 0.3721 |
| HEADCR | 0.3982 | 0.3874 | 0.4317 | 0.4095 | 0.4101 | 0.3481 |
| UPARM | 0.3246 | 0.4051 | 0.4238 | 0.3498 | 0.3684 | 0.2716 |
| CALFC | 0.3445 | 0.3995 | 0.4296 | 0.3960 | 0.3603 | 0.3095 |
| TRISKN | 0.3205 | 0.3639 | 0.3412 | 0.3195 | 0.3607 | 0.3053 |
| SUBSKN | 0.4316 | 0.4785 | 0.4340 | 0.4151 | 0.4690 | 0.4208 |
| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
| FOOTL | 0.2859 | | | | | |
| TFACHT | 0.3593 | 0.1924 | | | | |
| UFACHT | 0.3375 | 0.1438 | -0.0055 | | | |
| NOSEL | 0.3514 | 0.1896 | 0.0583 | 0.0538 | | |
| NOSEB | 0.4197 | 0.3995 | 0.3604 | 0.3486 | 0.2643 | |
| BICHUM | 0.3754 | 0.3422 | 0.2889 | 0.2881 | 0.4000 | 0.2954 |
| WRISTB | 0.3867 | 0.3205 | 0.2692 | 0.2591 | 0.3801 | 0.3157 |
| HANDB | 0.3410 | 0.3734 | 0.3740 | 0.3420 | 0.3369 | 0.3403 |
| HANDL | 0.3097 | 0.3815 | 0.3857 | 0.4116 | 0.4285 | 0.4034 |
| BICFEM | 0.4201 | 0.3831 | 0.3922 | 0.3840 | 0.4158 | 0.3879 |
| FOOTB | 0.3322 | 0.3609 | 0.3455 | 0.3368 | 0.3459 | 0.3423 |
| HEADL | 0.3615 | 0.2999 | 0.2915 | 0.3110 | 0.3846 | 0.3827 |
| HEADB | 0.3892 | 0.3058 | 0.2837 | 0.3048 | 0.3902 | 0.3511 |
| MFRONT | 0.4324 | 0.3590 | 0.3996 | 0.4151 | 0.4070 | 0.4253 |
| BIZYGO | 0.4145 | 0.3232 | 0.2799 | 0.3211 | 0.4089 | 0.3526 |
| BIGON | 0.4674 | 0.3630 | 0.3132 | 0.3513 | 0.3970 | 0.3614 |
| HEADCR | 0.4161 | 0.3041 | 0.2881 | 0.3146 | 0.4004 | 0.3896 |
| UPARM | 0.3858 | 0.2795 | 0.2373 | 0.2745 | 0.3812 | 0.3099 |
| CALFC | 0.3868 | 0.3191 | 0.2849 | 0.2852 | 0.4045 | 0.3291 |
| TRISKN | 0.3192 | 0.2815 | 0.3035 | 0.3520 | 0.3164 | 0.3341 |
| SUBSKN | 0.4029 | 0.3914 | 0.4226 | 0.4737 | 0.4029 | 0.4329 |
| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |

Exhibit 4.6 Common Environment (gamma) Correlations

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 0.2784 | | | | | |
| HANDB | 0.3173 | 0.1770 | | | | |
| HANDL | 0.4163 | 0.3376 | 0.2657 | | | |
| BICFEM | 0.3790 | 0.4083 | 0.4406 | 0.3341 | | |
| FOOTB | 0.3282 | 0.2203 | 0.3298 | 0.4170 | 0.2037 | |
| HEADL | 0.3717 | 0.3403 | 0.3691 | 0.4172 | 0.3519 | 0.1577 |
| HEADB | 0.3522 | 0.3854 | 0.3994 | 0.3748 | 0.3861 | 0.2893 |
| MFRONT | 0.4205 | 0.3768 | 0.4340 | 0.3917 | 0.3875 | 0.3345 |
| BIZYGO | 0.3620 | 0.4313 | 0.4298 | 0.3728 | 0.4040 | 0.3579 |
| BIGON | 0.3781 | 0.4363 | 0.4616 | 0.3867 | 0.4430 | 0.4073 |
| HEADCR | 0.3764 | 0.4013 | 0.4265 | 0.3992 | 0.4105 | 0.2381 |
| UPARM | 0.3057 | 0.3381 | 0.3942 | 0.3831 | 0.3300 | 0.3562 |
| CALFC | 0.3193 | 0.3318 | 0.4171 | 0.3801 | 0.3300 | 0.3871 |
| TRISKN | 0.3384 | 0.3133 | 0.2817 | 0.3249 | 0.3058 | 0.3215 |
| SUBSKN | 0.4355 | 0.3790 | 0.3587 | 0.4107 | 0.3726 | 0.4026 |
| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
| HEADB | 0.1686 | | | | | |
| MFRONT | 0.3236 | 0.1464 | | | | |
| BIZYGO | 0.2516 | 0.3471 | 0.1968 | | | |
| BIGON | 0.3025 | 0.3847 | 0.2971 | 0.1730 | | |
| HEADCR | 0.2105 | 0.3113 | 0.2988 | 0.3162 | 0.1811 | |
| UPARM | 0.2866 | 0.3915 | 0.2889 | 0.3178 | 0.3498 | 0.2440 |
| CALFC | 0.3208 | 0.4088 | 0.3357 | 0.3507 | 0.3622 | 0.3154 |
| TRISKN | 0.2607 | 0.2883 | 0.2793 | 0.2834 | 0.3050 | 0.2946 |
| SUBSKN | 0.3725 | 0.3518 | 0.3882 | 0.3842 | 0.4155 | 0.3917 |
| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
| CALFC | 0.2894 | | | | | |
| TRISKN | 0.3133 | 0.1094 | | | | |
| SUBSKN | 0.4245 | 0.1899 | 0.2503 | | | |
| | CALFC | TRISKN | SUBSKN | | | |

Exhibit 4.6 Common Environment (gamma) Correlations

environment. This value is higher than the 18% reported by Rao, et al. (1975) for height and weight in Brazil, although their estimates come from a different model based on a "national" sample. Despite this difference in actual values, both results emphasize the importance of the common environment. They also emphasize that heritability values based on sibs (or twins) would lead to inflated heritability estimates.

Turning to the matrix of genetic correlations between spouses (exhibit 4.7) we see that most of these are effectively zero. In a population with low heritability for most traits, the genetic correlation between spouses which is caused by phenotypic assortative mating is very low. It seems that in these populations at least, the parent-offspring correlation would be a reasonable estimate for heritability.

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 0.0077 | | | | | |
| SITHT | -0.0054 | 0.0113 | | | | |
| STAT | -0.0101 | -0.0043 | -0.0108 | | | |
| BIACROM | 0.0083 | 0.0019 | -0.0058 | -0.0095 | | |
| BICRIST | -0.0012 | -0.0023 | -0.0080 | 0.0077 | -0.0244 | |
| CHESTB | 0.0054 | -0.0031 | -0.0093 | -0.0071 | -0.0162 | -0.0198 |
| FOOTL | 0.0044 | 0.0039 | -0.0008 | -0.0031 | 0.0041 | 0.0007 |
| TFACHT | -0.0060 | -0.0038 | -0.0036 | -0.0011 | 0.0083 | -0.0004 |
| UFACHT | -0.0036 | 0.0017 | -0.0010 | 0.0066 | 0.0156 | 0.0225 |
| NOSEL | -0.0160 | -0.0094 | -0.0079 | -0.0083 | 0.0187 | -0.0069 |
| NOSEB | -0.0077 | -0.0003 | -0.0008 | -0.0088 | 0.0020 | -0.0141 |
| BICHUM | -0.0079 | -0.0068 | -0.0045 | -0.0105 | 0.0060 | -0.0195 |
| WRISTB | -0.0007 | -0.0029 | 0.0013 | -0.0094 | 0.0063 | -0.0202 |
| HANDB | -0.0279 | -0.0135 | -0.0142 | -0.0281 | -0.0112 | -0.0277 |
| HANDL | -0.0040 | -0.0039 | -0.0071 | -0.0001 | -0.0010 | 0.0000 |
| BICFEM | -0.0040 | -0.0157 | -0.0094 | -0.0032 | 0.0001 | -0.0072 |
| FOOTB | -0.0190 | 0.0003 | -0.0077 | -0.0231 | 0.0027 | -0.0172 |
| HEADL | -0.0157 | -0.0052 | -0.0080 | -0.0074 | -0.0082 | -0.0169 |
| HEADB | -0.0178 | -0.0085 | -0.0085 | -0.0178 | -0.0084 | -0.0239 |
| MFRONT | -0.0053 | -0.0016 | -0.0009 | -0.0020 | -0.0012 | -0.0064 |
| BIZYGO | -0.0077 | -0.0057 | -0.0002 | -0.0119 | 0.0046 | -0.0153 |
| BIGON | 0.0141 | -0.0010 | -0.0004 | 0.0021 | 0.0017 | 0.0053 |
| HEADCR | -0.0129 | -0.0054 | -0.0037 | -0.0072 | -0.0052 | -0.0131 |
| UPARM | 0.0302 | -0.0090 | -0.0053 | 0.0170 | 0.0070 | 0.0302 |
| CALFC | 0.0168 | -0.0054 | -0.0051 | 0.0127 | 0.0085 | 0.0245 |
| TRISKN | 0.0051 | 0.0005 | -0.0025 | 0.0049 | 0.0002 | 0.0036 |
| SUBSKN | 0.0034 | 0.0017 | -0.0008 | 0.0045 | 0.0001 | 0.0017 |

| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
|---|---|---|---|---|---|---|

| | | | | | | |
|---|---|---|---|---|---|---|
| FOOTL | 0.0051 | | | | | |
| TFACHT | 0.0077 | 0.0249 | | | | |
| UFACHT | 0.0112 | 0.0407 | 0.0892 | | | |
| NOSEL | 0.0077 | 0.0368 | 0.0549 | 0.0631 | | |
| NOSEB | 0.0027 | 0.0051 | -0.0007 | 0.0061 | -0.0173 | |
| BICHUM | 0.0055 | 0.0154 | 0.0128 | 0.0102 | 0.0078 | 0.0100 |
| WRISTB | 0.0022 | 0.0009 | -0.0018 | 0.0063 | 0.0123 | 0.0049 |
| HANDB | -0.0166 | -0.0042 | -0.0065 | -0.0027 | -0.0112 | -0.0053 |
| HANDL | 0.0049 | 0.0096 | 0.0114 | 0.0047 | -0.0036 | 0.0023 |
| BICFEM | 0.0010 | -0.0036 | -0.0005 | -0.0026 | 0.0004 | 0.0037 |
| FOOTB | 0.0033 | 0.0033 | -0.0022 | 0.0098 | -0.0118 | 0.0018 |
| HEADL | 0.0050 | -0.0036 | 0.0082 | -0.0050 | -0.0048 | -0.0050 |
| HEADB | -0.0084 | -0.0006 | 0.0075 | 0.0052 | -0.0008 | -0.0043 |
| MFRONT | -0.0027 | 0.0019 | 0.0014 | 0.0008 | -0.0068 | -0.0013 |
| BIZYGO | -0.0001 | 0.0142 | 0.0149 | 0.0158 | -0.0024 | 0.0063 |
| BIGON | 0.0011 | 0.0002 | -0.0003 | 0.0091 | -0.0011 | 0.0092 |
| HEADCR | 0.0001 | 0.0040 | 0.0131 | 0.0001 | -0.0027 | -0.0075 |
| UPARM | 0.0080 | 0.0160 | 0.0047 | -0.0041 | -0.0016 | 0.0009 |
| CALFC | -0.0000 | 0.0099 | 0.0113 | -0.0062 | -0.0133 | -0.0146 |
| TRISKN | 0.0004 | 0.0008 | 0.0027 | -0.0004 | 0.0030 | 0.0016 |
| SUBSKN | 0.0015 | 0.0001 | -0.0000 | -0.0028 | -0.0019 | 0.0000 |

| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |
|---|---|---|---|---|---|---|

Exhibit 4.7 Genetic correlations between spouses

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 0.0122 | | | | | |
| HANDB | -0.0066 | -0.0511 | | | | |
| HANDL | 0.0037 | -0.0253 | 0.0191 | | | |
| BICFEM | 0.0061 | -0.0070 | 0.0030 | 0.0064 | | |
| FOOTB | 0.0014 | -0.0346 | -0.0043 | -0.0008 | -0.0058 | |
| HEADL | -0.0008 | -0.0055 | -0.0014 | -0.0034 | -0.0105 | -0.0964 |
| HEADB | -0.0034 | -0.0044 | -0.0050 | -0.0126 | -0.0075 | -0.0325 |
| MFRONT | -0.0015 | -0.0087 | -0.0039 | -0.0062 | -0.0082 | -0.0136 |
| BIZYGO | -0.0024 | -0.0014 | 0.0020 | 0.0015 | -0.0013 | -0.0080 |
| BIGON | 0.0116 | 0.0041 | 0.0036 | 0.0079 | -0.0001 | -0.0012 |
| HEADCR | -0.0021 | -0.0038 | -0.0008 | -0.0079 | -0.0076 | -0.0617 |
| UPARM | -0.0024 | -0.0080 | -0.0008 | -0.0006 | -0.0010 | -0.0094 |
| CALFC | -0.0146 | -0.0307 | -0.0063 | -0.0024 | -0.0170 | -0.0077 |
| TRISKN | -0.0004 | -0.0021 | 0.0045 | 0.0009 | -0.0006 | -0.0004 |
| SUBSKN | 0.0002 | -0.0041 | 0.0021 | -0.0006 | -0.0034 | -0.0014 |

| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
|---|---|---|---|---|---|---|
| HEADB | -0.0550 | | | | | |
| MFRONT | -0.0194 | -0.0129 | | | | |
| BIZYGO | -0.0253 | -0.0088 | -0.0004 | | | |
| BIGON | -0.0116 | -0.0029 | -0.0050 | -0.0201 | | |
| HEADCR | -0.0676 | -0.0234 | -0.0208 | -0.0052 | -0.0904 | |
| UPARM | -0.0110 | -0.0024 | -0.0083 | 0.0149 | -0.0067 | 0.0541 |
| CALFC | -0.0081 | -0.0033 | -0.0084 | 0.0120 | -0.0087 | 0.0342 |
| TRISKN | 0.0055 | -0.0017 | -0.0007 | 0.0080 | -0.0003 | 0.0115 |
| SUBSKN | 0.0001 | -0.0023 | -0.0022 | 0.0127 | 0.0002 | 0.0088 |

| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
|---|---|---|---|---|---|---|
| CALFC | 0.0300 | | | | | |
| TRISKN | 0.0028 | 0.0214 | | | | |
| SUBSKN | 0.0019 | 0.0165 | 0.0096 | | | |

| | CALFC | TRISKN | SUBSKN |
|---|---|---|---|

Exhibit 4.7 Genetic correlations between spouses

## 4.3 Genetic Correlations Between Traits

### 4.3.1 Genetic and Environmental Correlation Matrices

The matrix of cross trait heritabilities was converted to a genetic correlation matrix by the GENSTAT macro shown in Appendix 1. The resulting matrix is shown in exhibit 4.8. The genetic correlations themselves are followed by a second matrix which gives the standard errors for the genetic correlations, calculated by the method of Turner and Young (1969:127). Briefly examining the genetic correlation matrix we note that it has a few small negative values, but all genetic correlations are in the theoretically acceptable range of -1.0 to 1.0. The standard errors are also reasonably low relative to the size of the correlations. This genetic correlation matrix is better behaved than those obtained by Leamy (1977) and Cheverud and Buikstra (1981b).

In contrast, the environmental correlation matrix (exhibit 4.9) is a complete mess. Most of the elements are outside the acceptable range -1.0 to 1.0, and the standard errors are usually uncalculateable because of negative variance estimates. Clearly the use of the gamma matrix as a basis for estimating genetic

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 1.0000 | | | | | |
| SITHT | 0.6104 | 1.0000 | | | | |
| STAT | 0.6145 | 0.7715 | 1.0000 | | | |
| BIACROM | 0.6399 | 0.5347 | 0.4987 | 1.0000 | | |
| BICRIST | 0.6104 | 0.5922 | 0.6053 | 0.6924 | 1.0000 | |
| CHESTB | 0.7072 | 0.4127 | 0.3423 | 0.6643 | 0.4555 | 1.0000 |
| FOOTL | 0.6757 | 0.5786 | 0.7628 | 0.5588 | 0.6041 | 0.4919 |
| TFACHT | 0.5342 | 0.3388 | 0.3487 | 0.3088 | 0.3260 | 0.3783 |
| UFACHT | 0.4069 | 0.2529 | 0.2975 | 0.2682 | 0.4103 | 0.2864 |
| NOSEL | 0.3190 | 0.2172 | 0.2949 | 0.1592 | 0.3707 | 0.1492 |
| NOSEB | 0.1297 | 0.1592 | 0.0739 | 0.1451 | 0.1705 | 0.0386 |
| BICHUM | 0.7962 | 0.6700 | 0.6264 | 0.5684 | 0.5031 | 0.4743 |
| WRISTB | 0.6596 | 0.5425 | 0.4550 | 0.5609 | 0.3285 | 0.4493 |
| HANDB | 0.7718 | 0.6245 | 0.5012 | 0.6219 | 0.3416 | 0.5809 |
| HANDL | 0.5596 | 0.5390 | 0.7605 | 0.5396 | 0.4681 | 0.3982 |
| BICFEM | 0.7503 | 0.6226 | 0.5433 | 0.5842 | 0.4974 | 0.5225 |
| FOOTB | 0.7374 | 0.4897 | 0.4916 | 0.5471 | 0.5439 | 0.5511 |
| HEADL | 0.1785 | 0.2226 | 0.2334 | 0.1255 | 0.0813 | 0.2362 |
| HEADB | 0.4448 | 0.2069 | 0.1988 | 0.2347 | 0.2432 | 0.3757 |
| MFRONT | 0.2852 | 0.1513 | 0.0824 | 0.0440 | 0.0954 | 0.2447 |
| BIZYGO | 0.6079 | 0.3708 | 0.3048 | 0.4092 | 0.4209 | 0.4418 |
| BIGON | 0.4916 | 0.3947 | 0.2544 | 0.3025 | 0.2171 | 0.2983 |
| HEADCR | 0.3383 | 0.2614 | 0.2596 | 0.2176 | 0.2183 | 0.3413 |
| UPARM | 0.7627 | 0.3020 | 0.2068 | 0.4278 | 0.2522 | 0.5099 |
| CALFC | 0.9119 | 0.4357 | 0.4025 | 0.4399 | 0.5429 | 0.5970 |
| TRISKN | 0.4119 | 0.0209 | 0.0188 | 0.1580 | -0.0111 | 0.2321 |
| SUBSKN | 0.3049 | -0.0047 | 0.0209 | 0.1553 | -0.0905 | 0.1407 |

| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
|---|---|---|---|---|---|---|

| | | | | | | |
|---|---|---|---|---|---|---|
| FOOTL | 1.0000 | | | | | |
| TFACHT | 0.3342 | 1.0000 | | | | |
| UFACHT | 0.3036 | 0.8723 | 1.0000 | | | |
| NOSEL | 0.2510 | 0.7469 | 0.8644 | 1.0000 | | |
| NOSEB | 0.1959 | 0.0865 | 0.1716 | 0.2589 | 1.0000 | |
| BICHUM | 0.5926 | 0.2052 | 0.0763 | 0.1560 | 0.1978 | 1.0000 |
| WRISTB | 0.5271 | 0.3455 | 0.1347 | 0.2228 | 0.3176 | 0.6743 |
| HANDB | 0.5278 | 0.2213 | 0.0075 | 0.0118 | 0.3259 | 0.5655 |
| HANDL | 0.8867 | 0.3580 | 0.3174 | 0.2267 | 0.1012 | 0.5187 |
| BICFEM | 0.5250 | 0.3478 | 0.2174 | 0.2679 | 0.3230 | 0.6838 |
| FOOTB | 0.5852 | 0.2918 | 0.1438 | 0.1521 | 0.2501 | 0.5172 |
| HEADL | 0.2548 | 0.3139 | 0.2462 | 0.1440 | 0.1096 | 0.1008 |
| HEADB | 0.2791 | 0.3042 | 0.2213 | 0.2040 | 0.0886 | 0.2067 |
| MFRONT | 0.1125 | 0.3608 | 0.1879 | 0.1459 | 0.0846 | 0.1678 |
| BIZYGO | 0.3356 | 0.2571 | 0.1929 | 0.1829 | 0.1940 | 0.4118 |
| BIGON | 0.2703 | 0.2151 | 0.1972 | 0.1937 | 0.2799 | 0.4678 |
| HEADCR | 0.3130 | 0.4036 | 0.2956 | 0.2398 | 0.1702 | 0.1505 |
| UPARM | 0.3631 | 0.4063 | 0.2066 | 0.1420 | 0.2847 | 0.6221 |
| CALFC | 0.5848 | 0.5454 | 0.3729 | 0.3971 | 0.1520 | 0.6640 |
| TRISKN | 0.0859 | 0.1521 | 0.0586 | -0.0467 | 0.0805 | 0.0873 |
| SUBSKN | 0.0781 | 0.1138 | 0.0054 | -0.1085 | 0.0880 | 0.1191 |

| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |
|---|---|---|---|---|---|---|

Exhibit 4.8 Genetic Correlation Matrix

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 1.0000 | | | | | |
| HANDB | 0.6421 | 1.0000 | | | | |
| HANDL | 0.5156 | 0.5618 | 1.0000 | | | |
| BICFEM | 0.7249 | 0.5143 | 0.4180 | 1.0000 | | |
| FOOTB | 0.5797 | 0.7377 | 0.5252 | 0.5884 | 1.0000 | |
| HEADL | 0.1514 | 0.2177 | 0.2509 | 0.0715 | 0.1740 | 1.0000 |
| HEADB | 0.1779 | 0.3124 | 0.2437 | 0.2598 | 0.2951 | 0.4108 |
| MFRONT | 0.2093 | 0.3028 | 0.0205 | 0.3189 | 0.2440 | 0.3230 |
| BIZYGO | 0.3538 | 0.3848 | 0.2441 | 0.4836 | 0.4587 | 0.2777 |
| BIGON | 0.3443 | 0.4444 | 0.2769 | 0.4346 | 0.3340 | 0.2388 |
| HEADCR | 0.2216 | 0.3535 | 0.3119 | 0.1808 | 0.2866 | 0.8402 |
| UPARM | 0.5992 | 0.6911 | 0.2954 | 0.5243 | 0.5754 | 0.1580 |
| CALFC | 0.6539 | 0.6666 | 0.4885 | 0.6877 | 0.7185 | 0.1606 |
| TRISKN | 0.0743 | 0.2229 | 0.1371 | 0.1964 | 0.0978 | -0.0450 |
| SUBSKN | 0.2079 | 0.3794 | 0.0972 | 0.3125 | 0.1718 | -0.0175 |

| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
|---|---|---|---|---|---|---|
| HEADB | 1.0000 | | | | | |
| MFRONT | 0.3869 | 1.0000 | | | | |
| BIZYGO | 0.5471 | 0.4503 | 1.0000 | | | |
| BIGON | 0.2703 | 0.2479 | 0.3949 | 1.0000 | | |
| HEADCR | 0.7438 | 0.4736 | 0.4457 | 0.3254 | 1.0000 | |
| UPARM | 0.4047 | 0.3017 | 0.4854 | 0.4677 | 0.2953 | 1.0000 |
| CALFC | 0.4714 | 0.2331 | 0.5658 | 0.4342 | 0.2943 | 0.7691 |
| TRISKN | 0.2169 | 0.0766 | 0.1578 | 0.1737 | 0.1062 | 0.3532 |
| SUBSKN | 0.1262 | 0.1570 | 0.1076 | 0.2350 | 0.0796 | 0.3537 |

| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
|---|---|---|---|---|---|---|
| CALFC | 1.0000 | | | | | |
| TRISKN | 0.2992 | 1.0000 | | | | |
| SUBSKN | 0.2658 | 0.8868 | 1.0000 | | | |

| | CALFC | TRISKN | SUBSKN |
|---|---|---|---|

Exhibit 4.8 Genetic Correlation Matrix

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 0.2083 | | | | | |
| SITHT | 0.2881 | 0.5334 | | | | |
| STAT | 0.3212 | 0.5792 | 0.7739 | | | |
| BIACROM | 0.1952 | 0.4305 | 0.4805 | 0.4887 | | |
| BICRIST | 0.1553 | 0.2542 | 0.2797 | 0.2029 | 0.1912 | |
| CHESTB | 0.0946 | 0.2046 | 0.2474 | 0.1270 | 0.1114 | 0.0776 |
| FOOTL | 0.1778 | 0.3114 | 0.2773 | 0.2662 | 0.1721 | 0.1433 |
| TFACHT | 0.1192 | 0.2521 | 0.2749 | 0.2078 | 0.1521 | 0.1065 |
| UFACHT | 0.1004 | 0.1608 | 0.1794 | 0.1492 | 0.0979 | 0.0828 |
| NOSEL | 0.1210 | 0.1744 | 0.1979 | 0.1661 | 0.1062 | 0.0944 |
| NOSEB | 0.2165 | 0.3380 | 0.3998 | 0.3024 | 0.2141 | 0.1609 |
| BICHUM | 0.0935 | 0.2557 | 0.3190 | 0.2021 | 0.1658 | 0.1111 |
| WRISTB | 0.1227 | 0.2613 | 0.3562 | 0.2012 | 0.1732 | 0.1041 |
| HANDB | 0.1023 | 0.1830 | 0.2041 | 0.1524 | 0.1198 | 0.0818 |
| HANDL | 0.1734 | 0.3119 | 0.2718 | 0.2487 | 0.1846 | 0.1392 |
| BICFEM | 0.2826 | 0.3744 | 0.5490 | 0.4368 | 0.3223 | 0.2164 |
| FOOTB | 0.1035 | 0.2281 | 0.2160 | 0.1651 | 0.1202 | 0.0897 |
| HEADL | 0.1696 | 0.2527 | 0.2861 | 0.2414 | 0.1729 | 0.1219 |
| HEADB | 0.1499 | 0.2738 | 0.3242 | 0.2476 | 0.1796 | 0.1191 |
| MFRONT | 0.1934 | 0.2894 | 0.3390 | 0.2781 | 0.1958 | 0.1413 |
| BIZYGO | 0.1337 | 0.2659 | 0.3255 | 0.2252 | 0.1742 | 0.1150 |
| BIGON | 0.1537 | 0.2441 | 0.3106 | 0.2405 | 0.1750 | 0.1227 |
| HEADCR | 0.1845 | 0.2749 | 0.3475 | 0.2717 | 0.1929 | 0.1316 |
| UPARM | 0.1248 | 0.2623 | 0.3126 | 0.1664 | 0.1587 | 0.0791 |
| CALFC | 0.1730 | 0.2913 | 0.3662 | 0.2679 | 0.1664 | 0.1138 |
| TRISKN | 0.2748 | 0.4245 | 0.4816 | 0.3843 | 0.2903 | 0.2037 |
| SUBSKN | 0.2454 | 0.3463 | 0.3978 | 0.3221 | 0.2437 | 0.1795 |
| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
| FOOTL | 0.1952 | | | | | |
| TFACHT | 0.1680 | 0.1124 | | | | |
| UFACHT | 0.1095 | 0.0358 | 0.0140 | | | |
| NOSEL | 0.1197 | 0.0514 | 0.0156 | 0.0236 | | |
| NOSEB | 0.2224 | 0.1899 | 0.1187 | 0.1242 | 0.1847 | |
| BICHUM | 0.1991 | 0.1728 | 0.1133 | 0.1137 | 0.2259 | 0.2314 |
| WRISTB | 0.2048 | 0.1508 | 0.1051 | 0.1033 | 0.2070 | 0.1291 |
| HANDB | 0.1147 | 0.1181 | 0.0781 | 0.0834 | 0.1254 | 0.1213 |
| HANDL | 0.1267 | 0.1601 | 0.1052 | 0.1165 | 0.2016 | 0.2001 |
| BICFEM | 0.3280 | 0.2578 | 0.1723 | 0.1823 | 0.3201 | 0.3096 |
| FOOTB | 0.1208 | 0.1292 | 0.0848 | 0.0916 | 0.1396 | 0.1359 |
| HEADL | 0.1664 | 0.1286 | 0.0869 | 0.0966 | 0.1749 | 0.1860 |
| HEADB | 0.1893 | 0.1407 | 0.0949 | 0.1042 | 0.1891 | 0.1864 |
| MFRONT | 0.1950 | 0.1523 | 0.1004 | 0.1094 | 0.1879 | 0.2055 |
| BIZYGO | 0.1898 | 0.1393 | 0.0910 | 0.1022 | 0.1879 | 0.1698 |
| BIGON | 0.1809 | 0.1403 | 0.0884 | 0.0984 | 0.1666 | 0.1632 |
| HEADCR | 0.2002 | 0.1365 | 0.0915 | 0.1032 | 0.1921 | 0.2003 |
| UPARM | 0.1763 | 0.1260 | 0.0996 | 0.1164 | 0.1815 | 0.1107 |
| CALFC | 0.1986 | 0.1503 | 0.1105 | 0.1233 | 0.2175 | 0.1311 |
| TRISKN | 0.2750 | 0.2267 | 0.1467 | 0.1582 | 0.2725 | 0.2981 |
| SUBSKN | 0.2262 | 0.1903 | 0.1200 | 0.1276 | 0.2236 | 0.2467 |
| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |

Exhibit 4.8b Standard Errors of Genetic Correlations

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 0.2010 | | | | | |
| HANDB | 0.1063 | 0.0455 | | | | |
| HANDL | 0.2026 | 0.1019 | 0.1420 | | | |
| BICFEM | 0.2899 | 0.2074 | 0.3075 | 0.5165 | | |
| FOOTB | 0.1221 | 0.0383 | 0.1100 | 0.2381 | 0.0722 | |
| HEADL | 0.1735 | 0.1072 | 0.1515 | 0.2703 | 0.1218 | 0.0875 |
| HEADB | 0.1808 | 0.1233 | 0.1716 | 0.2650 | 0.1385 | 0.1296 |
| MFRONT | 0.1952 | 0.1187 | 0.1734 | 0.2699 | 0.1351 | 0.1408 |
| BIZYGO | 0.1695 | 0.1283 | 0.1741 | 0.2470 | 0.1373 | 0.1440 |
| BIGON | 0.1638 | 0.1147 | 0.1611 | 0.2342 | 0.1295 | 0.1375 |
| HEADCR | 0.1868 | 0.1268 | 0.1802 | 0.2828 | 0.1438 | 0.1154 |
| UPARM | 0.1111 | 0.1033 | 0.1621 | 0.2416 | 0.1110 | 0.1461 |
| CALFC | 0.1189 | 0.1094 | 0.1963 | 0.2712 | 0.1164 | 0.1772 |
| TRISKN | 0.2846 | 0.1771 | 0.2308 | 0.4106 | 0.1979 | 0.2180 |
| SUBSKN | 0.2351 | 0.1430 | 0.1901 | 0.3360 | 0.1594 | 0.1784 |

| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
|---|---|---|---|---|---|---|
| HEADB | 0.1113 | | | | | |
| MFRONT | 0.1468 | 0.1014 | | | | |
| BIZYGO | 0.1021 | 0.1488 | 0.1102 | | | |
| BIGON | 0.1262 | 0.1409 | 0.1106 | 0.0775 | | |
| HEADCR | 0.0780 | 0.1435 | 0.1301 | 0.1292 | 0.1116 | |
| UPARM | 0.1295 | 0.1609 | 0.1084 | 0.1251 | 0.1500 | 0.1294 |
| CALFC | 0.1606 | 0.1921 | 0.1490 | 0.1525 | 0.1778 | 0.1399 |
| TRISKN | 0.2210 | 0.2227 | 0.2187 | 0.2006 | 0.2335 | 0.2352 |
| SUBSKN | 0.1882 | 0.1784 | 0.1871 | 0.1679 | 0.1968 | 0.2027 |

| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
|---|---|---|---|---|---|---|
| CALFC | 0.2040 | | | | | |
| TRISKN | 0.2812 | 0.2941 | | | | |
| SUBSKN | 0.2446 | 0.1624 | 0.1714 | | | |

| | CALFC | TRISKN | SUBSKN |
|---|---|---|---|

Exhibit 4.8b Standard Errors of Genetic Correlations

| | | | | | | |
|---|---|---|---|---|---|---|
| WEIGHT | 1.0000 | | | | | |
| SITHT | 1.1900 | 1.0000 | | | | |
| STAT | 1.1447 | 1.1170 | 1.0000 | | | |
| BIACROM | 1.0721 | 1.1850 | 1.1273 | 1.0000 | | |
| BICRIST | 1.1459 | 1.1880 | 1.1455 | 1.1170 | 1.0000 | |
| CHESTB | 1.1437 | 1.3964 | 1.4038 | 1.1786 | 1.2977 | 1.0000 |
| FOOTL | 1.2240 | 1.2943 | 1.1067 | 1.2257 | 1.2425 | 1.4952 |
| TFACHT | 1.2169 | 1.4759 | 1.3925 | 1.3182 | 1.3789 | 1.3860 |
| UFACHT | 0.4502 | 0.6047 | 0.5700 | 0.5070 | 0.4763 | 0.4862 |
| NOSEL | 2.1778 | 2.5267 | 2.4828 | 2.3007 | 2.1283 | 2.2677 |
| NOSEB | 1.4087 | 1.4537 | 1.4298 | 1.3430 | 1.4561 | 1.6405 |
| BICHUM | 1.0594 | 1.1687 | 1.1700 | 1.1118 | 1.1839 | 1.2234 |
| WRISTB | 1.1128 | 1.2126 | 1.2635 | 1.1365 | 1.2452 | 1.2171 |
| HANDB | 1.3959 | 1.5200 | 1.4636 | 1.4028 | 1.5126 | 1.5280 |
| HANDL | 1.3304 | 1.4687 | 1.1931 | 1.3019 | 1.4356 | 1.6580 |
| BICFEM | 1.1903 | 1.1393 | 1.1957 | 1.2135 | 1.3270 | 1.4582 |
| FOOTB | 1.2750 | 1.5343 | 1.3473 | 1.3146 | 1.3489 | 1.4646 |
| HEADL | 1.6672 | 1.6305 | 1.5546 | 1.6120 | 1.7825 | 1.8695 |
| HEADB | 1.3949 | 1.6061 | 1.5874 | 1.4889 | 1.6542 | 1.6021 |
| MFRONT | 1.8978 | 1.9180 | 1.8721 | 1.9431 | 2.1418 | 2.3320 |
| BIZYGO | 1.3133 | 1.5314 | 1.5513 | 1.3975 | 1.5810 | 1.5756 |
| BIGON | 1.5604 | 1.6502 | 1.7987 | 1.6762 | 1.9410 | 1.9799 |
| HEADCR | 1.5697 | 1.5475 | 1.6269 | 1.5954 | 1.7559 | 1.8098 |
| UPARM | 1.1025 | 1.3940 | 1.3761 | 1.1740 | 1.3591 | 1.2164 |
| CALFC | 1.0743 | 1.2625 | 1.2809 | 1.2204 | 1.2207 | 1.2729 |
| TRISKN | 1.6254 | 1.8701 | 1.6544 | 1.6016 | 1.9874 | 2.0423 |
| SUBSKN | 1.4471 | 1.6259 | 1.3913 | 1.3756 | 1.7086 | 1.8613 |

| | WEIGHT | SITHT | STAT | BIACROM | BICRIST | CHESTB |
|---|---|---|---|---|---|---|
| FOOTL | 1.0000 | | | | | |
| TFACHT | 1.5319 | 1.0000 | | | | |
| UFACHT | 0.6312 | 0.3278 | -0.0055 | | | |
| NOSEL | 2.8339 | 1.8640 | 0.2513 | 1.0000 | | |
| NOSEB | 1.5267 | 1.7716 | 0.7010 | 2.9237 | 1.0000 | |
| BICHUM | 1.2916 | 1.4354 | 0.5315 | 2.2856 | 1.4312 | 1.0000 |
| WRISTB | 1.3707 | 1.3848 | 0.5102 | 2.1176 | 1.4013 | 1.1008 |
| HANDB | 1.5158 | 2.0237 | 0.8889 | 3.5059 | 1.5573 | 1.4880 |
| HANDL | 1.1238 | 1.6876 | 0.7482 | 3.4434 | 1.6170 | 1.4398 |
| BICFEM | 1.3503 | 1.5111 | 0.6785 | 2.8650 | 1.3992 | 1.2347 |
| FOOTB | 1.3768 | 1.8230 | 0.7656 | 3.2182 | 1.4906 | 1.3952 |
| HEADL | 1.7026 | 1.7217 | 0.7340 | 3.3773 | 1.8836 | 1.7730 |
| HEADB | 1.7729 | 1.6980 | 0.6910 | 3.2015 | 1.8485 | 1.5730 |
| MFRONT | 2.1136 | 2.1391 | 1.0443 | 4.6779 | 2.0687 | 2.0446 |
| BIZYGO | 1.7477 | 1.6612 | 0.6310 | 3.1213 | 1.7930 | 1.4625 |
| BIGON | 2.1021 | 1.9900 | 0.7532 | 3.6427 | 1.8566 | 1.5988 |
| HEADCR | 1.8286 | 1.6292 | 0.6770 | 3.1874 | 1.8300 | 1.6841 |
| UPARM | 1.4608 | 1.2899 | 0.4803 | 2.3964 | 1.5007 | 1.1540 |
| CALFC | 1.3446 | 1.3522 | 0.5296 | 2.2862 | 1.4625 | 1.1256 |
| TRISKN | 1.8048 | 1.9402 | 0.9175 | 4.5884 | 1.8605 | 1.8582 |
| SUBSKN | 1.5060 | 1.7836 | 0.8446 | 4.0828 | 1.5665 | 1.5920 |

| | FOOTL | TFACHT | UFACHT | NOSEL | NOSEB | BICHUM |
|---|---|---|---|---|---|---|

Exhibit 4.9 Environmental Correlation Matrix

| | | | | | | |
|---|---|---|---|---|---|---|
| WRISTB | 1.0000 | | | | | |
| HANDB | 1.4293 | 1.0000 | | | | |
| HANDL | 1.5309 | 1.5567 | 1.0000 | | | |
| BICFEM | 1.2428 | 1.6791 | 1.4787 | 1.0000 | | |
| FOOTB | 1.3783 | 1.1601 | 1.4177 | 1.5983 | 1.0000 | |
| HEADL | 1.7737 | 2.0370 | 1.8028 | 1.8175 | 1.9635 | 1.0000 |
| HEADB | 1.6259 | 2.2310 | 1.8870 | 1.5793 | 2.0832 | 1.7743 |
| MFRONT | 2.0830 | 2.3405 | 2.2004 | 1.7712 | 2.2436 | 2.2015 |
| BIZYGO | 1.5468 | 2.3109 | 1.8800 | 1.4539 | 2.0181 | 2.0318 |
| BIGON | 1.7233 | 2.4938 | 2.1536 | 1.6089 | 2.3602 | 2.4661 |
| HEADCR | 1.6762 | 2.2413 | 1.9442 | 1.6226 | 2.1373 | 1.4085 |
| UPARM | 1.1729 | 1.6270 | 1.5483 | 1.3415 | 1.4801 | 1.8156 |
| CALFC | 1.1250 | 1.4658 | 1.5043 | 1.2225 | 1.3594 | 1.8121 |
| TRISKN | 1.9388 | 2.2514 | 1.6520 | 1.6994 | 2.0481 | 2.4470 |
| SUBSKN | 1.6499 | 1.8005 | 1.3909 | 1.4201 | 1.6501 | 2.0264 |
| | WRISTB | HANDB | HANDL | BICFEM | FOOTB | HEADL |
| HEADB | 1.0000 | | | | | |
| MFRONT | 2.0597 | 1.0000 | | | | |
| BIZYGO | 1.3815 | 2.0450 | 1.0000 | | | |
| BIGON | 1.7717 | 2.4173 | 1.6106 | 1.0000 | | |
| HEADCR | 1.2044 | 1.9117 | 1.5829 | 1.7862 | 1.0000 | |
| UPARM | 1.4128 | 2.0712 | 1.3185 | 1.5468 | 1.6637 | 1.0000 |
| CALFC | 1.4521 | 1.9858 | 1.4068 | 1.5677 | 1.5819 | 1.1869 |
| TRISKN | 1.9191 | 2.2779 | 1.9037 | 2.0601 | 2.1663 | 1.8029 |
| SUBSKN | 1.8132 | 1.8376 | 1.7494 | 1.8466 | 1.9511 | 1.5848 |
| | HEADB | MFRONT | BIZYGO | BIGON | HEADCR | UPARM |
| CALFC | 1.0000 | | | | | |
| TRISKN | 1.7606 | 1.0000 | | | | |
| SUBSKN | 1.5773 | 1.1476 | 1.0000 | | | |
| | CALFC | TRISKN | SUBSKN | | | |

Exhibit 4.9 Environmental Correlation Matrix

correlations has fared no better than other analyses based on the residuals after calculating genetic correlations (Leamy 1977; Cheverud and Buikstra 1981b). This very poorly formed environmental correlation matrix may have arisen for any number of reasons. I have not yet been able to find a more successful solution to the problem. Since the environmental correlation matrix obviously contains no useful information, its structure will not be examined by any of the subsequent data analysis techniques.

### 4.3.2 Cluster Analysis of Genetic Correlations

A centroid cluster analysis of the genetic correlation matrix is presented in exhibit 4.10. As in the case of the phenotypic correlation matrix, a transform was used to place all the correlations in the range 0-1. The transform used here replaces negative correlations with a small positive value. A different transform (absolute value) was apparently used by Buikstra and Cheverud (1979), although they don't mention it in their article. It can be inferred from the fact that large negative correlations reported on page 54 appear as positive in the cluster diagram two pages later! If negative correlations are quite small then either an absolute value transform, or the one used here, will have no significant effect on the results. If however, the largest value (ignoring the sign) in a row or

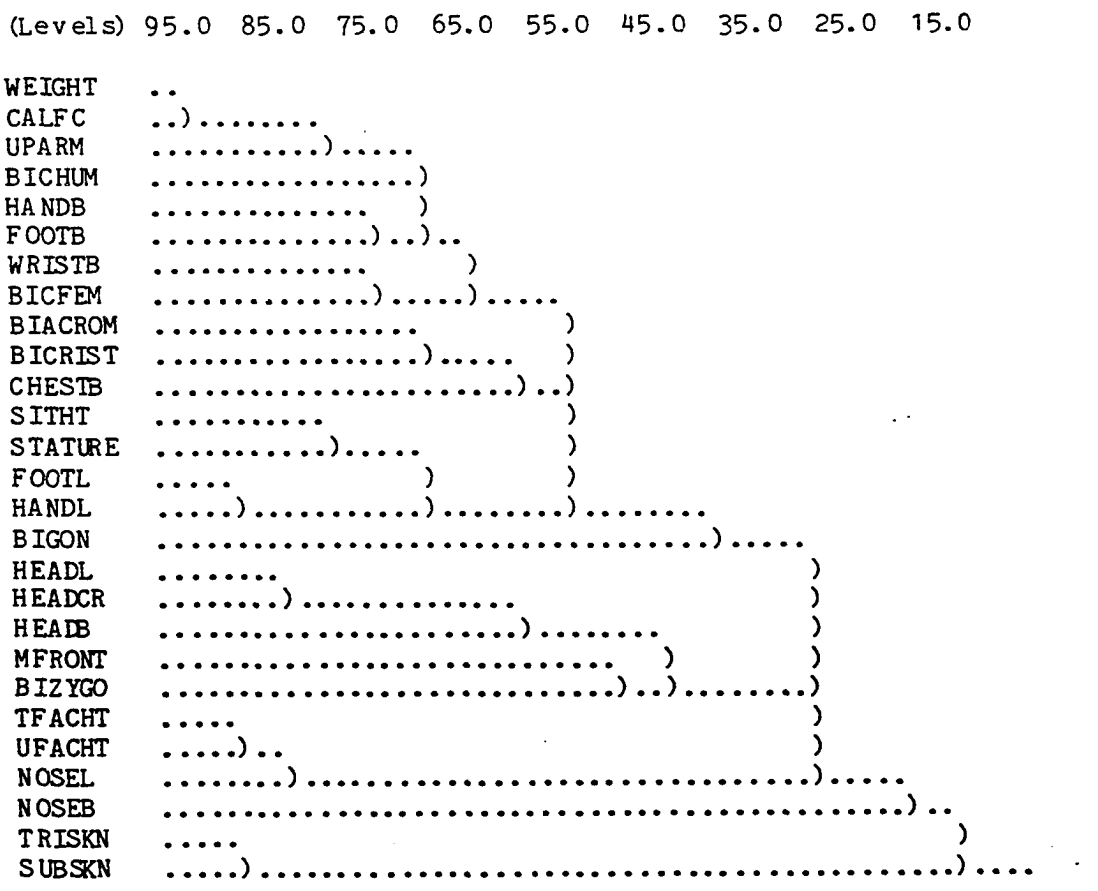



Exhibit 4.10 Cluster analysis of genetic correlations

column of the matrix is negative then such a transform may be questionable. It raises the issue of what a negative genetic correlation actually means. This is not discussed by Cheverud and Buikstra (1979). In the present study all of the small negative genetic correlations may be transformed without afftecting the results.

Examining the tree in exhibit 4.10 there are a number of clusters which are obvious in the diagram. Primary clusters are made up of the following variable pairs: (1) weight and calf circumference, (2) triceps skinfold and subscapular skinfold, (3) foot length and hand length, (4) head length and head circumference. The trio of facial height measurements (total facial height, upper facial height, nose length) also forms a primary cluster.

At a slightly lower level of similarity, upper arm circumference joins in with weight and calf circumference in forming a "bulk and circumference" cluster. Sitting height and stature are linked as a pair, and in turn are joined by the foot length-hand length pair in a "linear" cluster. Hand breadth and foot breadth join in with the "bulk and circumference" cluster rather than the corresponding length measures. The transverse diameters of limbs also form a cluster. Wrist breadth and bicondylar femur are most closely associated with one another, and bicondylar humerus joins in with this pair.

There is a loose association between the transverse diameters of the trunk and shoulders (biacromial diameter, bicristal diameter, chest breadth) and this cluster is relatively independent of the other major clusters of the body.

The head measurements (other than head length and head circumference) are only loosly integrated, yet they are more similar to one another than they are to other clusters. The facial height cluster is distinct from the head measures, and in fact quite distinct from the other clusters. Both bigonial diameter and nose breadth act independently as well, and they are not closely associated with any other measurements. The two skinfolds as a pair are also quite independent of the other measures.

### 4.3.3 Genetic vectors and PCA

The matrix of genetic correlations is unsuitable for PCA because it has large negative latent roots (is not positive semidefinite). However, Hashiguchi and Morishima (1969) have presented a method of analysis which allows latent roots and vectors to be extracted from the phenotypic correlation matrix and then transformed to "genetic vectors". This process bypasses the difficulties of performing an eigenanalysis on a genetic

correlation matrix. In their article, genetic vectors were extracted by this method from the phenotypic correlation matrix, and compared to latent vectors obtained directly from the genetic correlation matrix. In the particular data set they used, PCA could be done on the genetic correlation matrix. The two sets of vectors were extremely close. However, the authors point out that the performance of the method cannot be guaranteed when the genetic correlation matrix has elements with values greater than one and/or large negative latent roots.

A GENSTAT macro to perform genetic vector analysis is given in Appendix 2. This macro was used to obtain the solution given in exhibit 4.11. The first 10 genetic vectors (after Varimax rotation) are shown along with the estimated heritability for each vector.

In describing the PCA of phenotypic correlations, variables were considered important if they had a loading with an absolute value of 0.3 or greater. Examining the genetic vectors, there are very few loadings in this range. It is as if all the loadings are scaled down in the process of translation into "genetic space". Accordingly, variables with a loading greater than 0.1 will be included in the discussion of the genetic vectors.

Heritability of Genetic Vectors (1 - 27)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 0.32 | 0.28 | 0.46 | 0.38 | 0.29 | 0.25 | 0.29 | 0.32 |
| 0.41 | 0.40 | 0.39 | 0.29 | 0.27 | 0.32 | 0.22 | 0.19 |
| 0.27 | 0.19 | 0.18 | 0.20 | 0.12 | 0.16 | 0.20 | 0.25 |
| 0.19 | 0.35 | 0.16 | | | | | |

Genetic Vectors

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| WEIGHT | -0.0771 | -0.0125 | 0.0074 | 0.0378 | -0.0603 | 0.0099 |
| SITHT | -0.0624 | -0.0465 | -0.0552 | -0.0147 | -0.0016 | 0.0620 |
| STAT | -0.0596 | -0.0582 | -0.0715 | 0.0030 | 0.0326 | 0.0554 |
| BIACROM | -0.0448 | -0.0119 | -0.0334 | 0.0171 | -0.0176 | 0.0275 |
| BICRIST | -0.0591 | -0.0531 | -0.0405 | 0.0336 | -0.0026 | 0.0791 |
| CHESTB | -0.0658 | -0.0070 | 0.0164 | 0.0220 | 0.0011 | -0.0120 |
| FOOTL | -0.0833 | -0.0580 | -0.0768 | 0.0038 | 0.0240 | 0.0098 |
| TFACHT | -0.0657 | -0.1205 | 0.1217 | 0.1431 | 0.0177 | -0.0087 |
| UFACHT | -0.0554 | -0.1564 | 0.1224 | 0.1844 | 0.0240 | 0.0631 |
| NOSEL | -0.0433 | -0.1452 | 0.0869 | 0.1449 | -0.0321 | 0.0516 |
| NOSEB | -0.0331 | -0.0266 | 0.0292 | -0.0369 | -0.1341 | -0.0178 |
| BICHUM | -0.0619 | -0.0043 | -0.0590 | -0.0091 | -0.0725 | 0.0388 |
| WRISTB | -0.0592 | -0.0144 | -0.0369 | -0.0004 | -0.0813 | -0.0383 |
| HANDB | -0.0762 | 0.0175 | -0.0216 | -0.0406 | -0.0486 | -0.0721 |
| HANDL | -0.0776 | -0.0632 | -0.0833 | 0.0131 | 0.0372 | 0.0036 |
| BICFEM | -0.0723 | -0.0089 | -0.0186 | 0.0113 | -0.1033 | 0.0451 |
| FOOTB | -0.0708 | -0.0103 | -0.0277 | -0.0123 | -0.0525 | -0.0708 |
| HEADL | -0.0564 | -0.0917 | 0.1743 | -0.1432 | 0.1881 | -0.1333 |
| HEADB | -0.0671 | -0.0348 | 0.1790 | -0.0949 | 0.0490 | -0.0113 |
| MFRONT | -0.0571 | -0.0371 | 0.1981 | -0.1070 | -0.0086 | -0.0641 |
| BIZYGO | -0.0709 | -0.0182 | 0.0952 | -0.0737 | -0.0548 | 0.0519 |
| BIGON | -0.0667 | -0.0135 | 0.0633 | -0.0514 | -0.1200 | 0.1112 |
| HEADCR | -0.0760 | -0.0851 | 0.2189 | -0.1446 | 0.1403 | -0.0939 |
| UPARM | -0.0637 | 0.0181 | 0.0450 | 0.0144 | -0.1000 | -0.0522 |
| CALFC | -0.0821 | -0.0179 | 0.0252 | 0.0524 | -0.0910 | -0.0255 |
| TRISKN | -0.0326 | 0.0931 | 0.0850 | 0.0783 | -0.0552 | 0.0351 |
| SUBSKN | -0.0317 | 0.0934 | 0.0697 | 0.0538 | -0.0853 | -0.0064 |

Exhibit 4.11 Genetic Vector Solution

| | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|
| WEIGHT | 0.0810 | -0.0532 | 0.0036 | -0.0270 | 0.0599 | -0.0181 |
| SITHT | 0.0276 | -0.0292 | 0.0529 | -0.0219 | -0.0430 | 0.0142 |
| STAT | -0.0224 | -0.0251 | 0.0295 | -0.0245 | 0.0839 | 0.0009 |
| BIACROM | 0.0410 | 0.0161 | -0.0388 | 0.0349 | 0.0344 | 0.0152 |
| BICRIST | 0.0430 | 0.0568 | -0.0992 | -0.0362 | 0.0400 | 0.1301 |
| CHESTB | 0.1129 | -0.0213 | -0.0676 | 0.0485 | 0.0398 | 0.0178 |
| FOOTL | -0.0093 | 0.0232 | 0.0174 | -0.0169 | 0.2325 | -0.0196 |
| TFACHT | 0.0340 | -0.0341 | 0.0462 | -0.0553 | 0.0026 | -0.0023 |
| UFACHT | 0.0125 | 0.0664 | 0.0440 | -0.0382 | 0.0391 | 0.0345 |
| NOSEL | 0.0120 | 0.0814 | 0.0215 | -0.0372 | -0.0146 | 0.0269 |
| NOSEB | -0.0583 | 0.2733 | 0.1172 | -0.0688 | -0.0636 | -0.0620 |
| BICHUM | 0.0534 | -0.0324 | 0.0346 | 0.0017 | -0.0264 | -0.0217 |
| WRISTB | 0.0303 | -0.0119 | 0.0423 | 0.0069 | -0.0315 | -0.0342 |
| HANDB | 0.0891 | -0.0064 | 0.0794 | -0.0472 | 0.0443 | -0.0733 |
| HANDL | -0.0209 | -0.0062 | 0.0649 | 0.0203 | 0.2838 | -0.0843 |
| BICFEM | 0.0315 | -0.0144 | 0.0125 | -0.0575 | -0.0398 | 0.0406 |
| FOOTB | 0.1044 | 0.0189 | -0.0098 | -0.0569 | 0.0731 | 0.0620 |
| HEADL | -0.0577 | -0.0127 | 0.1360 | 0.2638 | 0.0272 | 0.0329 |
| HEADB | 0.0810 | -0.0574 | -0.1581 | 0.0596 | 0.1339 | -0.1494 |
| MFRONT | 0.0620 | -0.1893 | -0.0105 | -0.2742 | -0.0943 | 0.1337 |
| BIZYGO | 0.1221 | -0.0403 | -0.0837 | -0.0502 | 0.0407 | 0.0335 |
| BIGON | 0.1569 | -0.0059 | 0.2838 | 0.0811 | 0.0494 | 0.0156 |
| HEADCR | -0.0081 | -0.0320 | 0.0219 | 0.1711 | 0.0950 | -0.0424 |
| UPARM | 0.1050 | -0.0262 | 0.0446 | -0.0199 | 0.0031 | -0.0902 |
| CALFC | 0.1108 | -0.0390 | -0.0147 | -0.0166 | 0.0771 | -0.0206 |
| TRISKN | -0.1068 | -0.0571 | 0.0822 | -0.0541 | 0.1805 | -0.1578 |
| SUBSKN | -0.1051 | -0.0841 | 0.1304 | -0.0600 | 0.1416 | -0.1186 |

Exhibit 4.11 Genetic Vector Solution

| | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|
| WEIGHT | 0.0734 | 0.0365 | 0.0043 | 0.0502 | 0.0228 | 0.0451 |
| SITHT | 0.0927 | -0.0213 | 0.0250 | 0.0206 | 0.0188 | 0.0752 |
| STAT | 0.0880 | 0.0276 | 0.0320 | 0.0439 | 0.0060 | 0.0451 |
| BIACROM | -0.0125 | -0.0488 | 0.0140 | 0.0035 | 0.0137 | 0.0461 |
| BICRIST | 0.0966 | 0.0662 | 0.0893 | -0.0358 | -0.0162 | -0.0117 |
| CHESTB | -0.0150 | -0.0029 | 0.0039 | 0.0803 | 0.1031 | 0.1549 |
| FOOTL | 0.0697 | 0.1165 | 0.0347 | 0.0444 | 0.0778 | 0.0019 |
| TFACHT | -0.0154 | 0.1093 | -0.0507 | 0.0046 | 0.1341 | -0.0212 |
| UFACHT | 0.0090 | 0.1380 | -0.0089 | -0.0218 | 0.0984 | -0.0612 |
| NOSEL | 0.0571 | 0.1713 | -0.0289 | -0.0347 | 0.0596 | -0.1469 |
| NOSEB | -0.0013 | -0.0205 | -0.0343 | -0.0324 | 0.0514 | -0.0635 |
| BICHUM | 0.0620 | 0.1121 | 0.0521 | 0.0638 | 0.0216 | -0.0129 |
| WRISTB | 0.0014 | 0.0480 | -0.0819 | -0.0431 | 0.0956 | -0.0362 |
| HANDB | 0.0155 | -0.0931 | 0.0238 | 0.0337 | 0.1061 | 0.0588 |
| HANDL | 0.0548 | 0.0426 | 0.0298 | 0.0363 | 0.0767 | 0.0390 |
| BICFEM | 0.0420 | 0.0677 | -0.1611 | 0.0639 | 0.0792 | 0.0020 |
| FOOTB | 0.0850 | -0.0160 | -0.0081 | 0.0249 | 0.0158 | 0.0173 |
| HEADL | -0.0366 | 0.0611 | 0.1144 | 0.0548 | 0.0118 | 0.0508 |
| HEADB | 0.1385 | 0.0486 | 0.0076 | 0.0591 | 0.0814 | -0.1146 |
| MFRONT | -0.2375 | 0.1254 | -0.0362 | 0.1388 | 0.2320 | -0.0433 |
| BIZYGO | 0.0150 | 0.1165 | -0.0170 | -0.0934 | -0.1574 | 0.0974 |
| BIGON | 0.0375 | 0.0084 | 0.0370 | 0.1234 | 0.1249 | -0.0760 |
| HEADCR | 0.0114 | 0.0247 | 0.0864 | 0.0579 | 0.0955 | -0.0452 |
| UPARM | 0.0306 | 0.0459 | 0.0174 | 0.0106 | 0.0561 | -0.0083 |
| CALFC | 0.1279 | 0.1079 | -0.0190 | -0.0023 | 0.0484 | 0.0053 |
| TRISKN | -0.0169 | -0.2279 | -0.1056 | 0.1093 | -0.0368 | -0.0123 |
| SUBSKN | -0.0606 | -0.2639 | -0.1453 | 0.1286 | 0.0134 | -0.0242 |

Exhibit 4.11 Genetic Vector Solution

| | 19 | 20 | 21 | 22 | 23 | 24 |
|---|---|---|---|---|---|---|
| WEIGHT | 0.0202 | 0.0276 | -0.1189 | 0.0051 | -0.0611 | -0.0492 |
| SITHT | -0.0337 | -0.0222 | -0.0083 | -0.0524 | -0.1500 | -0.1828 |
| STAT | -0.0031 | -0.0031 | 0.0370 | -0.0323 | -0.0167 | 0.0280 |
| BIACROM | -0.0285 | 0.0264 | -0.0090 | -0.0187 | -0.0342 | -0.1412 |
| BICRIST | -0.0485 | 0.0277 | -0.0554 | 0.0301 | -0.0946 | -0.1211 |
| CHESTB | 0.1223 | -0.0914 | -0.1228 | 0.0123 | -0.0032 | -0.2316 |
| FOOTL | 0.0745 | 0.0305 | -0.0648 | -0.1129 | -0.0689 | -0.1523 |
| TFACHT | 0.0400 | 0.1270 | -0.0138 | 0.1011 | -0.0377 | -0.0102 |
| UFACHT | -0.0177 | 0.0630 | -0.0122 | 0.1377 | 0.0378 | -0.0427 |
| NOSEL | -0.0678 | -0.0645 | -0.0567 | 0.1724 | -0.0142 | 0.0756 |
| NOSEB | -0.1048 | -0.0333 | -0.0976 | -0.0175 | 0.0894 | -0.1817 |
| BICHUM | 0.0245 | -0.0073 | 0.0014 | -0.0613 | -0.0775 | -0.0675 |
| WRISTB | 0.0471 | 0.0001 | 0.0256 | -0.0625 | -0.0960 | -0.0562 |
| HANDB | -0.0649 | -0.0449 | 0.0261 | -0.0743 | -0.1699 | -0.0774 |
| HANDL | 0.0543 | 0.0799 | 0.0328 | 0.0158 | -0.1201 | -0.1202 |
| BICFEM | -0.0078 | -0.0326 | 0.0085 | -0.0982 | -0.0873 | -0.0645 |
| FOOTB | 0.0423 | 0.0040 | 0.0407 | -0.0203 | -0.0705 | -0.0683 |
| HEADL | 0.0204 | 0.0621 | 0.0317 | -0.0146 | 0.0667 | -0.0763 |
| HEADB | -0.0173 | 0.0359 | -0.0996 | 0.0748 | -0.0423 | -0.0594 |
| MFRONT | -0.0064 | -0.0965 | 0.0499 | -0.0373 | 0.0317 | -0.0750 |
| BIZYGO | 0.0511 | -0.0574 | -0.0629 | -0.0489 | 0.0082 | -0.0543 |
| BIGON | -0.1137 | -0.0078 | -0.0235 | -0.0059 | -0.0906 | -0.1167 |
| HEADCR | -0.0232 | 0.0451 | -0.0210 | 0.0518 | 0.0124 | -0.1114 |
| UPARM | -0.0054 | 0.0893 | -0.0597 | -0.0287 | 0.0483 | -0.1286 |
| CALFC | 0.0271 | 0.0424 | -0.1212 | 0.0091 | -0.1525 | -0.0123 |
| TRISKN | 0.0265 | 0.0532 | -0.1437 | 0.0390 | -0.1582 | 0.1033 |
| SUBSKN | -0.0585 | 0.0499 | -0.0511 | -0.1141 | -0.1445 | 0.1804 |

Exhibit 4.11 Genetic Vector Solution

| | 25 | 26 | 27 |
|---|---|---|---|
| WEIGHT | -0.0373 | -0.0337 | 0.1516 |
| SITHT | 0.0120 | 0.0026 | 0.0621 |
| STAT | 0.0340 | -0.0118 | 0.1036 |
| BIACROM | -0.0680 | -0.0014 | 0.0533 |
| BICRIST | -0.1427 | 0.1007 | 0.1169 |
| CHESTB | -0.0941 | -0.0686 | 0.1820 |
| FOOTL | -0.0591 | -0.1056 | 0.2021 |
| TFACHT | -0.0484 | 0.0230 | 0.2196 |
| UFACHT | -0.2996 | -0.0663 | 0.0830 |
| NOSEL | -0.0855 | 0.0954 | 0.1374 |
| NOSEB | -0.0238 | 0.0541 | 0.2610 |
| BICHUM | 0.1042 | -0.0911 | 0.0212 |
| WRISTB | 0.1164 | -0.0075 | 0.1711 |
| HANDB | 0.1228 | 0.0608 | 0.2303 |
| HANDL | -0.0839 | -0.0143 | 0.2708 |
| BICFEM | 0.0638 | -0.0469 | 0.2404 |
| FOOTB | 0.0915 | 0.0237 | 0.2269 |
| HEADL | 0.0081 | -0.3513 | 0.2894 |
| HEADB | -0.0563 | 0.2041 | 0.2733 |
| MFRONT | 0.1372 | 0.0698 | 0.3073 |
| BIZYGO | 0.0123 | -0.0831 | 0.1224 |
| BIGON | 0.0258 | 0.0258 | 0.2161 |
| HEADCR | 0.0003 | 0.2308 | 0.2913 |
| UPARM | 0.1007 | -0.0743 | 0.2570 |
| CALFC | 0.0585 | -0.1253 | 0.2519 |
| TRISKN | -0.1201 | 0.0904 | 0.2410 |
| SUBSKN | -0.0861 | 0.0328 | 0.5396 |

Exhibit 4.11 Genetic Vector Solution

Varimax Rotated Genetic Vectors

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| WEIGHT | -0.0206 | -0.0248 | 0.0412 | 0.0301 | -0.1108 | 0.0240 |
| SITHT | 0.0015 | -0.1143 | 0.0082 | 0.0211 | -0.0288 | 0.0561 |
| STAT | -0.0005 | -0.1330 | 0.0146 | 0.0199 | 0.0148 | 0.0075 |
| BIACROM | 0.0351 | -0.0232 | 0.0059 | 0.0151 | -0.0253 | 0.0055 |
| BICRIST | 0.0714 | -0.0540 | 0.0548 | 0.0799 | 0.0073 | -0.0295 |
| CHESTB | 0.0569 | 0.0162 | 0.0224 | -0.0272 | -0.0787 | -0.0031 |
| FOOTL | 0.0246 | -0.1220 | 0.0158 | 0.0047 | -0.0202 | -0.0234 |
| TFACHT | -0.0418 | -0.0244 | 0.2274 | -0.0322 | -0.0559 | -0.0088 |
| UFACHT | -0.0157 | -0.0349 | 0.2927 | -0.0057 | 0.0125 | 0.0160 |
| NOSEL | 0.0026 | -0.0221 | 0.2403 | 0.0225 | -0.0088 | 0.0118 |
| NOSEB | -0.0162 | 0.0072 | 0.0550 | 0.0248 | -0.0442 | 0.0329 |
| BICHUM | -0.0104 | -0.0636 | -0.0224 | 0.0407 | -0.0830 | 0.0610 |
| WRISTB | -0.0143 | -0.0344 | -0.0090 | 0.0025 | -0.1083 | 0.0161 |
| HANDB | -0.0031 | -0.0335 | -0.0294 | -0.0106 | -0.1594 | 0.0280 |
| HANDL | 0.0054 | -0.1383 | 0.0148 | -0.0284 | -0.0169 | 0.0033 |
| BICFEM | -0.0413 | -0.0454 | 0.0185 | 0.0748 | -0.0857 | 0.0302 |
| FOOTB | 0.0496 | -0.0129 | 0.0000 | 0.0255 | -0.1495 | -0.0245 |
| HEADL | 0.0193 | -0.0118 | -0.0003 | -0.4449 | 0.0563 | 0.0453 |
| HEADB | 0.0625 | 0.0818 | 0.0166 | -0.1498 | -0.0086 | -0.0379 |
| MFRONT | -0.0830 | 0.0157 | 0.0481 | -0.0101 | -0.1278 | -0.0554 |
| BIZYGO | 0.0320 | 0.0280 | 0.0150 | 0.0052 | -0.0812 | 0.0346 |
| BIGON | -0.0630 | -0.0493 | 0.0378 | -0.0694 | -0.1482 | 0.3346 |
| HEADCR | 0.0289 | 0.0283 | 0.0221 | -0.3602 | 0.0283 | 0.0064 |
| UPARM | -0.0301 | 0.0352 | 0.0250 | -0.0022 | -0.1675 | 0.0415 |
| CALFC | -0.0038 | 0.0110 | 0.0583 | 0.0239 | -0.1538 | 0.0113 |
| TRISKN | -0.2201 | 0.0209 | 0.0374 | 0.0262 | 0.0070 | 0.0108 |
| SUBSKN | -0.2361 | 0.0119 | 0.0096 | 0.0135 | -0.0406 | 0.0239 |

Exhibit 4.11 Genetic Vector Solution

| | 7 | 8 | 9 | 10 |
|---|---|---|---|---|
| WEIGHT | -0.0055 | -0.0405 | -0.0332 | -0.0469 |
| STHT | -0.0024 | -0.0083 | -0.0028 | -0.0201 |
| STAT | -0.0049 | -0.0128 | -0.0021 | -0.0023 |
| BIACROM | -0.0056 | -0.0077 | -0.0805 | -0.0047 |
| BICRIST | 0.0101 | 0.0187 | -0.0953 | -0.0609 |
| CHESTB | 0.0211 | -0.0637 | -0.0897 | -0.0436 |
| FOOTL | 0.0075 | 0.0254 | -0.0211 | 0.0154 |
| TFACHT | 0.0095 | -0.0425 | 0.0299 | -0.0304 |
| UFACHT | 0.0160 | 0.0251 | -0.0231 | -0.0045 |
| NOSEL | -0.0226 | 0.0573 | -0.0316 | -0.0057 |
| NOSEB | 0.0007 | 0.3304 | 0.0169 | 0.0492 |
| BICHUM | -0.0271 | -0.0067 | -0.0383 | -0.0102 |
| WRISTB | -0.0393 | 0.0200 | -0.0125 | 0.0220 |
| HANDB | 0.0381 | 0.0307 | 0.0396 | -0.0078 |
| HANDL | -0.0024 | -0.0013 | -0.0080 | 0.0553 |
| BICFEM | -0.0317 | 0.0282 | -0.0299 | -0.0500 |
| FOOTB | 0.0248 | 0.0253 | -0.0010 | -0.0303 |
| HEADL | 0.0015 | -0.0027 | 0.0386 | 0.0450 |
| HEADB | -0.0040 | -0.0667 | -0.0699 | -0.2087 |
| MFRONT | 0.0240 | -0.0594 | 0.2268 | -0.3000 |
| BIZYGO | -0.0024 | -0.0139 | -0.0404 | -0.1999 |
| BIGON | 0.0023 | 0.0562 | -0.0031 | 0.0052 |
| HEADCR | 0.0001 | -0.0147 | 0.0127 | -0.0900 |
| UPARM | 0.0014 | 0.0022 | -0.0042 | -0.0288 |
| CALFC | -0.0160 | -0.0337 | -0.0488 | -0.0449 |
| TRISKN | 0.0083 | 0.0062 | 0.0221 | 0.0008 |
| SUBSKN | -0.0134 | 0.0098 | 0.0667 | 0.0205 |

Exhibit 4.11 Genetic Vector Solution

The first genetic vector includes the four variables representing linearity (sitting height, stature, foot length, hand length). The second represents the skinfolds, and the third is the facial height measures (total facial height, upper facial height, nose length). General measures of head size are important in genetic vector four. The major contribution comes from head length and head circumference, with a lesser one for head breadth. Head measurements reappear in the tenth genetic vector where head breadth, minimum frontal diameter and bizygomatic diameter make almost equal contributions.

Genetic vector number five contains a mixture of variables which are separate in the dendrogram. Bulk and circumferential measures appear (weight, upper arm circumference, calf circumference) along with extremety breadths (foot breadth, hand breadth). Although this grouping parallels the cluster results so far, wrist breadth, bigonial diameter and minimum frontal diameter also appear in the component. Bigonial diameter and minimum frontal diameter appear in the sixth and ninth components, respectively, with much larger loadings than they do in this component. Their inclusion in the fifth component is less striking than their independence as expressed in each having a component to itself. Nose breadth is also an independent variable and has the eighth component to itself.

There are no variables which contribute significantly to the

seventh genetic vector. My experience with other genetic vector solutions suggests that this is not uncommon. Several other data sets also produced what are essentially latent vectors with no variables loading on them. These "dud" genetic vectors also tend to have quite low heritabilities, although a low heritability for a genetic vector does not automatically imply that there will be no significant loadings. For example, the second and fifth genetic vectors have lower heritabilites than the seventh.

### 4.3.4 Cluster Analysis and Genetic Vectors Compared

The cluster and genetic vector solutions have some points of similarity, but they give some different details to the picture of the genetic correlations between traits. Nose breadth is picked up as an independent in both representations. The dendrogram places bigonial diameter as an independent measure, but the genetic vector solution presents a more complicated picture. Bigonial diameter appears alone in the sixth genetic vector. It appears again in the heterogeneous component five.

The genetic vector solution and cluster analysis are in close agreement in the independence of the skinfolds, and the close association of head length and head circumference. In the genetic vector solution, head breadth is associated with two

different components. First, head breadth is important in the general head size component (along with head length and head circumference). Secondly, head breadth is associated with the face breadth measures (genetic vector 10: minimum frontal diameter and bizygomatic diameter).

The genetic vector solution identifies minimum frontal diameter as an independent. Although minimum frontal diameter is fairly independent in the dendrogram, it does share some similarity with the other head measurements.

There is a contrast between the genetic vector solution (which picks out an integrated head/face breadth component), and the cluster analysis which leaves head breadth and the measures of face/head breadth only loosely associated. In this instance the ability of a PCA solution to split the influence of variables adds greater clarity.

The integration of bulk/circumference measures plus extremety breadths (hand breadth, foot breadth) is found in both solutions. The genetic vector solution is less discriminating, however, as it includes some additional variables (wrist breadth, minimum frontal diameter, bigonial diameter) in the fifth genetic vector. Missing entirely from the genetic vector solution are most of the transverse measures of the body (biacromial diameter,

bicristal diameter, chest breadth, bicondylar humerus, bicondylar femur).

The cluster analysis and genetic vectors seem to be in general agreement, especially concerning the more closely related clusters of variables. Thus a consistent picture is available of the genetic relationships among the variables measured. This genetic correlation structure can now be compared with that obtained from phenotypic correlations.

# Chapter 5

## Synthesis

### 5.1 Genetic and Phenotypic Correlations Compared

Having generated phenotypic and genetic correlation matrices, we can now compare them. The two correlation matrices are independent in the sense that they arise from different sources (individual vs. familial correlations). However, as the measurements themselves are all made on the same individuals the two matrices cannot be truely independent. At this exploratory stage it is worthwhile to use measurements on the same individuals so that we can be sure that the two matrices refer to the same gene pool. Replication on other populations can be undertaken at a later stage.

The phenotypic and genetic correlation matrices have each

been summarized by cluster analysis and latent vectors. The easiest way to compare the two sets of solutions is to begin by comparing the two cluster diagrams, followed by a comparison of the latent vectors (components).

The two dendrograms are presented side by side in exhibit 5.1. Ignoring differences in secondary structure, the two trees show the same primary clusters. These common primary clusters are: (1) weight, calf circumference, (2) total facial height, upper facial height, nose length, (3) head length, head breadth, (4) bicondylar humerus, wrist breadth, bicondylar femur, (5) triceps skinfold, subscapular skinfold, (6) stature, sitting height, and (7) foot length, hand length. The two independent variables bigonial diameter and nose breadth remain separate from the other clusters in both trees, although bigonial diameter shifts its position. However, the positioning of variables which have low similarity with all others is fickle. Thus the apparently large movement of bigonial diameter simply serves to emphasize its distinctiveness, rather than suggesting a major difference between the trees. For the same reason, the locations of the tertiary clusters may change from one tree to the next without implying a radically different structure. For this reason the shift of the skinfolds cluster from being closely linked with weight/circumference/trunk breadths in the phenotypic tree, to being completely alone in the genetic tree is not particularly worrying. Again this emphasizes the relative independence of the skinfold measurements from all others, in

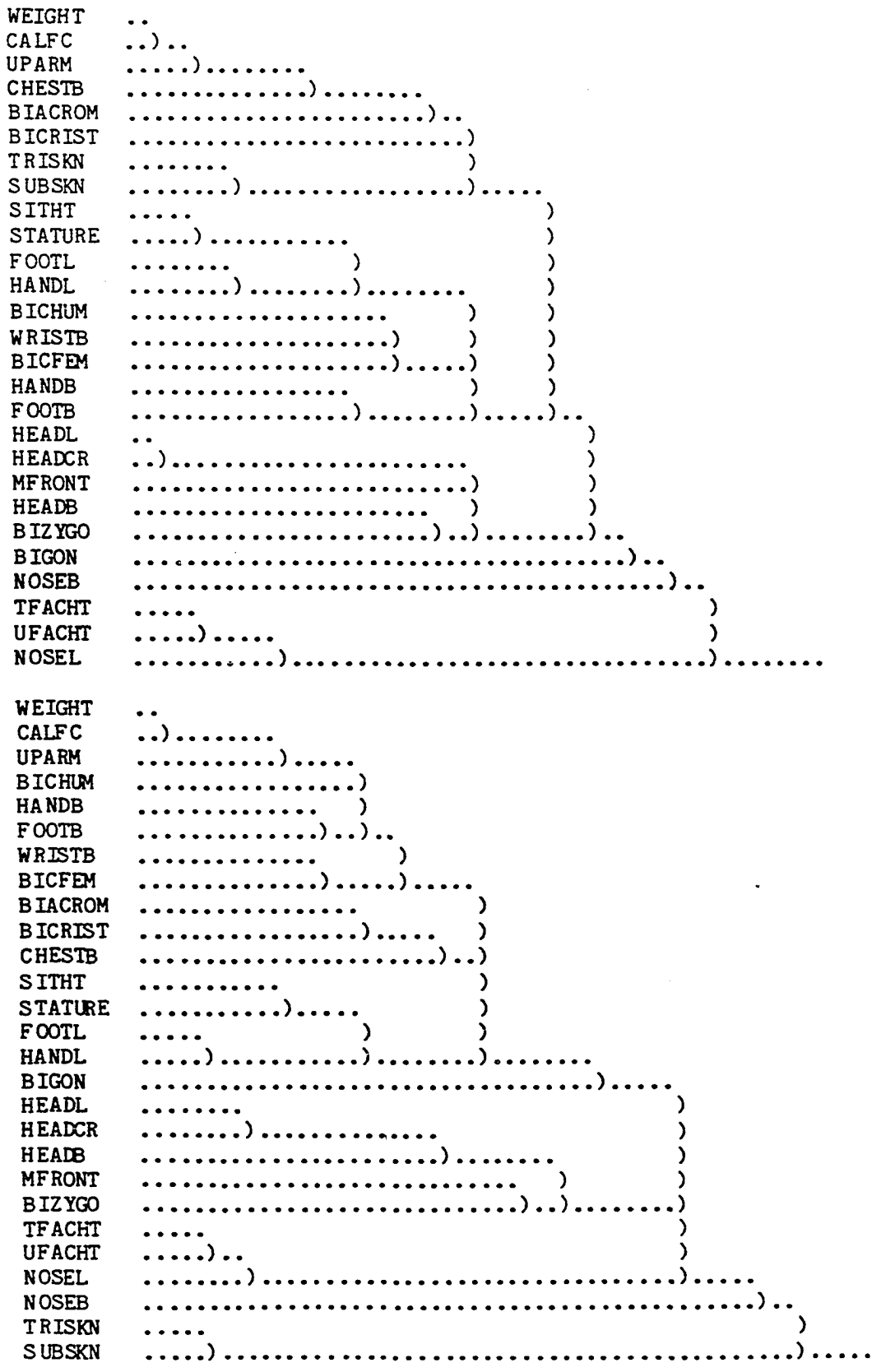



Exhibit 5.1 Phenotypic (above) and Genotypic Clusters

both the genetic and phenotypic cases. It also casts doubt on the idea of a common genetic influence on weight/circumference and skinfolds.

A final difference between the two trees lies in the positioning of extremety breadths. In the tree for genetic correlations extremety breadths are linked to the weight/circumference cluster. There is a separate cluster containing trunk and shoulder breadths (biacromial diameter, bicristal diameter, chest breadth) which is not present in the phenotypic tree. In contrast, the phenotypic tree has the trunk and shoulder breadths only tenuously related to the weight/circumference cluster and there is no suggestion of a "trunk and shoulder breadths" cluster. The view from genetic correlations suggests that the trunk and shoulder breadth area is more closely integrated than is apparent in phenotypic correlations. Similarly, the genetic tree suggests a link between extremety breadths and weight/circumference which is not apparent in the phenotypic correlations. Despite these distinctions, the overall impression is that of a close similarity of the primary clusters.

Turning to the latent vector solutions (exhibits 3.48 and 4.12) it is obvious that the ordering of the components has changed in the two solutions. For this reason Procrustes rotation is of little help. However, there is a clear

correspondence between most of the components. These are listed by an identifying label, followed by the genetic vector number and phenotypic vector number, respectively. The similar components are: (1) linearity [1,3], (2) facial height [3,2], (3) head size [4,4], (4) head and face breadths [10,5], (5) skinfolds [2,7], (6) nose breadth [8,8], and (7) bigonial diameter [6,9]. Contrasts between the two solutions appear in the other components.

Minimum frontal diameter is spread over two (phenotypic) versus three (genetic) components in the two solutions. It appears on its own in the ninth genetic vector, suggesting that it is independent in at least a portion of its variance. Minimum frontal diameter also plays a part in the tenth phenotypic component, where it is contrasted with biacromial diameter and chest breadth. In the phenotypic solution bicristal diameter splits its influence between limb circumference/extremety breadth (component 1) and this tenth component, but neither loading is above 0.3. In contrast, the genetic vector solution excludes biacromial diameter, bicristal diameter and chest breadth entirely. This suggests that the genetic similarity of the trunk breadth measures (reflected in the dendrogram) is outside of the genetic vector solution.

The genetic vector solution has a mixture of weight/circumference with extremety breadths on component five

(along with some other variables). This echoes the cluster solution for genetic correlations, and is similar to the phenotypic component which links extremety breadths and circumferences. Differences creep in, however, because the genetic vector also has significant loadings for wrist breadth, minimum frontal diameter, and bigonial diameter. These last two variables are independents, and minimum frontal diameter has already been mentioned as spreading its influence across several variables. The existance of wrist breadth on this fifth genetic vector highlights a further difference between the genetic and phenotypic solutions. The phenotypic solution includes a component reflecting transverse diameters of limbs (component 7; bicondylar humerus, wrist breadth, bicondylar femur). This component does not appear in the genetic solution. Wrist breadth joins in with the mixed fifth genetic vector, while bicondylar humerus and bicondylar femur do not occur in the solution at all. Nonetheless, these three do appear to be related in the genetic tree. Once again it may be that the similarity of the measures of transverse limb diameters is outside the genetic vector solution.

One other topic which was introduced briefly in Chapter 1.2.4 is the correlation of two physical measurements due to their definition as part and whole. Examples of this situation in the variable set used in this study are: (1) total facial height, upper facial height, nose length, and (2) stature, sitting height. These are defined as parts and wholes in one

individual, and it may be that high phenotypic correlations between them are due to this confounding. However, when stature is measured on one member of a family and sitting height on a different member the parts and wholes dependency is not present. Thus the genetic correlations allow a check against serious dependency due to the definition of measurements. The fact that both of these variable sets show levels of genetic correlation similar to that for phenotypic correlation can be taken as evidence against the influence of measurement definition dependency. This argument can only be developed further once reasonable estimates of environmental correlation have been obtained.

Summarizing what we have learned so far, there is a fairly close agreement between the genetic and phenotypic correlation matrices, as summarized by cluster analysis and PCA-genetic vectors. This is a reassuring finding given the long history of using phenotypic correlations without examining their genetic basis. It is also in marked contrast to the results reported by Cheverud and Buikstra (1981b) for nonmetric skeletal traits, where they report large differences between genetic correlations and phenotypic correlations. This may be because of smaller sample sizes in their study, the use of mother-offspring correlations to estimate heritability (less likely), and a fundamental difference in nonmetric versus continuous traits. It emphasizes the need for this study to be replicated in other areas.

## 5.2 Discrimiant Analysis and Between Group Heritability

It is now time to return to an examination of between group variation. The pattern of between group variation has already been examined by discriminant analysis. Since that point we have travelled through a multivariate maze examining the genetic basis of within population variation. Can the insights gained by studying the heritability of within population variation aid in the interpretation of the genetic basis of between population variation?

Recalling the discussion of between group heritability in Chapter 1.3.1, we see that there is limited value in using the within group heritability estimates. Making a list of highly heritable traits and then seeing how many of these figure in the between group variation is a less than satisfactory approach from a theoretical standpoint. However, it is possible to use equation [1.10] to derive estimates for the heritability of group means. This between group component of heritability can be compared more productively with the pattern of between group variation.

The calculation of the heritability of group means requires estimates for r (the genotypic intraclass correlation) and t (the

phenotypic intraclass correlation), as well as the pooled within group heritability which was obtained in chapter 4.2. The values for pooled within group heritability appear in the first column of exhibit 5.2, followed by the phenotypic intraclass correlation (t). The values of t are quite straightforward to obtain, as they are based on phenotypic values. A value for the genetic intraclass correlation (r) requires a lot more detective work, since genotypic variation cannot be observed directly.

A value for r can be calculated as twice the average F value (Falconer 1960:233) in the sample. F values can be obtained from individual pedigrees, and averaged over the study population. Friedlaender (1975:70) reports a value of F = 0.008 for seven neighboring villages in the Siwai area of Bougainville (an area not included in this study). He comments that the Siwai genealogical data is the best available for Bougainville, but that there are still many shallow genealogies (limited to two generations). Under these circumstances many pedigrees will have an F value of 0, and the average over all pedigrees is a best a lower bound. The value of F=0.008 is certainly in the right range given other estimates for non-Western societies (Spuhler 1967).

The genealogical information from the six study populations was checked for validity and consistency, and loaded into a data base by special purpose programs. F values were computed for

Calculation of between group heritability estimates and the eta-squared values for each variable for males and females.

| | $h^2$ Within | T | Factor | $h^2$ Between | $Eta^2$ M | $Eta^2$ F |
|---|---|---|---|---|---|---|
| WEIGHT | 0.420 | 0.181 | 0.562 | 0.236 | 0.149 | 0.189 |
| SITHT | 0.290 | 0.068 | 1.702 | 0.494 | 0.101 | 0.030 |
| STATURE | 0.248 | 0.129 | 0.839 | 0.208 | 0.099 | 0.141 |
| BIACROM | 0.301 | 0.277 | 0.324 | 0.098 | 0.190 | 0.294 |
| BICRIST | 0.433 | 0.141 | 0.757 | 0.328 | 0.100 | 0.162 |
| CHESTB | 0.583 | 0.294 | 0.298 | 0.174 | 0.235 | 0.290 |
| FOOTL | 0.430 | 0.193 | 0.519 | 0.223 | 0.153 | 0.210 |
| TFACHT | 0.520 | 0.139 | 0.769 | 0.400 | 0.089 | 0.168 |
| UFACHT | 0.843 | 0.353 | 0.228 | 0.192 | 0.252 | 0.389 |
| NOSEL | 0.775 | 0.347 | 0.234 | 0.181 | 0.243 | 0.374 |
| NOSEB | 0.438 | 0.096 | 1.170 | 0.513 | 0.062 | 0.130 |
| BICHUM | 0.404 | 0.246 | 0.381 | 0.154 | 0.207 | 0.240 |
| WRISTB | 0.425 | 0.248 | 0.377 | 0.160 | 0.177 | 0.259 |
| HANDB | 0.673 | 0.374 | 0.208 | 0.140 | 0.293 | 0.400 |
| HANDL | 0.481 | 0.292 | 0.301 | 0.145 | 0.251 | 0.280 |
| BICFEM | 0.294 | 0.108 | 1.026 | 0.302 | 0.086 | 0.110 |
| FOOTB | 0.595 | 0.311 | 0.275 | 0.164 | 0.252 | 0.334 |
| HEADL | 0.562 | 0.149 | 0.709 | 0.399 | 0.175 | 0.106 |
| HEADB | 0.521 | 0.074 | 1.554 | 0.811 | 0.068 | 0.102 |
| MFRONT | 0.537 | 0.037 | 3.233 | 1.737 | 0.042 | 0.028 |
| BIZYGO | 0.523 | 0.172 | 0.598 | 0.313 | 0.136 | 0.188 |
| BIGON | 0.583 | 0.177 | 0.578 | 0.337 | 0.100 | 0.199 |
| HEADCR | 0.521 | 0.051 | 2.311 | 1.204 | 0.035 | 0.078 |
| UPARM | 0.496 | 0.283 | 0.315 | 0.156 | 0.213 | 0.305 |
| CALFC | 0.423 | 0.083 | 1.372 | 0.580 | 0.060 | 0.095 |
| TRISKN | 0.368 | 0.172 | 0.598 | 0.220 | 0.055 | 0.147 |
| SUBSKN | 0.450 | 0.112 | 0.985 | 0.444 | 0.143 | 0.150 |

$$\text{Factor} = \frac{(1 - t)\, r}{(1 - r)\, t}$$

Exhibit 5.2 Between Group Heritability

each individual by a program which accessed the information in the genealogical data base. In three of the populations (Reefs, Kwaio, Lau) the genealogical records were so shallow that all individuals had F values of 0.0. In the remaining groups the values were:

| | |
|---|---|
| Nagovisi | F(ave) = 0.0167 |
| Aita | F(ave) = 0.002 |
| Baegu | F(ave) = 0.0005 |

These values can be taken as a lower bound on the true value of F(ave), and combined into an overall average F of 0.0064. This is comfortingly close to Friedlaender's estimate for the Siwai.

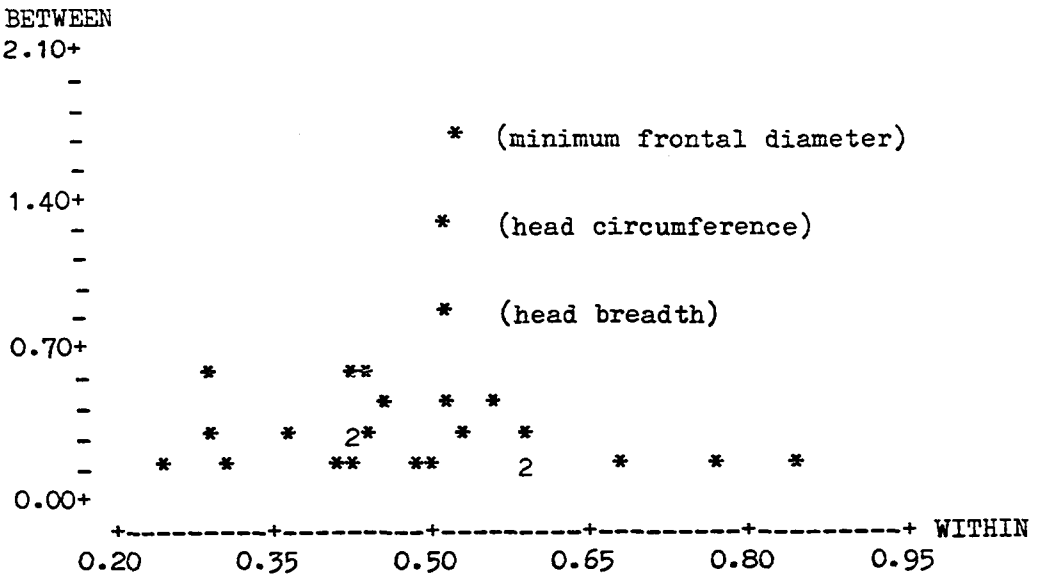
This value of F(ave) is the inbreeding of individuals relative to their subpopulation (F(is)). In addition, members of a subpopulation will share more genes in because of the subdivided population structure (Wright 1968-1977). This additional source of inbreeding can be incorporated into the estimate by calculating F(st), the inbreeding of a subpopulation relative to the total. The value we use for F(st)=0.04916 is based on Friedlaender's work on Bougainville (Friedlaender, et al. 1971; Friedlaender 1975). In using this value we tacitly assume that it is a reasonable estimate from Malaita and the Reef

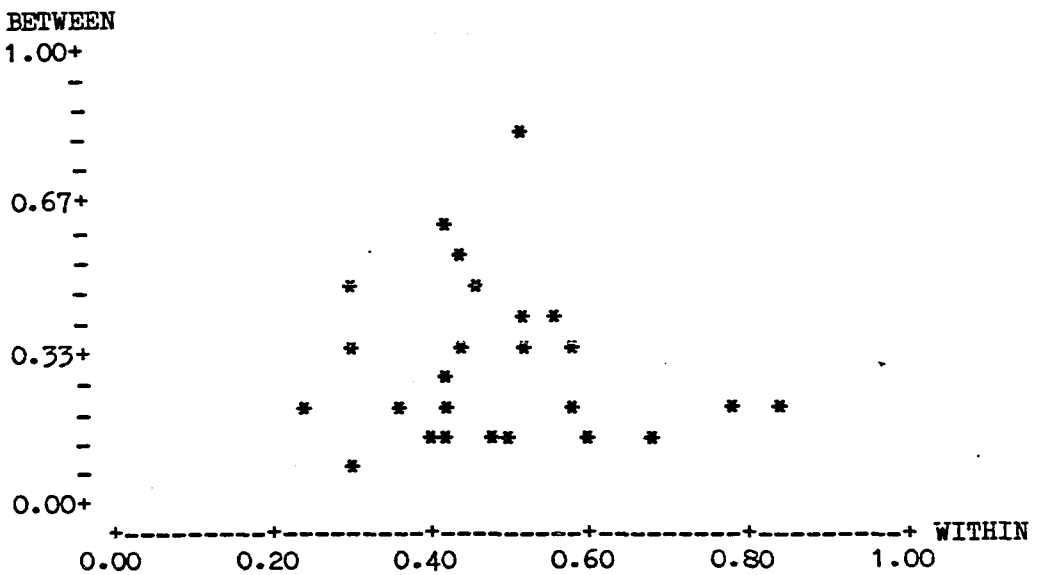
Islands as well. The equation for estimating the inbreeding of the individual relative to the total population (F(it)) is:

$$F(it) = F(st) + F(is)\ (1 - F(st)). \qquad [5.1]$$

Doubling the value of F(it) we obtain the estimate of the parameter r=0.11049. The calculations involved in substituting the value for r into the expression for heritability of group means are shown in the next two columns of exhibit 5.2. The estimates for between group heritability range from 0.09 to 1.73, the later value serving to remind us that these estimates are far from perfect. In fact, considering the number of assumptions (or educated guesses) involved in obtaining an estimate for the parameter r, we have probably been quite lucky. The estimation equation for the heritability of group means is one of the "nasty equations" of population biology which multiplies and divides very small numbers by other equally small numbers (which are both imprecisely estimated), and hopes to come up with an answer in the expected range of 0-1! Accordingly, the values for $h^2_g$ must be seen as very approximate, and perhaps only worthy of gross distinctions such as "high", "medium" or "low". Nonetheless it is impossible to resist the temptation to take them at face value and compare them to the levels of phenotypic variation between groups.

The relationship between the pooled within group heritability and the heritability of group means is plotted in



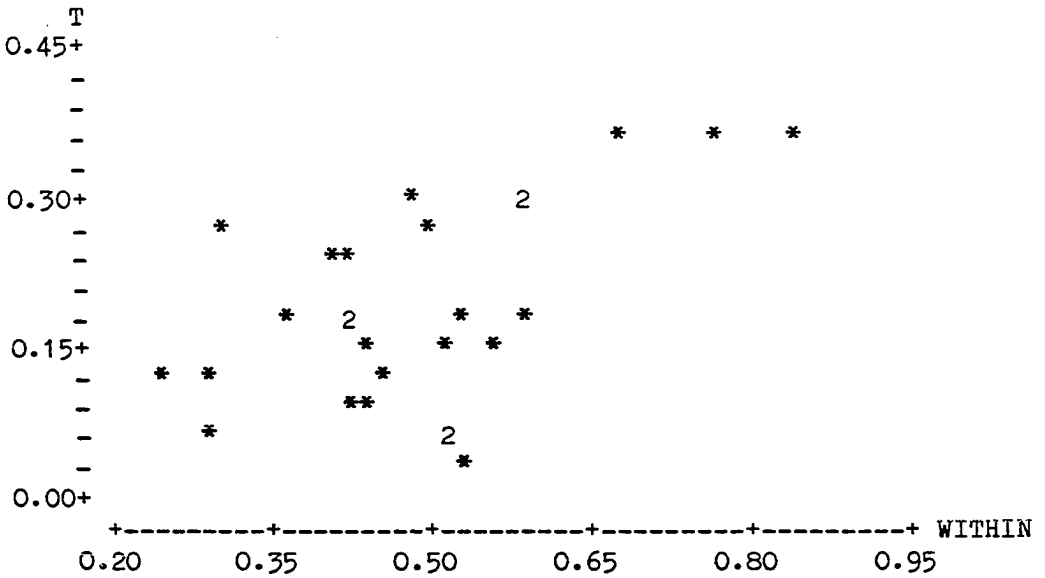



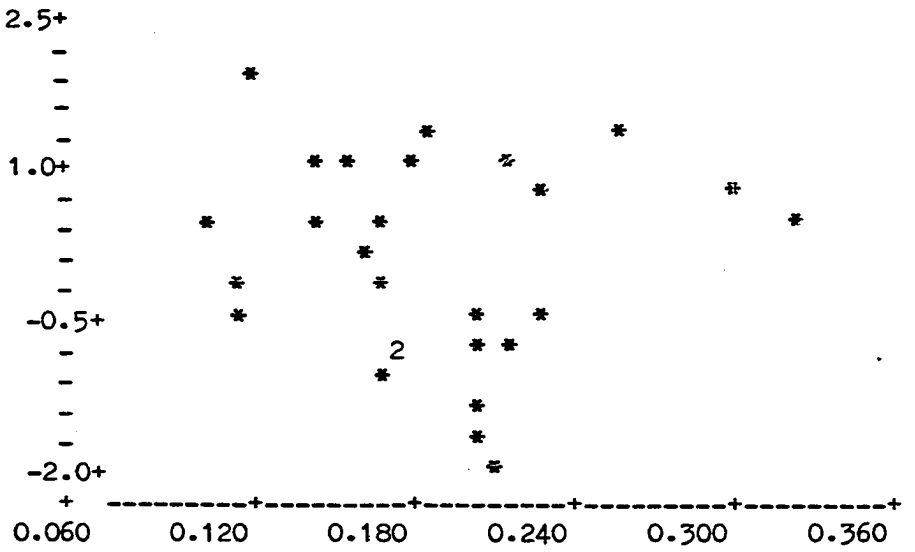

2 POINTS OUT OF BOUNDS

Exhibit 5.3 Plot of within vs. between group heritability

exhibit 5.3. Two variables with between-group heritability estimates over one tend to dominate the display. If these points are deleted the remaining 25 show little relationship between within- and between-group heritability (the lower plot). The linear relationship accounts for less than 11% of the variation in either variable. There is also little relationship between the intraclass phenotypic correlation (t) for a given variable, and its within group heritability (exhibit 5.4). The linear relationship between t and within group heritability accounts for only 3% of the variation in either variable. These two plots emphasize the danger of substituting within group heritability when the heritability of group means should be used.

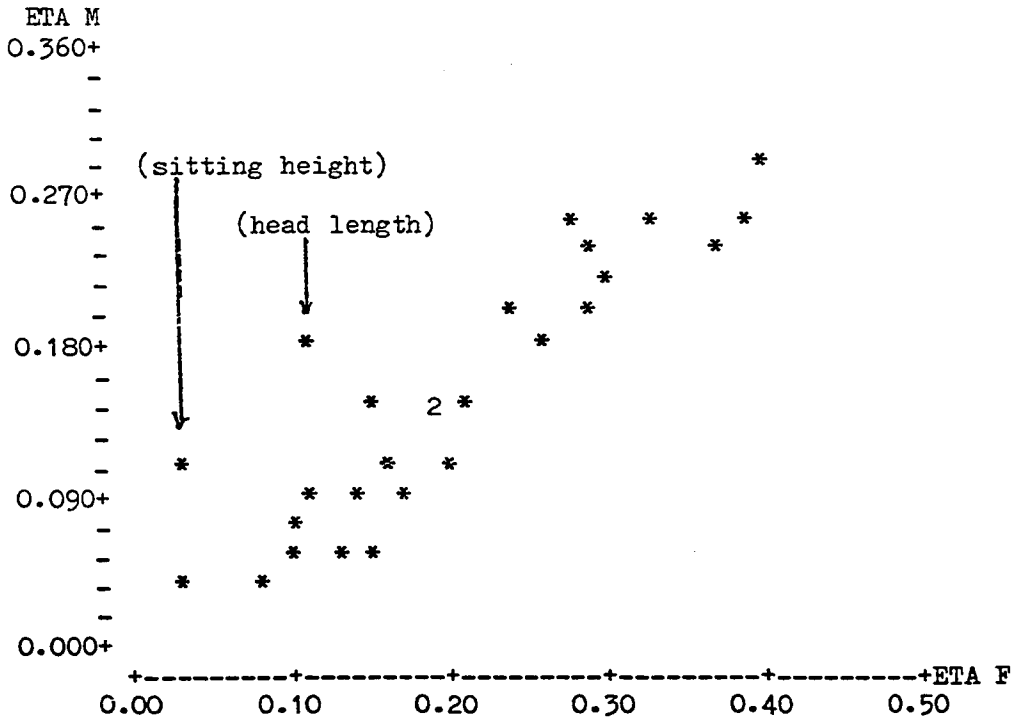
Turning to the relationship between the heritability of group means and the phenotypic variation between groups, we examine the last two columns of exhibit 5.2. These columns contain the eta-squared values for males and females for each variable. This statistic is the ratio of between group to total variation in each trait, larger values indicating greater variability between groups (Blalock 1960:266). As shown in exhibit 5.5 there is a close association between the eta-squared vectors for males and females, particularly among the variables with larger eta-squared values (>0.25). This reconfirms the general similarity of the patterns of male and female between group variation. The two noted exceptions are sitting height and head length which have different levels of between group variation judged by univariate eta-squared values. Note however

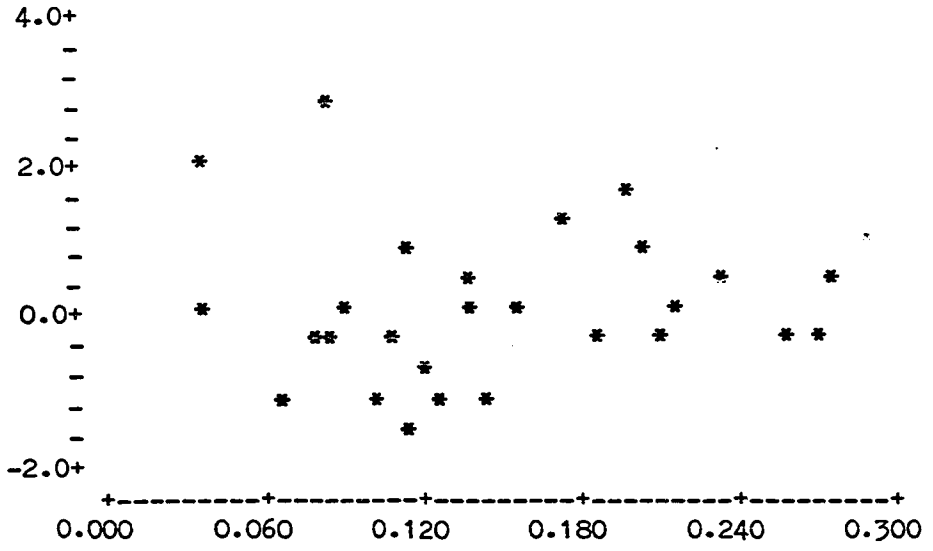



Plot of predicted values against standardized residuals.

Exhibit 5.4 Plot of t vs. within group heritability




Predicted value against standardized residual.

Exhibit 5.5 Plot of eta-squared values for males and females

that the univariate pattern based on eta-squared values does not reproduce the pattern of multivariate residuals following a Procrustes rotation of two discriminant analyses (see pages 132-134).

Between group heritability is plotted against eta-squared values for females (exhibit 5.6) and males (exhibit 5.7). There is obviously some negative relationship between eta-squared value and between group heritability. Once again the two largest values of between-group heritability dominate the plots. When these values are deleted the pattern of the negative relationship is clearer (lower plot). In both sexes this linear relationship accounts for about 50% of the variation in eta-squared. Although this is a comforting percentage in some ways, it still leaves half of the variation unexplained.

The 27 estimates of between group heritability may be ranked and then divided into three sets. These groups will be referred to as "high", "medium" and "low" between group heritability sets. Values greater then 0.6 are classed as "high". Values less than 0.19 are classed as "low". Remaining values are termed "medium".

The high between group heritability set contains the following variables: minimum frontal diameter, head circumference and head breadth. The low heritability set

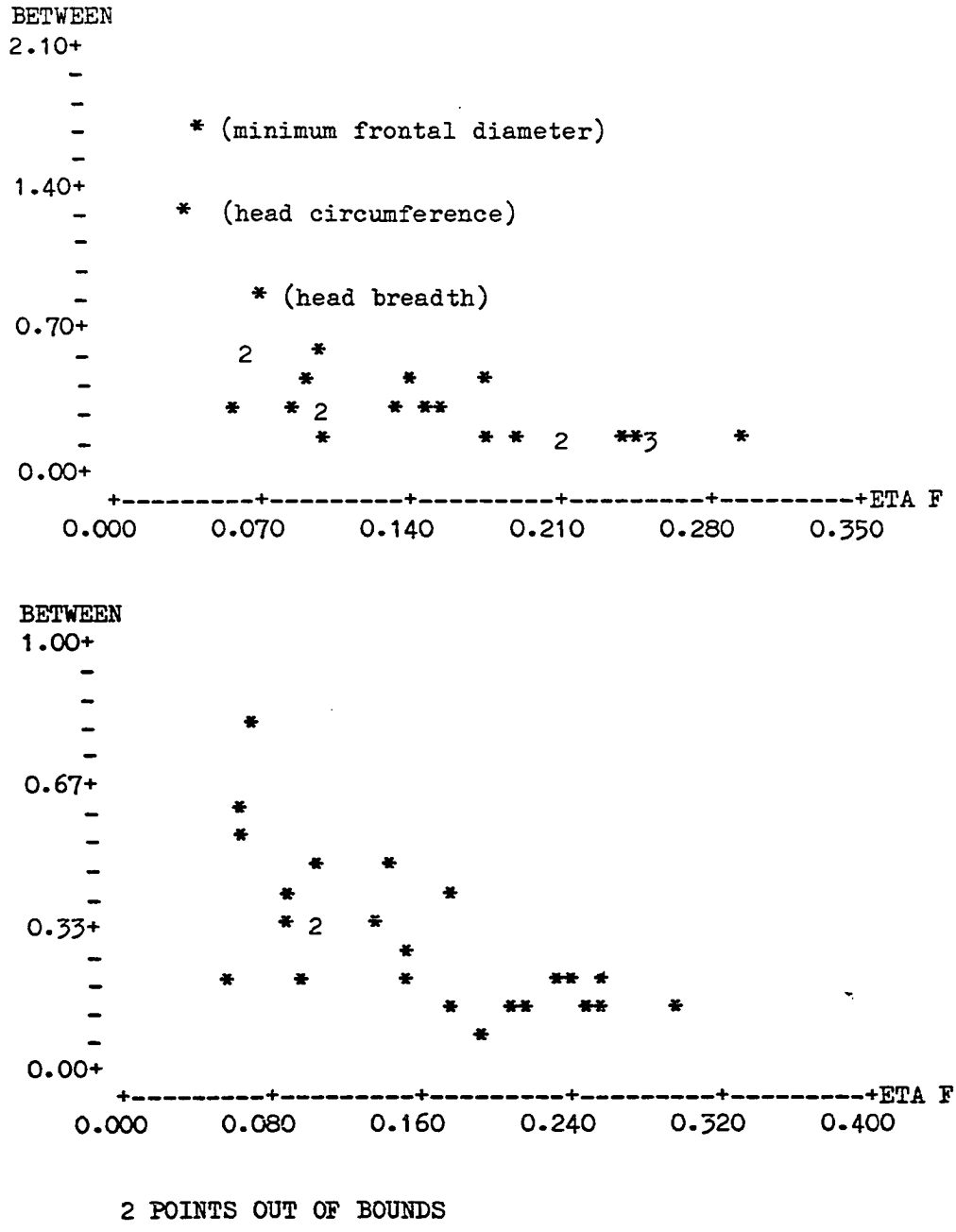



Exhibit 5.6 Eta-squared vs. between group heritability (females)

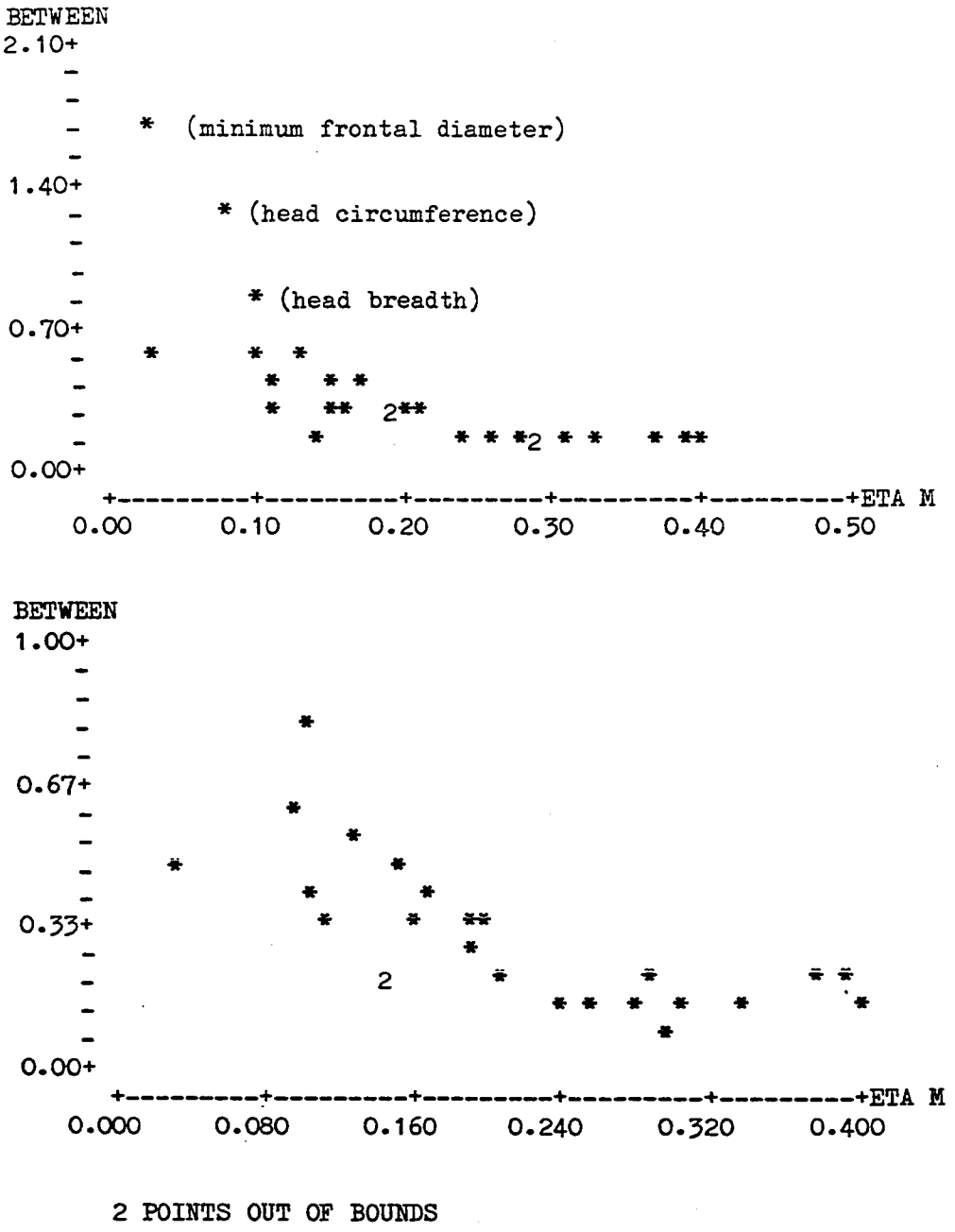



Exhibit 5.7 Eta-squared vs. between group heritability (males)

contains: biacromial diameter, chest breadth, nose length, bicondylar humerus, wrist breadth, hand breadth, hand length, foot breadth, and upper arm circumference.

Examining those variables with the higher eta-squared values (say the ranked upper third in both males and females), the following between-group phenotypic variation appears to be primarily environmental in origin: chest breadth, nose length, bicondylar humerus, hand breadth, foot breadth, and upper arm circumference. The variables with high between-group heritability values are conspicuous by thier absence from the list of high eta-squared variables. This situation in fact points up a danger in relying on univariate eta-squared values in judging which variables make a ccntribution to between-group variation. In the previous discriminant analyses head shape (represented most often by head length and head circumference) played an important role in between group variation. This information has been lost in the examination of eta-squared values for one variable at a time.

Note that the high between group heritability set contains head breadth, which has proved important in the discriminant functions for both sexes, and in discriminant functions derived by Friedlaender (1975) for Bougainville males. In Friedlaender's discriminant functions, head length is paired with head breadth, and highlights differences in head shape (cranial index in fact)

between groups. Head breadth was generally less important in the discriminant analysis results in this study, and apparently replaced in importance by head circumference. Friedlaender (1975:158) interprets differences in head shape as reflecting genetic variation, on the (possibly misleading) grounds that head length and head breadth have relatively high within group heritability values in some other populations. This conclusion is supported by these results, which are correctly based on the heritability of group means. This result looks promising for those who would claim that discriminant analysis is picking up primarily genetic differences in the second discriminant function for both males and females. Unfortunately this simple view is contradicted by the observation that hand breadth and foot breadth are also important in the same function. Between-group variation in hand breadth and foot breadth is judged to be primarily environmental in origin! Taken at face value, this suggests that the discriminant function mixes variables which represent both genetic and environmental group differences. This may in fact be a very successful strategy for maximizing genetic between group differences. Given a positive genetic and phenotypic correlation between head measures and extremety breadths the contrast of these two measurement pairs in the discriminant function may successfully extract the environmental variation in extremety breadths (as if covariates) from the genetic contrast based on the head measurements. This would mean that the canonical variate formed as a weighted combination of the original variables might represent primarily genetic differences. Unfortunately, the univariate study of

between-group heritability cannot illuminate this area further. What is required here is some multivariate generalization of between group heritability which can include the interrelationships between the variables. Such a formulation might start with cross trait intraclass correlations and cross trait heritabilities. However, this is something to be left for future work.

Summarizing the observations made in this section, between group heritability presents a different picture from that of within group heritability. The claim that between group variation is genetic in origin for traits with significant within group heritability may be seriously misleading. In this study upper facial height is an example of a variable with a substantial within group heritability (0.84) but a low between group heritability (0.19). The phenotypic variation between the six populations studied does appear to have a significant genetic basis as judged by the between group component of heritability. In partiular, variation in head circumference, minimum frontal diameter and head breadth between these groups seems to reflect genetic differences. Between group variation in extremety breadths, biacromial diameter, chest breadth and upper arm circumference appears to be primarily environmental in origin. Several facial measures (bizygomatic diameter, bigonial diameter, total facial height) appear to be intermediate in the genetic component of between group variation. Some strong contrasts appear in a single organ. This is demonstrated in the nose where

nose breadth has slightly higher values for between (0.51) than for within (0.44) group heritatibiliy. In contrast, nose length has a substantial value for within group heritability (0.77) but a low between group heritability value (0.18). Clearly there is still much work to be done in relating between group heritabiity to phenotypic differences, especially when several variables are interrelated in some fashion.

## 5.3 Prospects

This work has been directed by two themes concerning the nature of anthopometric variation. The first theme concerns anthropometric variation and covariation within populations, and might be summarized as follows:

phenotypic (co)variation = genetic (co)variation
+
environmental (co)variation
+
residual (co)variation.

This is a rather bald summary of a very complex process, but it is given here to emphasize the need to look beyond phenotypic variation and covariation. In particular, the phenotypic correlation between traits must be decomposed into its component

parts if progress is to be made on the underlying components of physical variation. The examination of genetic correlations in the Solomon Islands data set led to the same picture of covariation between variables as did the phenotypic correlations. This is certainly reassuring, but does not excuse us from examining genetic and environmental components of phenotypic variation in other populations.

The calculation of an environmental correlation matrix between traits was entirely unsuccessful in the Solomon Islands data set. It is not clear why the process failed, but more work clearly needs to be done in this area. In fact, the whole problem of defining and collecting suitable measures of environment reamains the most pressing problem in the study of physical variation and its causes. Although environmental indexing (Morton 1974; Gulbrandsen, Morton, Rhoads, Kagan and Lew 1977; Morton and Chung 1978; Morton and Rao 1978; Rao et al. 1975,1976) makes a start, it is but a small beginning. One particularly difficult problem is that the "environment" experienced by a growing child is actually a series of related events ordered in time. When measurements on children are included in estimates of heritability, the calculations will inevitably become involved with quantities which vary over time. For this reason the calculation of familial correlations must sooner or later consider temporal variation in more detail. Studies of temporal variation in parent-offspring and sib-sib correlations produce a variety of interesting patterns suggesting

transient environmental effects and age limited genes. Likewise, careful attention to the sex of individuals in calculating correlations has led to observed patterns suggesting maternal effects and sex linked genes. At present, however, there is no way to bring this view of the causes of variation in familial correlations into line with the rather static concept of heritability. The population norm or range of reaction (Lewontin 1974, 1975) may ultimately prove a more useful concept than heritability. Longitudinal studies of child growth, which include appropriate measures of environment plus parents measurements, may eventually prove of greater value to understanding the causes of physical variation than studies of adults.

The path models themselves may need to be extended to include factors such as gene-environment covariance, maternal effects, dominance, and genotype-environment interactions. However, it seems to me that simpler models are more likely to be successful in the study of anthropometric variation. Very large samples (and observations on more remote biological relationships) are required to fit the more sophisticated models. But in order to get these larger samples it may be neccessary to include individuals from different subpopulations, a procedure which raises its own problems (see below).

The second theme which has guided this work considers

variation between populations versus variation within populations. The calculation of heritability estimates based on "national" samples (which ignore the differentiation of subpopulations) has been shown to give inflated heritability estimates. In addition, the data from the Solomon Islands has been used to show that the heritability of a trait within a population is not very useful in predicting the proportion of variation between groups which is genetic in origin. The correct statistic for estimating the genetic proportion of betwen group variation is the heritability of group means. The heritability of group means is examined in a univariate fashion in this study, but it is clear that a multivariate generalization is neccessary. This should be an important goal in future work on between group variation.

The pooling of data from six populations was neccessary in the Solomon Islands data set in order to obtain reasonable estimates for genetic correlation matrices. This arises in part because the asymptotic behaviour of the genetic correlation coefficient is to tend to infinity when it should tend to zero. Also, the probability of obtaining genetic correlations outside the range -1.0 to 1.0 increases as the number of measurements increases (Hill and Thompson 1978). These observations raise two points, the first concerning the need for more robust estimation techniques and the second concerning the number of variables examined.

My experiences with the calculation of innumerable correlation coefficients is that they are too susceptible to outliers and non-normally distributed data. Although Tukey (1977) and others (Devlin, Gnanadesikan and Kettenring 1975) have examined the performance of a number of robust correlation-like coefficients, there is still a need for further work in this area. There is also a need for a general reformulation of the genetic and environmental correlation equations in ways which render them less susceptible to giving outrageously large results for traits of essentially zero heritability.

The size of the variable set used in this study has proved a burden, as 27 X 27 matrices are not easy to take in at a glance, or even summarize with a multivariate technique. The idea of measuring everything possible because we never know what will be important (the "shotgun approach") must be replaced by the use of a few selected variables (less than 10 if the matrices are to be manageable). One suggestion which arises from the analysis of the Solomons data is that craniofacial variables be analyzed separately. There appears to be only a low phenotypic or genetic correlation between craniofacial variables and the rest of the body. Separate analysis of craniofacial and body variables using the set of multivariate heritability techniques would lead to two smaller and more manageable matrices. Careful consideration should also be given to choosing the minimal set of variables which are neccessary in a particular analysis. Unfortunately, however, the interesting data on relative proportions is only

likely to emerge when a sufficient number of variables are included.

Finally, the most important prospect for future work is that these techniques be replicated on other populations. As Sewell Wright (1968:141) has observed: "The scientific process consists to a large extent of an indefinitely extended alteration of a priori inferences and empirical tests." The attempt to apply these techniques to other populations will help to identify the deficiencies and weaknesses of the present models and conclusions.

The following is the text of a GENSTAT macro to solve the matrix equations for heritability based on the path model proposed by C.C. Li. The first macro is followed immediately by a second macro which takes the cross trait heritaility matrix and converts it to a genetic correlation matrix. Suitable changes to the declarations in the second macro allow it to produce an environmental correlations matrix.

```
'MACRO' LISOLVE $
''
  SOLVING LI EQUATIONS FOR HERITABILITY

  THIS MACRO EXPECTS THE FOLLOWING STRUCTURES TO HAVE BEEN
  DECLARED IN THE CALLING PROGRAM:

  'POINTER' P = TRAITS          P POINTS TO A LIST OF THE TRAITS.
  'SYMMAT' RPP $ P              CORRELATION BETWEEN PARENTS
  'SYMMAT' RPO $ P              CORRELATION BETWEEN PARENTS AND
                                  OFFSPRING
  'SYMMAT' ROO $ P              CORRELATION BETWEEN OFFSPRING
  'SYMMAT' HSQUARED $ P         HERITABILITES TO BE RETURNED

''
'LOCAL' P,MO,GAMMA
'POINTER' P = TRAITS
'SYMMAT' MO $ P
'SYMMAT' GAMMA $ P
''SOLVE FOR H SQUARED VALUES''
'CALC' HSQUARED = RPO / (0.5 * (1.0 + RPP))
'LINES' 5
'CAPTION'  ''MATRIX OF H SQUARED VALUES''
'PRINT' HSQUARED $ 9.4
''SOLVE FOR GENETIC CORRELATION BETWEEN SPOUSES (MO)''
'CALC' MO = HSQUARED * RPP
'LINES' 5
'CAPTION' ''MATRIX OF GENETIC CORRELATIONS BETWEEN SPOUSES''
'PRINT' MO $ 9.4
''SOLVE FOR COMMON ENVIRONMENT FACTOR GAMMA''
'SYMMAT' GAMMA $ P
'CALC' GAMMA = ROO - (0.5 * (1.0 +MO) * HSQUARED)
'LINES' 5
'CAPTION' ''COMMON ENVIRONMENT FACTOR GAMMA''
'PRINT' GAMMA $ 9.4
'DEVALUE' P,MO,GAMMA
'ENDMACRO'
```

```
'MACRO' GMATRIX $
 ''
   RETURNS A GENETIC CORRELATION MATRIX WHEN SUPPLIED WITH A
   MATRIX OF CROSS TRAIT HERITABILITY VALUES.

   THIS MACRO EXPECTS THE FOLLOWING STRUCTURES TO HAVE
   BEEN DECLARED IN THE CALLING PROGRAM:

    'SYMMAT' RG            GENETIC CORRELATION MATRIX RETURNED
    'SYMMAT' HSQUARED         HERITABILITIES TO BE SUPPLIED
    'SYMMAT' SERROR      STANDARD ERRORS OF GENETIC CORRELATIONS
    'POINTER' P = TRAITS      P POINTS TO A LIST OF THE TRAITS
    'SYMMAT' R           PHENOTYPIC CORRELATIONS TO BE SUPPLIED
    'SCALAR' N                NUMBER OF OBSERVATIONS

   RETURNS STANDARD ERROR = 10 FOR NEGATIVE VARIANCE ESTIMATES
 ''
'LOCAL' DVEC,DENOM,TEMP1,HVEC,DRECIP,HVALS,HVALST,SUMS,SIGLEV
'MATRIX' SIGLEV $ P,P
'DIAGMAT' DVEC $ P
''EXTRACT DIAGONAL OF H SQUARED VALUES''
'CALC' DVEC = HSQUARED
''FORM A MATRIX OF SUITABLE DENOMINATORS''
'VARIATE' HVEC $ P
'MATRIX' DENOM $ P,P
'EQUATE' HVEC = DVEC
'CALC' DENOM = PDTT(HVEC;HVEC)
'CALC' DENOM = SQRT(DENOM)
''ELEMENT DIVIDE H SQUARED BY DENOMINATOR''
'CALC' RG = HSQUARED/DENOM
'LINES' 5
'CAPTION' ''GENETIC CORRELATION MATRIX''
'PRINT' RG $ 9.4
''
  COMPUTE THE STANDARD ERRORS FOR GENETIC CORRELATIONS USING THE
  FORMULA GIVEN BY TURNER AND YOUNG P.127
  PLACE HiHj IN DENOM FOR C
''
'CALC' DENOM = PDTT(HVEC;HVEC)
''SET UP RECIPROCAL OF D''
'SYMMAT' DRECIP $ P
'MATRIX' SUMS,HVALS,HVALST $ P,P
'EQUATE' HVALST = 27(DVEC)
'CALC' HVALS = TRANS(HVALST)
'CALC' HVALS = 1.0 / HVALS
'CALC' HVALST = 1.0 / HVALST
'CALC' SUMS = HVALS + HVALST
'CALC' DRECIP = 0.5 * SUMS
'DEVALUE' SUMS,HVALS,HVALST
''WORK ON STANDARD ERRORS IN SEVERAL STEPS''
'CALC' SERROR = (( RG * DRECIP ) - ( R / DENOM ))
'CALC' SERROR = 4 * SERROR * SERROR        ''LAST TERM''
'SYMMAT' TEMP1  $ P
'CALC' TEMP1 = 2*( 1 - (RG*RG))*(1 - (R*R)) / (DENOM*DENOM)
```

```
'CALC' TEMP1 = (0.5 * ((1 - (RG * RG))**2)) + TEMP1
'' FIRST TERM ''
'CALC' SERROR = (TEMP1 + SERROR) / N
''SET VARIANCE TO 100 IF .LE. 0''
'CALC' SERROR = (SERROR.GT.0)*SERROR + (SERROR.LE.0)*100.0
'CALC' SERROR = SQRT(SERROR)
'LINES' 5
'CAPTION' ''STANDARD ERRORS FOR GENETIC CORRELATIONS''
'PRINT' SERROR  $ 9.4
'DEVALUE' P,DVEC,HVEC,DENOM,DRECIP,TEMP1
'LINES' 5
'CAPTION' ''NON ZERO ELEMENTS OF RG MARKED AS 1.0''
''
  TEST SIGNIFICANCE OF ELEMENTS OF GENETIC CORRELATION MATRIX
  AGAINST THE STANDARD ERROR OF THAT ELEMENT
''
'CALC' SIGLEV = (RG .GE. (2.0 * SERROR))
'PRINT' SIGLEV $ 3.0
'ENDMACRO'
```

The text of a GENSTAT macro to perform extraction of genetic vectors by the method of Hashiguchi and Morishima (1969) is included here. It also extracts latent roots and vectors from the phenotypic correlation matrix for comparison with the genetic vectors.

```
'MACRO' GENVEC $
''
  GENETIC VECTORS BY THE METHOD OF HASHIGUCHI AND MORISHIMA
  BIOMETRICS 25:9-15.    (1969).

 THE MACRO ASSUMES THE FOLLOWING STRUCTURES HAVE BEEN DECLARED IN
 THE CALLING PROGRAM:

 'SCALAR' NUMVEC            NUM OF GENETIC VECTORS TO ROTATE
 'SCALAR' TOTVEC            TOTAL NUMBER OF VARIATES IN ANALYSIS
 'SYMMAT' R $ TRAITS        PHENOTYPIC CORRELATIONS
 'SYMMAT' RG $ TRAITS        GENETIC CORRELATIONS
 'NAME' TRAITS               POINTS TO NAMES OF TRAITS
 'VARIATE' HVEC $ TRAITS     VECTOR OF HERITABILITY ESTIMATES
                                FOR TRAITS
 'MATRIX' ROTATED $ TRAITS,NUMVEC  ROTATED GENETIC VECTORS
 'MATRIX' ROTATEDP $ TRAITS,NUMVEC  ROTATED PHENOTYPIC VECTORS
 'MATRIX' GVECTORS $ TRAITS,TRAITS    FULL GENETIC VECTORS MATRIX
''
'LOCAL' LOADINGS,VECTORS,EVALUES,TRCE,GVEC(1...TOTVEC),
        PERCENT,H1,H2,LROOT(1...TOTVEC),BITS(1...TOTVEC),
        TEMP(1...TOTVEC),TRANSLOAD,GENHSQR
'VARIATE' GENHSQR
'MATRIX' VECTORS $ TRAITS,TRAITS
'DIAGMAT' EVALUES, PERCENT $ TRAITS
'SCALAR' TRCE
''
  EIGEN ANALYSIS OF R
''
'LRV' R;VECTORS,EVALUES,TRCE
'LINES' 5
'CAPTION' ''** PHENOTYPIC LATENT ROOTS AND PERCENT OF TRACE **''
'PRINT/LABC=1' EVALUES $ 9.4
'LINES' 1
'CALC' PERCENT = 100.0 * EVALUES / TRCE
'PRINT/LABC=1' PERCENT $ 9.2
'LINES' 2
'CAPTION' '' ** PHENOTYPIC LATENT VECTORS (COLUMNWISE) ** ''
'PRINT/LABC=1' VECTORS $ 9.4
''
  FIND HERITABILITY OF LATENT ROOTS

  BEGIN BY BUILDING K*SIGMA-G*K IN H1
''
'CALC' HVEC = SQRT(HVEC)
'MATRIX' H1,H2 $ TRAITS,TRAITS
```

```
'EQUATE' H1 = HVEC
'CALC' H2 = TRANS(H1)
'CALC' H1 = H1 * H2 * RG
''
  NOW PREMULT BY THE TRANSPOSE OF VECTORS TO GET THE (ROW WISE)
  GENETIC VECTORS
''
'CALC' GVECTORS = TPDT(VECTORS;H1)
''
  NOW SCALE THE GENETIC VECTORS BY THE LATENT ROOTS FROM R
''
'VARIATES' GVEC(1...TOTVEC) $ TRAITS
'SCALAR' LROOT(1...TOTVEC)
''
  UNRAVEL ROW WISE INTO VARIATES
''
'EQUATE' GVEC(1...TOTVEC) = GVECTORS
'EQUATE' LROOT(1...TOTVEC) = EVALUES
'CALC' GVEC(1...TOTVEC) = GVEC(1...TOTVEC) / LROOT(1...TOTVEC)
''
  TRANSPOSE BACK INTO GVECTORS SO A COL IS A GENETIC VECTOR
''
'EQUATE' GVECTORS = GVEC(1...TOTVEC)
'CALC' GVECTORS = TRANS(GVECTORS)
'LINES' 5
'CAPTION' '' ** GENETIC VECTORS (COLUMNWISE) ** ''
'PRINT/LABC=1' GVECTORS $ 9.4
''
  COMPUTE HERITABILITY OF GENETIC VECTORS

  UNRAVEL VECTORS INTO VARIATES GVEC
''
'CALC' VECTORS = TRANS(VECTORS)
'VARIATES' TEMP(1...TOTVEC) $ TOTVEC
'SCALAR' BITS(1...TOTVEC)
'EQUATE' GVEC(1...TOTVEC) = VECTORS
'CALC' TEMP(1...TOTVEC) = PDT(H1;GVEC(1...TOTVEC))
'CALC' BITS(1...TOTVEC) = TPDT(TEMP(1...TOTVEC);GVEC(1...TOTVEC))
''
  SCALE BITS BY EIGENVALUES IN LROOT
''
'CALC' BITS(1...TOTVEC) = BITS(1...TOTVEC) / LROOT(1...TOTVEC)
'EQUATE' GENHSQR = BITS(1...TOTVEC)
'LINES' 3
'CAPTION' '' ** HERITABILITY OF GENETIC VECTORS ** ''
'PRINT/LABR=1,VAR=1' GENHSQR $ 9.4
''
  PREPARE TO VARIMAX ROTATE THE FIRST NUMVEC GENETIC VECTORS
  SAVING THE LOADINGS VECTORS IN MATRIX ROTATED
''
'MATRIX' LOADINGS  $ TRAITS , NUMVEC
'MATRIX' TRANSLOAD $ NUMVEC , TRAITS
''
  PLACE GVECTORS BACK INTO GVEC AND THEN GRAB THE FIRST NUMVEC
```

```
  COLS FOR THE ROTATION
''
'CALC' GVECTORS = TRANS(GVECTORS)
'EQUATE' GVEC(1...TOTVEC) = GVECTORS
'EQUATE' TRANSLOAD = GVEC(1...NUMVEC)
'CALC' LOADINGS = TRANS(TRANSLOAD)
'FACROT' LOADINGS;ROTATED
'CAPTION' '' GENETIC VECTORS   ***** ''
'PRINT' ROTATED $ 9.4
''
  PREPARE TO VARIMAX ROTATE THE FIRST NUMVEC PHENOTYPIC VECTORS

  UNRAVEL VECTORS COLUMNWISE INTO VARIATES GVEC REMEMBERING
  THAT VECTORS HAVE ALREADY BEEN TRANSPOSED
''
'EQUATE' GVEC(1...TOTVEC) = VECTORS
'EQUATE' TRANSLOAD = GVEC(1...NUMVEC)
'CALC' LOADINGS = TRANS(TRANSLOAD)
'FACROT' LOADINGS;ROTATEDP
'CAPTION'   '' PHENOTYPIC VECTORS   ***** ''
'PRINT' ROTATEDP $ 9.4
'DEVALUE' LOADINGS,GVEC(1...TOTVEC),LROOT(1...TOTVEC),
          PERCENT,BITS(1...TOTVEC),TEMP(1...TOTVEC),
          TRANSLOAD,GENHSQR,
          H1,H2,VECTORS,EVALUES,TRCE
'ENDMACRO'
```

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