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I am submitting herewith a dissertation written by Samantha M. Hens entitled "Stature Estimation in Fossil Hominids." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Anthropology.

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We have read this dissertation
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Associate Vice Chancellor
and Dean of The Graduate School

Stature Estimation in Fossil Hominids

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Samantha M. Hens

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Dedication

This work is lovingly dedicated
to those who have waited so long.

My mother, Elaine,
for her support, encouragement and love.
You are my best friend.

My brother Joe and his family,
Monica, David and Eric
for smiles, laughter and so much to come home to.

Finally, although they do not understand the words,
they feel the emotion behind them,
Cherokee, Alex and Sinje (because the heart does go on),
for enriching the quality of my life
and easing the loneliness.

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Abstract

Researchers have long appreciated the significant relationship between body size and an animal's overall adaptive strategy and life history. However, much more emphasis has been placed on interpreting body size than on the actual calculation of it. One measure that is especially important for human evolutionary studies is stature. References to stature estimation can be found in the literature from over one hundred years. Despite this long history, stature estimation remains plagued by two methodological problems: 1) the choice of statistical estimator, and 2) the choice of reference population upon which to derive the parameters.

This work addresses both of these problems. Three reference samples of known stature with maximum humerus and femur lengths recorded are used in this study: a large (N=2,209) modern human sample from North America, a smaller sample of modern African pygmies (N=19) from West Africa and a sample of African great apes (N=85). First, the performance of five commonly used regression models is examined: classical calibration, inverse calibration, major axis, reduced major axis and the zero intercept regression (ratio) model. These five techniques are rigorously tested in both univariate and multivariate categories for their ability to predict stature in situations where there is both extrapolation beyond the mean of the reference sample and differences in limb proportions. The performance of the five estimators is measured using both the root mean squared error and bias. Stature is also estimated for two well-known fossil

hominids, A.L. 288-1 ("Lucy") and KNM-WT 15000 ("The Boy") using parameters derived from the reference samples.

Results indicate that the choice of regression estimator remains unclear in situations where the allometry differs between the reference population and the sample population, which is often the case with fossil remains. Classical calibration performed best in almost all multivariate analyses of stature. However, results varied between the reduced major axis, inverse calibration and ratio models in univariate situations.

Results of the fossil stature estimations vary depending on whether the data is univariate or multivariate. When estimating the stature of A.L. 288-1, results indicate that because of unique limb proportions, the human pygmy sample works best with the univariate data, but the chimpanzee sample came closest to Lucy's actual stature with multivariate data. However, since the limb proportions of the Nariokotome Boy are well within the modern human range, the large sample of modern humans was the best reference sample and the ratio model and the classical calibration estimator provided the closest estimates of stature to published values.

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Chapter 1

Introduction

Biologists have long recognized the significance of body size in relation to an animal's overall adaptive strategy. During an address to the American Society of Naturalists, Hutchinson (1959) postulated that much of the diversity of life could be explained by differences in body size. Even earlier in time, Haldane (1932: 18) discusses how each animal has a "most convenient size" and how through evolution by natural selection, animals increase their surface area in proportion to volume. Research on mammalian paleoecology has relied heavily on body size as a useful predictor of an individual's or a species' adaptations. The relationship between body size and ecological factors assists in making inferences about more complex and diverse life history issues, i.e. social behavior, feeding behavior, energetic costs of locomotion and physiological correlates (Damuth and MacFadden, 1990; Fleagle, 1978; Martin, 1990).

An organism's body size and the range in size within and between taxa are easily observed. However, the factors that determine body size are not so obvious (Roff, 1981). Several researchers have worked to show the relationship between body size and other morphological, biomechanical, physiological, ecological and demographic features (Barbault, 1988; Bonner, 1988; Calder, 1984; Clutton-Brock and Harvey, 1977, 1983; Ford, 1984; Peters, 1983; Roff, 1981; Smith, 1985; Went, 1968). Clutton-Brock and Harvey (1983) examine the relationship between body size and a host of other variables including: reproductive rate, maternal investment, climate, predation, food handling,

feeding range, energetic requirements, food quality and interspecific competition among a variety of mammals. Although the specific relationships between any of the variables and body size may not be completely understood, it is clear that in order to understand an animal's adaptation and evolution, size must be taken into account (Jungers, 1990b). Indeed, Damuth and MacFadden (1990) believe the most useful single predictor of a species' adaptations is body size.

Physical anthropologists, in particular, are interested in estimating body size in both extant and extinct primates, including hominid fossils. Biological anthropologists have related body size to dietary adaptations (Fleagle, 1978; Kay, 1984, 1985), positional behaviors (Aiello, 1981; Jungers, 1982, 1984) and brain size/degree of encephalization (Conroy, 1987; Gingerich, 1977; Hofman, 1983; Jerison, 1973; McHenry, 1975, 1976, 1982, 1988; Radinsky, 1974). While studies examining these relationships are important, they all rely on accurate predictions of body size, especially for fossil remains, which are often fragmented and incomplete.

Body mass or weight, is the most commonly used measure of body size. Mass is an excellent measure of total volume and does not depend on shape (Hills and Wood, 1984; Jungers, 1984, 1990b), making it one of the single best measures for representing overall size (Smith, 1993b). An extensive literature has been generated by using estimates of body weight in allometric studies of brain size (Jerison, 1973; McHenry, 1976, 1982, 1988; Radinsky, 1974), dental dimensions (Fleagle, 1978; Jungers and Grine, 1986; McHenry, 1982, 1984a, 1988; Wolpoff, 1973), and bipedalism and limb proportions (Aiello, 1981; Jungers, 1978, 1982, 1984, 1985b, 1988 a,b,c; McHenry 1978,

1982, 1986a, 1992a,b). With such wide usage, it would seem that body weight would not be a problematical character to estimate from fossil specimens (Damuth and MacFadden, 1990). However, due to the fragmented and incomplete fossil remains, researchers focus on different cranial and postcranial elements to estimate overall body weight. Problems also exist in the choice of reference sample and regression equations upon which to base the estimations.

Another measure of body size and an important component in its own right, especially for humans and our bipedal ancestors, is stature or body length. The estimation of adult stature from skeletal remains is a part of the reconstruction of the individuals' physique during life, provides an impression of size and clearly influences body weight. While body weight may be difficult to estimate, stature is simpler. The length of the long limb bones was found to be highly correlated with stature, especially the weight bearing bones of the lower limbs (Trotter and Gleser, 1952, 1958). Several regression equations have since been proposed by which stature can be estimated using the limb bones, particularly the femur. However, the relationship between stature and long bone length may differ among populations and as a consequence, population specific regression equations are often used for individuals from different populations. Several researchers have attempted stature reconstructions on fossil specimens (Geissmann, 1986; Leakey and Walker, 1985, Lovejoy and Heiple, 1970; McHenry, 1974; Trinkaus, 1981, 1983; Wolpoff, 1973). The recovery of fossil specimens with smaller body sizes, out of the range of modern human reference samples and with clearly distinct body proportions, has complicated attempts at stature reconstruction even further (Johansen et al., 1987;

Johansen and White, 1979; Jungers, 1988c). To combat these problems, researchers derived alternate procedures involving the use of reference populations that are more similar in size to the fossil specimens (e.g. human pygmies, great apes) and various regression models including the Model II regression techniques in addition to the more traditional Model I type regressions (Feldesman, 1992; Feldesman et al., 1989,1990; Feldesman and Lundy, 1988; Jungers, 1988c; Olivier, 1976). This classification of regression models into type I equations and type II equations is explained by Graybill (1961). Graybill describes the differences between the two classifications: where Model I is defined as the regression of an observable variable (y) onto known variables (X) and unknown parameters (β) with an error term (ε) and is written as:

$$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + ... + \beta_k X_k + \varepsilon$$

The Model II classification is a functionally related model with each of the variables subject to measurement error. Here, Y^* and $X_1^*,..., X_k^*$ are not observable, but y and $x_1,..., x_k$ can be observed where $y = Y^* + \varepsilon$ and $x_i = X_i^* + \varepsilon$. This model takes the form:

$$Y^* = \beta_0 + \beta_1 X_1^* + \beta_2 X_2^* + ... + \beta_k X_k^*$$

The Model I type regressions are commonly known as ordinary least squares regressions, while the Model II type regressions are known as the major axis (principal axis) and reduced major axis regressions. Further detail describing these models is incorporated into Chapter 2 - Statistical Considerations in Body Size Estimation.

Statement of Purpose

Since body size is an important aspect of an organism's adaptation and evolution, both taxonomic and behavioral reconstructions are hampered without accurate and reliable estimates of the relevant parameters. The estimation of these parameters (weight, stature) involves the use of different statistical approaches. More emphasis has been placed on interpreting body size than on the calculation of it. This dissertation addresses univariate and multivariate models for predicting stature in fossil hominids. Two major issues in stature estimation are explored: 1) the choice of regression estimator, and 2) the choice of reference sample. Shea (1995) acknowledges that the fitting of a line to the relationship and the choice of reference sample are usually considered purely statistical issues. However, Shea points out that these methodological concerns should be grounded in the biology of organisms. He indicates that preference for a particular regression model should be based on biological factors, and the decision to utilize a particular reference sample should also be based on the biological context.

A review of the appropriate literature reveals five models most commonly used in stature estimation. These estimators include both the Model I and Model II type equations: standard least squares regression of x on y and y on x, major axis and reduced major axis regressions and lastly, a zero intercept regression (ratio) model relating stature to long bone length. The ability of these five models to predict stature is rigorously tested in this dissertation in scenarios of extreme extrapolation and differing allometries. At first this analysis may appear unreasonable, however, it is deemed valuable because the

fragmentary nature of the fossil record may not always allow for an understanding of the allometry of extinct specimens who have no modern representative. Likewise, even when the allometric relationships are known, fossil specimens do not belong to any living reference population. Thus, the second issue, choice of reference sample, becomes an important one. This study uses three comparative reference samples: a large sample of modern humans (Americans of European and African ancestry), a smaller sample of modern human pygmies from West Africa, and a sample of African great apes.

In order to test the predictive ability of the five estimators under rigorous conditions, the parameters derived from the modern human sample (excluding pygmies) are used to estimate stature in the great ape sample and the great ape regression parameters are used to estimate stature in the large modern human sample. Both univariate and multivariate analyses are included. The next step is to determine which regression model provides the best estimates of stature on two well-known fossil hominids: A.L. 288-1 ("Lucy") and KNM-WT 15000 ("The Boy"). Due to the extreme extrapolation necessary for the Lucy specimen, the five models are tested on human pygmy and great ape reference samples. However, The Boy's stature and limb proportions are shown to be well within modern human ranges and his stature is estimated from the large modern human sample.

This brief introductory chapter is followed by a review of the literature. Chapter 2 considers in detail the five regression models tested in this thesis. An examination of the theoretical background behind each estimator is essential for an understanding of their subsequent performances in this study. Chapter three has three parts. The first and

longest section reviews the historical background of stature estimation in physical anthropology. The second section provides a brief review of some of the most significant studies in weight estimation and their importance in the study of body size. Finally, a discussion of the relevant allometric literature pertaining to the fossil hominids examined here is included. The samples, measurements and statistical methods used in this study are described in Chapter 4 followed by the results of the present analysis (Chapter 5) and discussion (Chapter 6).

Chapter 2

Statistical Considerations in Body Size Estimation

Introduction

The estimations of body length and body weight are essential for providing an impression of size for individuals, populations, or taxa. These estimations are also useful in biomechanical research. Body size comparisons between taxa can test hypotheses about functional and adaptive significance in morphology, behavioral variation, and size prediction. However, certain methodological problems must first be addressed.

This section addresses the statistical problem of fitting a straight line to a two dimensional cluster of points by providing a summary of possible models and their pitfalls. Researchers customarily use three statistical models: least squares regression, major axis analysis, and reduced major axis analysis. The recent development of a long bone/body size ratio warrants a discussion of its usefulness in body size estimation.

Before exploring these models in detail, I must lay some groundwork. The next section briefly describes some basics about line fitting, including: error terms, dependence, and correlation. This is followed by a detailed discussion of each of the regression models used in this study.

Aspects of Line Fitting

A linear relation is often sought because there is some *a priori* suggestion that the sample comes from a population with an underlying linear relationship. Logic then dictates fitting a line to the sample in order to clarify the relationship (Rayner, 1985). With biological data, two main types of error affect the observed variables (x and y): measurement error and error due to "real" biological variation. Measurement error in x and y is assumed to be uncorrelated unless evidence exists to the contrary (Rayner, 1985). Harvey and Mace (1982) show that error results from a lack of dependence. If two variables cannot be explained by each other, but can be somewhat explained by a third variable, dependence does not exist. They are not independent and dependent variables. The error found in one variable may result from a lack of total dependence on the second variable. Smith (1994b) states that measurement error may not be as difficult to model as it appears. The statistical theory behind measurement error is based on random imprecision and inaccuracy of measurement as typically found in the physical sciences, not the meaningful deviations from a perfect bivariate relationship seen in biological measures.

If one assumes a normal distribution of data points and a linear relationship, it is important to emphasize the distinction between strength (correlation) and form (parameters of the best fit line) (Harvey and Mace, 1982). The correlation coefficient will decrease as the amount of error variance increases. So the correlation coefficient should not necessarily be a component for calculating the best fit line. Before choosing the best

fit line, it is also important to distinguish between intraspecific scaling and interspecific scaling (Martin and Barbour, 1989). Intraspecific scaling involves all points derived from a single species. Intraspecific scaling can be ontogenetic, where the points refer to individuals at different stages of development, or inter-adult, where the sample shows correlated variation in body size and in the measurement being increased. In interspecific scaling, each point represents the average values determined for a single species. In the total distribution, each point is a target for the individual species, and the overall pattern represents the result of speciation and evolutionary change.

Model Comparison

The different approaches to line fitting can result in major distinctions in biological interpretation. Pearson (1899) first introduced least squares regression to estimate stature from skeletal measurements (see also: Haldane, 1950). Today, the wide availability of standard least squares regression in statistical software packages makes it one of the most commonly used models. Least squares regression minimizes the sum of squared residuals. This works well with a unilateral causal relationship, where one character causes another, but the causality cannot be reversed. LSR assumes that there is measurement error only in the dependent variable and not in the independent variable. The LSR of y on x minimizes the vertical departures from the line (Fig. 1). This has the advantage of ease of calculation, but it is an asymmetrical approach to line fitting. Thus, LSR is known as a Model I type regression (Martin and Barbour, 1989; Harvey and

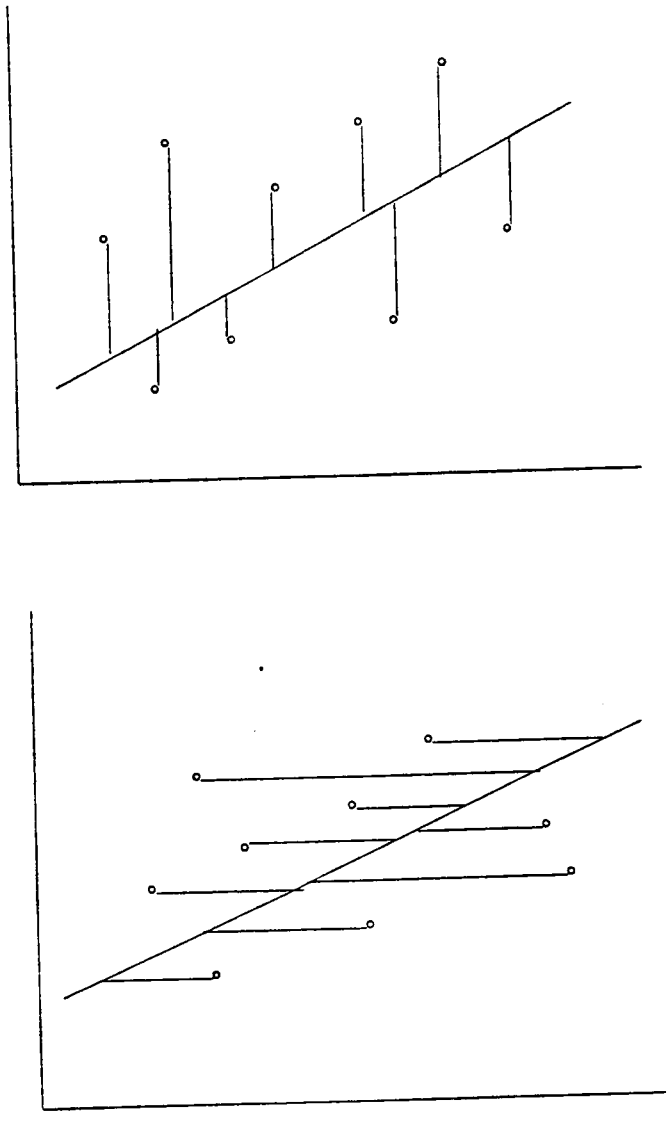

Figure 1. Differences between the two least squares regression lines determined for a bivariate data set showing a weak linear relationship (r = 0.45). The least squares regression of y on x (top) minimizes the sum of the squared deviations in a vertical dimension. The least squares regression of x on y (bottom) minimizes the sum of the squared deviations in a horizontal direction.
Source: Adapted from Martin RD, and Barbour AD (1989) Aspects of line-fitting in bivariate allometric analysis. Folia Primatol. 53:65-81.

Mace, 1982). When y is regressed on x, the assumption is that y is dependent on x and x is measured without error (inherent asymmetry). LSR of y on x will only provide an unbiased estimate of the best fit line when the variables have no error on the x axis. As error is introduced into the x axis, the slope will become shallower. Error in the y axis does not affect the regression of y on x (Harvey and Mace, 1982). However, it is rare to say one variable has accuracy at the expense of another (Rayner, 1985).

An important aspect of LSR is that a second line can be fit to the data if x is dependent and y is independent (x on y). Here, LSR will minimize the horizontal distance from each point to the line (Fig. 1). When x is regressed on y, y is assumed to be measured without error, with error in the x axis. In an LSR analysis, these two lines, y on x and x on y, will cross at a point representing the mean of the x and the mean of the y variables (Aiello, 1992). The degree to which these lines diverge from one another is inversely proportional to the correlation coefficient (Sokal and Rohlf, 1981). So a decreased correlation coefficient will mean increased divergence, while an increased correlation coefficient indicates convergence (Fig. 2).

Numerous authors from the general statistics literature view least squares regression as a calibration problem (Hoadley, 1970; Hunter and Lamboy, 1981; Lwin and Maritz, 1982), while some anthropologists have become interested in the controversy as well (Aykroyd, et al., 1997; Konigsberg and Frankenberg, 1994; Konigsberg and Hens, n.d.; Konigsberg, et al., 1996; 1998). Two methods of calibration can be compared and contrasted: inverse calibration and classical calibration. Krutchkoff (1967) coined the term "inverse calibration" because the independent variable x (body size-in the case of

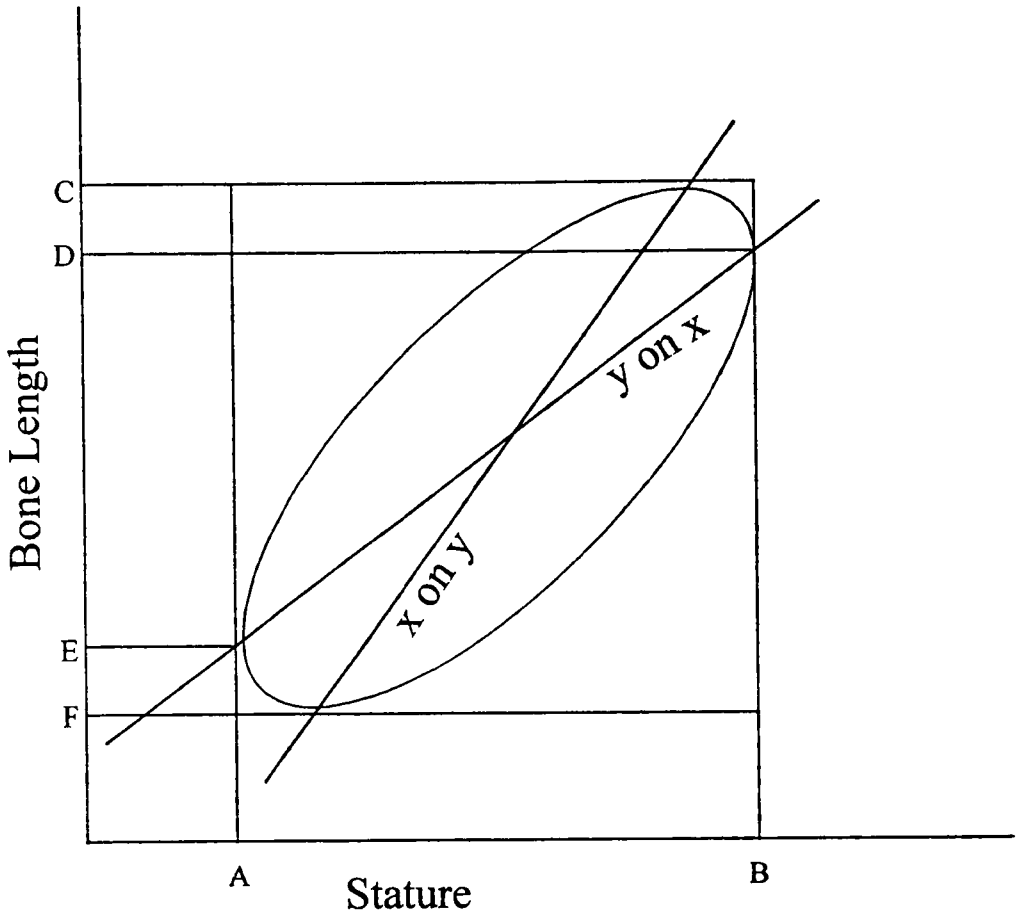

Figure 2. Certain properties of bivariate regression showing both the y on x and x on y least squares lines. The x on y least squares line represents when long bone measurement is independent and stature is dependent. The range of variation according to some iso-density ellipse is between A and B, and between C and F, respectively. Estimating stature by means of the regression line from the value E, yields the estimate A, and from D the estimate B is obtained. This shows that inverse regression tends to overestimate the shortest individuals, underestimate the tallest, and narrow the range of variation. The other line is the y on x line when stature is independent and long bone measurement is the dependent variable.
Source: Adapted from Sjøvold T (1990) Estimation of stature from long bones utilizing the line of organic correlation. Hum. Evol. 5:431-447.

this dissertation) is regressed on the dependent variable y (long bone measurement-in this dissertation), which is the x on y situation described above. This regression is the inverse of how the problem is regarded in the allometric literature. Classical calibration (y on x) involves the regression of y on x followed by solving for x. Thus, the long bone measurement (y) regresses on the body size variable (x). This model makes better sense in allometric studies, where the long bone measurement is considered the dependent variable and the body size measurement may partly explain the long bone size.

The inverse calibration estimator produces a Bayes estimator (Hoadley, 1970; Hunter and Lamboy, 1981; Lwin and Maritz, 1982). Although Konigsberg and Frankenberg (1994) work with age estimators, their work can be thought about in the light of body size estimation. Thus, the posterior probability for a body size variable will be proportional to the product of the likelihood and an informative prior for body size (from the normal distribution of the reference sample). Forensic situations commonly use this approach, where a body size variable such as stature or weight becomes the dependent variable that regresses on the independent variable, usually a long bone measurement. The body size estimate will regress toward the mean of the reference population in LSR (see Fig. 2). The inverse approach decreases the variation so that the predictions of body size will vary less than body size itself (Sjøvold, 1990). Numerous studies demonstrate this point (Aykroyd, et al., 1997; Hens, et al., 1998; Konigsberg and Hens, n.d.; Rogers, 1996), while finding support for classical calibration estimators in certain contexts.

Classical calibration produces a maximum likelihood estimator. Konigsberg and Frankenberg's (1994) work can be adapted to show that in this situation the posterior probability for a body size variable is proportional to the product of the likelihood and an uninformative (uniform) prior. The likelihood is proportional to the probability that an individual of a specific body size will have a long bone measurement identical to a bone from the reference sample.

A drawback of LSR is in the dependence and independence of the variables. A long bone measurement may explain body size, but body size may also explain the long bone measurement (Sjøvold, 1990). It is difficult to argue a direct dependence of y on x or x on y in allometric studies. In another example, brain size and body size are both end products of similar developmental lines (Martin and Barbour, 1989). This causes the error in biological studies to be unclear. LSR will model the error unrealistically when both the x and y variables consist of uncontrolled measures (Rayner, 1985), as is often the case with biological data. Due to these methodological difficulties, many researchers seek other methods to account for the bilaterality and confusion in error variability.

Common alternatives to standard LSR are the more symmetrical Model II regressions: major axis and reduced major axis. These models assume that error exists in both the dependent and independent variables (Sokal and Rohlf, 1981). With these models, one variable just as easily estimates a second as the second estimates the first (Sjøvold, 1990). The major axis and reduced major axis techniques are generally preferred when determining the central tendency of a sample and estimating functional

relationships (Martin and Barbour, 1989; Rayner, 1985; Ricker, 1973). According to Sprent (1969), a functional relationship occurs when all variables are subject to error.

The major axis (MA), or principal axis, minimizes the sum of squared deviations perpendicular to the line of best fit (Fig 3) and is seen as the greatest extension of an iso-density ellipse (Fig. 4). Thus, the major axis accounts for the maximum amount of variation in the data. The reduced major axis (RMA) minimizes the sum of areas of a triangle bounded on one side by the line of best fit and on the other two sides by lines passing parallel to the two axes (Figs. 3 and 4). The RMA is "reduced" because the variables are standardized by dividing them by their standard deviations (Hills and Wood, 1984). Both the MA and the RMA can fit only one line to the two dimensional data set. If the variables are reversed (x on y), the slope of the line is the inverse of the slope of the line when y is regressed on x (Aiello, 1992; Kermack and Haldane, 1950). The MA and RMA respond differently to the sample correlation coefficients and the ratio of variances of the x and y variables. The RMA is unaffected by the correlation coefficient. It is always the geometric mean of the two least squares lines (x on y and y on x) regardless of the correlation coefficient. The RMA is a ratio of the standard deviation of the x and y variables (s_y/s_x) (Kermack and Haldane, 1950). As long as the variance ratio remains constant (s^2y/s^2x), the slope of the RMA will remain the same. This is because the covariance of the x and y variables is not part of the equation used to compute the RMA, but it is used to compute the correlation coefficient (Seim and Saether, 1983).

The slope of the MA is dependent upon the variance ratio and the correlation coefficient because the formulae used to derive the equations depend on both the variance

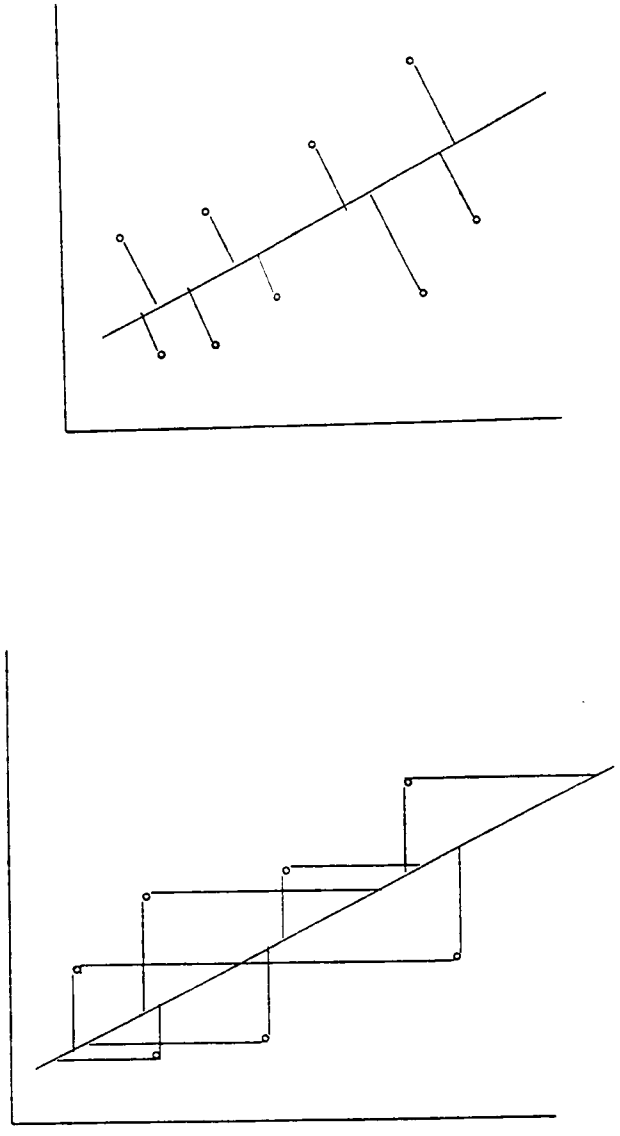

Figure 3. Differences between the major axis and reduced major axis lines determined for a bivariate data set showing a weak linear relationship (r = 0.45). The major axis (top) minimizes the sum of the squared deviations perpendicular to the line. The reduced major axis (bottom) minimizes the sum of the areas of the triangles subtended by the points on the line.
Source: Adapted from Martin RD, and Barbour AD (1989) Aspects of line-fitting in bivariate allometric analysis. Folia primatol. 53:65-81.

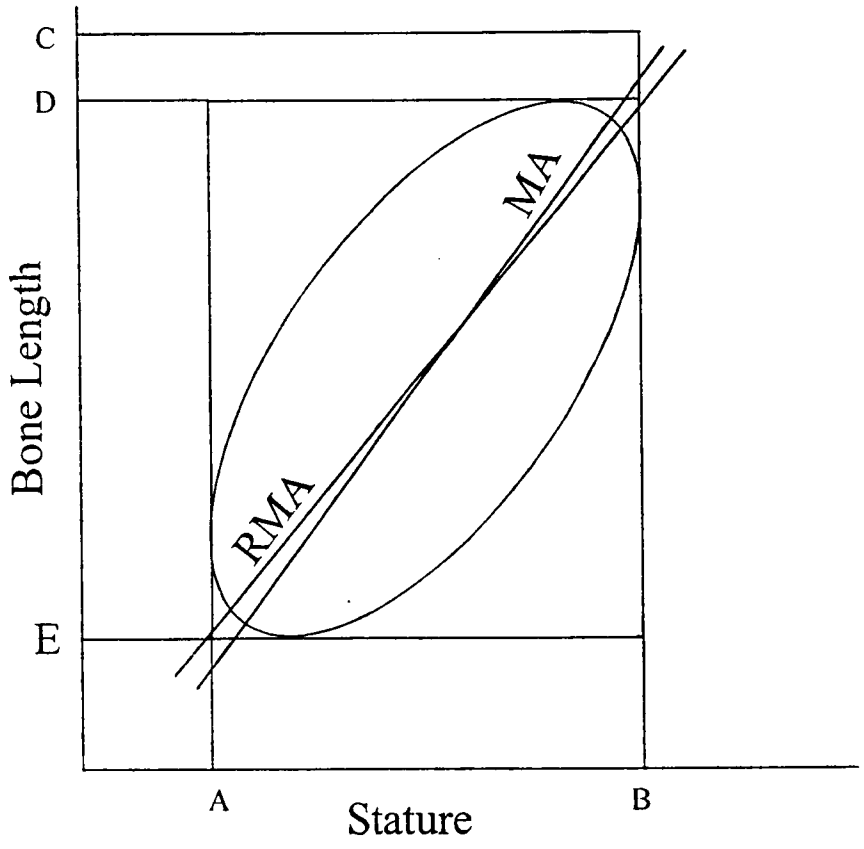

Figure 4. This illustrates the major axis (principal axis of the ellipse) and reduced major axis (the diagonal of the rectangle) of a bivariate regression using the same iso-density ellipse as in Figure 2. The reduced major axis (theoretically) reproduces the actual range of variation, whereas the major axis tends to underestimate the shortest individual (A) and overestimate the tallest (B) based on the extreme values E and D.
Source: Adapted from Sjøvold T (1990) Estimation of stature from long bones utilizing the line of organic correlation. Hum. Evol. 5:431-447.

and covariance of x and y. When the variance ratio is equal to one (unity), the slope of the MA is independent of the correlation coefficient and identical to the RMA. However, as the variance ratio drops below unity, the correlation coefficient will have a stronger effect on the MA. A decreased correlation coefficient will equal a decreased slope. Above unity, a decreased correlation coefficient will cause an increase in the slope (Seim and Saether, 1983; McArdle, 1988).

The slope of the LSR line is also dependent on the variance ratio and the correlation coefficient. However, it reacts differently than the MA. When the correlation coefficient is high, the LSR approaches the RMA. A lower correlation coefficient will decrease the LSR slope when compared to the MA (Aiello, 1992).

One last disadvantage of the MA deserves attention. The MA is affected by changes in the scale of measurement. There is a need with this technique to use log transformed data so that the slope of the best fit line is not affected (Harvey and Mace, 1982; Kermack and Haldane, 1950; McArdle, 1988). The RMA is unaffected by changes in scale either way (Rayner, 1985) and will work equally well on transformed and untransformed data.

The choice of method, whether LSR, MA, or RMA, should depend on the assumptions present and the purpose of the analysis. MA and RMA are of value when estimating a functional relation. The MA will provide consistent estimates of the parameters when the two error variances are equal. The RMA is consistent when the relative sizes of the two error variances are equal (Seim and Saether, 1983; McArdle, 1988). The RMA is the maximum likelihood or least biased estimator of a functional

relation when errors cannot be determined (Rayner, 1985). Rayner (1985) shows that the RMA exhibits the least biased estimations of unobserved variables within and between populations, allowing for multiple population analysis.

Martin and Barbour (1989) and Smith (1994b) discuss the rationale behind the use of LSR. When confronted with a bivariate normal distribution, these authors feel that predictions should be based on the LSR because the bivariate normal distribution exhibits special properties relating to the vertical and horizontal deviations from the mean values. For a bivariate normal distribution, the major axis of an ellipse indicates the overall biological trend in the data (Martin and Barbour,1989). If mean values of y are determined for a series of x, the line passing through those mean values will be the y on x least squares line. Conversely, if the values of x are determined from y, the line will be the x on y least squares line. Smith (1994b) argues that least squares regression is preferable because it accurately reflects the actual distribution of error between the variables. This is especially true when one of the axis traits is highly variable and hard to measure, as is the case with life history parameters. LSR also works well when the range of variation on one axis is much greater than the range of variation on the other axis. This makes measurement error negligible relative to the second axis.

Finally, attention has turned recently to a long bone/body size ratio in body size estimation. The work of Feldesman (1992), Feldesman and Lundy (1988), Feldesman et al. (1989, 1990), and Lundy and Feldesman (1987) supports the ratio model. These authors use the model to estimate stature from femoral length in modern and fossil

hominids. To obtain stature, the observed femur length is divided by the ratio of mean femur length to mean stature following the equation:

stature (cm) = femur length (cm)/0.2674

Logically then this equation could also model body weight from a long bone measurement, where to obtain the weight of an individual, the observed long bone measurement is divided by the ratio of the mean long bone measurement to mean weight.

Konigsberg et al. (1998) treat the average stature to femur length ratio as a regression parameter. This parameter is multiplied by an actual femur length to obtain an estimate of stature:

$$\hat{X}_i = \frac{\bar{x}}{\bar{y}} y_i$$

In this equation, the regression line passes through the origin and bivariate mean and becomes a least squares line when the femur and stature are isometric. Hens et al. (1998) and Konigsberg (1997) shows that with this special case of femur/stature isometry, the classical calibration estimator defaults to the ratio estimator. So, classical calibration and the femur/stature ratio work equally well in cases of isometry, but classical calibration outperforms the ratio estimator in other non-isometric situations.

Multivariate Conditions

So far, I have only examined the bivariate situation where there is one variable that predicts a second variable. In this work, the bivariate case is based on the variables

femur and stature. However, I also explore the multivariate case, where two or more variables are used to predict an unknown variable. Here, humerus length and femur length are measured variables used to predict stature. The multivariate condition is a logical extension of the single predictor condition described earlier. Konigsberg et al. (1998) describe the multivariate situation for each model in detail, which is summarized here. Each method (inverse, classical, MA, RMA, and ratio) fits a plane through the data, which in this case is trivariate. Once the plane is fit through the data, stature is estimated by projecting humerus and femur values onto the plane. Inverse calibration fits the plane so that it minimizes the distances of actual statures to the plane. Classical calibration minimizes the distances of the humeral and femoral measurements to the plane. The ratio estimator is similar to the classical method, however, in the ratio model the plane must pass through the origin. The MA fits the plane so that the perpendicular distances of points to the plane are minimized. The RMA fits the plane to minimize the distances of humerus, femur and stature measurements to the plane simultaneously, which minimizes the volume of the tetrahedron.

The multivariate generalization of the inverse calibration method is the well known multiple regression model. The classical calibration parameters are written as vectors, where the intercept is a vector of y-intercepts and the slope is a vector of regression coefficients for measurements taken from the reference collection. Also included in this model is the variance-covariance matrix among bone measurements after regression on stature in the reference collection. Standard statistical software packages can obtain the regression coefficients and the variance-covariance matrix needed with this

estimator. In the multivariate generalization of the ratio model, the intercepts remain at zero, and the slope is a vector of mean bone measurements divided by the mean stature in the reference collection. The residual variance-covariance matrix remains in the equation. The multivariate extensions of the MA and RMA are described in detail in McArdle (1988). In the MA estimator, the eigenvector of the variance-covariance matrix (**V**) associated with the smallest eigenvalue is needed. If this is written as **e**, the column vector where the first element (e_1) refers to stature, and the remaining elements ($e_{2...n}$) refer to long bones and the vector of regression coefficients for stature on long bones is -$e_{2...n}/e_1$. For the RMA, the eigenvector associated with the smallest eigenvalue from the correlation matrix is needed. The regression coefficients are then the same as in the major axis model, but for the RMA the coefficients are scaled by the ratios of the standard deviation of stature to the standard deviations of each long bone (Konigsberg et al., 1998).

Summary

This chapter has examined the five regression models in some detail, including the theory behind each model as well as the appropriate situations where the models may be employed. An understanding of these theoretical backgrounds will assist in understanding and interpreting the models' subsequent performance later in this study. The next chapter highlights the important studies done in stature estimation and the role

these five regression models have played in those studies. Brief sections on weight estimation and allometry are also included.

Chapter 3

Survey of the Literature

Studies in Stature Estimation

The first contribution to the field of stature estimation came in 1712, by an English anatomist and surgeon, William Cheselden. Cheselden analyzed the skeletal remains of a Romano-British individual and attempted to reconstruct the stature. This work remained alone for over 150 years until American and British researchers renewed interest in stature estimation from skeletal remains (Dwight, 1894; Manouvrier, 1893; Pearson, 1899; Rollet, 1888, cited in Wells, 1963; Topinard, 1885). At this time period stature was primarily reconstructed from the reassembled bones of the skeleton while accounting for soft tissue and spinal curvature. However, several of these early researchers worked with the limb bones of the skeleton and their proportion to stature. The work of Manouvrier (1893) and Pearson (1899) especially, remained popular for several decades. Despite the contributions of these early studies, the estimation of stature was not fully explored until the 1950's with the work of Trotter and Gleser (1952, 1958). In their 1952 study, Trotter and Gleser used both American White and Negro males and females from the modern Terry cadaver collection and the repatriated remains of American servicemen from World War II. Trotter and Gleser updated their study in 1958 with further repatriated skeletal material from the Korean War, which included a Mexican

sample. The samples were subdivided into categories based on sex and race. This partitioning provided numerous least squares regression equations applicable to a variety of human groups. Trotter and Gleser argued against the use of averaging techniques for all bones or bone combinations and supported the use of a single estimate with a low standard error. Trotter and Gleser's work culminated in the regression equations widely used in the estimation of stature today.

Trotter and Gleser pointed out the difficulties inherent in applying their equations to other human populations. Specifically, skeletal remains are measured with error, body proportions may vary according to sex and race, and most importantly, the formulae are population specific and not well adapted to populations that differ from the reference sample. Shortly thereafter, Wells (1963) noted that stature regressions show the least accuracy above and below the range of the population from which they were calculated.

The work of Trotter and Gleser inspired many researchers to develop regression formulae for numerous contemporary and archaeological populations (see for example: Formicola, 1983; Genoves, 1967; Lundy and Feldesman, 1987; Mo, 1983; Olivier et al., 1978; and Rösing, 1983). Due to its central role in bipedal posture and locomotion, the femur has become a large and robust bone that lends a high contribution to the overall stature of an individual. Numerous investigations in stature estimation show the femur, along with other lower limb bones, as the most reliable indicators for stature predictions (Lovejoy and Heiple, 1970; Trotter and Gleser, 1952, 1958).

Despite the warnings expressed by Trotter and Gleser (1952, 1958) and Wells (1963) concerning the population specificity of regression equations, regression formulae

have been applied to numerous human groups and fossil hominids, notably australopithecines (Lovejoy and Heiple, 1970; McHenry, 1974; Reed and Falk, 1977; Robinson, 1972; White, 1980; White and Suwa, 1987; Wolpoff, 1973), *Homo erectus* (Leakey and Walker, 1985; Ruff, 1988), and Neandertals (Trinkaus 1981, 1983).

Early work by Wolpoff (1973) attempted to counterbalance the difficulties pointed out by Wells (1963). In trying to relate posterior tooth size to diet, Wolpoff needed estimates of body size for three South African *Australopithecus africanus* specimens. Because the australopithecines are small, Wolpoff sought regressions based on a short-statured population. The Mesoamerican sample examined by Genoves (1967) extended the range of variation into the australopithecine range. Wolpoff utilized the short-statured Mesoamericans to predict stature in the fossil sample. Although Wolpoff recognized the possibility of differing limb proportions, he was unable to account for this because the fossil sample did not have upper and lower limbs associated for each individual.

McHenry (1974) was the first to systematically reconstruct stature from the remains of numerous fossil hominids. He used the Trotter and Gleser formulae on 18 Plio-Pleistocene fossil hominids and concluded that the two forms of early South African hominids, gracile and robust, were more similar in size than previously thought. Although later researchers did not give him credit, McHenry realized that the equations were not totally reliable because they were derived from a modern reference sample. However, McHenry believed the equations could provide rough approximations for an overall impression of size. McHenry also recognized that the values derived from the forelimb and hindlimb should not be compared because the fossil limb proportions

differed from the modern limb proportions. The stature estimations from the forelimb were probably too high, while those from the hindlimb were probably too low.

In 1976, Olivier challenged McHenry's (1974) results. Olivier faulted McHenry's reference population and his choice of regression equations. Olivier began by examining the reference population. The Trotter and Gleser formulae and standard least squares regression techniques based on modern human samples overestimated the stature of early hominids. Consequently, the estimation of australopithecine stature seems impossible without an appropriate reference population. Olivier suggested two solutions: either Model II regressions or Model I regressions that use contemporary African Pygmies as the reference population. Using the principal axis or major axis technique on McHenry's sample of 18 australopithecine long bones, Olivier calculated an average stature of 150 cm. This value is smaller than the 156 cm reported by McHenry (1974). Olivier's second technique involved the hindlimb dimensions of 91 "Baka" Pygmies from Cameroon. Measurements on living individuals were used to translate the skeletal height and limb dimensions. The resulting values for the regression line and major axis averaged 152.0 cm and 149.9 cm, respectively. These results correspond with the values obtained by the Model II equations; thus the methods confirm each other.

These two solutions, either a Model II regression technique or a Model I technique with a shorter-statured reference population, are alternate procedures that appear in most of the recent attempts to predict stature for fossil hominids. In this way, many researchers tried to combat the error problems inherent in stature prediction.

In a very thorough study, Geissmann (1986) tested 45 different regression equations for their ability to correctly determine the stature of the *A. afarensis* specimen, "Lucy" (A.L. 288-1). Early reports by Johanson (1976) and Johanson and White (1979) on the hindlimb bones estimated Lucy's stature at between 107-122 cm. However, later estimates based on all preserved parts suggested a height of about 107 cm (Johanson and Edey, 1981). Reconstruction of the entire skeleton by Schmid (1986) provided a living stature of 105 cm. Schmid's reconstructed value was compared to the estimates derived from the equations. Geissmann used two criteria to assess the applicability of the regression formulae: 1) the consistency of the results judged by its range of estimates, and 2) the similarity of the results to Schmid's (1986) stature reconstruction. Using these criteria, results that range less than 10 cm were consistent and results between 90-120 cm were "similar". The results of Geissmann's study show that 12 out of 40 of the regression formulae ranged less than 10 cm, two of which were major axis regressions. The stature estimates derived from the femur were the shortest, while the stature estimates derived from the humerus were the tallest. Three formulae estimated the stature of A.L. 288-1 below 120 cm. Two of these were based on the major axis, and the third from a short-statured Hindu population. Geissmann concludes that between the inconsistent results and overestimations, none of the regression formulae he tested provides a reliable means to predict stature in gracile australopithecines.

Jungers (1988c) was not surprised by Geissmann's results. The living stature of many fossil hominids is outside the range of variation seen in modern human groups, making extrapolation difficult. Least squares regression performs poorly as the sample

values move away from the mean of the x and y variables. These circumstances render standard least squares regression techniques based on modern human reference samples inappropriate (Jungers, 1988c).

Several researchers report non-human limb proportions for Lucy. McHenry (1974) and Johanson and Edey (1981) state that australopithecines had disproportionately longer arms, while Jungers (1982), and Jungers and Stern (1983) believe australopithecines have shorter legs compared to modern humans. An alternative view is provided by Wolpoff (1983), who believes Lucy's legs were the right size for a human of that body size. All of this suggests to Jungers (1988c) that models other than modern humans should be considered (i.e. apes, as well as the modern African pygmy groups).

In his 1988c study, Jungers focused on estimating stature in A.L. 288-1 from femur length using a sample of modern African pygmies and pygmy chimpanzees. Seven males and eight females composed the human pygmy skeletal sample. Four males and four females made up the pygmy chimpanzee sample. Extrapolation still occurred because all of the human femora were longer than Lucy's. Although Jungers prefers the Model II predictors, he compared least squares, major axis, and reduced major axis estimators on both the raw and log transformed data.

The Model II techniques drawn from the human pygmies estimated Lucy's stature at 105.5 cm. The least squares estimate was slightly higher. The Model II results based on the pygmy chimpanzees suggested an average stature of 109 cm. These values are remarkably close to Schmid's value of 105 cm from the anatomical reconstruction of the skeleton.

Around the same time period, Feldesman and Lundy (1988) also attempted to revise the stature estimates for 15 Plio-Pleistocene African hominids, including new estimates for A.L. 288-1. They used both least squares and major axis estimators developed from a contemporary South African Black tribal population housed in the Raymond Dart collection at the University of Witwatersrand. Stature was reconstructed for the sample using Fully's (1956) anatomical method, which provided a "known" height population for deriving the equations. The South African Blacks were of smaller stature and more homogenous than Trotter and Gleser's reference samples. The authors rejected using human pygmies because of the rarity of skeletal data and the low bivariate correlations between femur length and stature. Results indicated that the Trotter and Gleser equations overestimated stature when compared to estimates from the South African sample. The Model II results were lower than the Model I values. The least squares technique estimated Lucy at 115 cm, while the major axis estimated her at 106 cm. The MA value is nearly identical to Schmid's value of 105 cm.

At the close of the article, Feldesman and Lundy (1988) discuss the differences in intermembral proportions for the Lucy specimen. They feel the weight of evidence favors the Jungers (1982) and Jungers and Stern (1983) assessments. Regardless of the comparative sample, Lucy's femur is small for a human of that estimated body *weight*. This leads Feldesman and Lundy to contemplate another approach to stature estimation: a comparison of femur length to *stature*. The femur/stature ratio traces back to 19th century workers (Dwight, 1894; Pearson, 1899; Topinard, 1885), but was not consistently used to predict stature.

Using Schmid's estimate, Feldesman and Lundy find that Lucy's femur has the same relative proportion to stature as contemporary human populations, including the African pygmies. The authors determine that several human groups have a femur/stature ratio times 100 of 26.7. This value is similar to Lucy's femur/stature ratio, which is estimated between 26.5-27.0. Thus, although Lucy's lower limb may be small for her estimated body weight, Lucy's proportions show she did not have short legs compared to her estimated total height.

Further research by Feldesman and coworkers (1989, 1990) supports the femur length/stature ratio model. Analyzing over 10,000 contemporary individuals, the authors computed a mean ratio of femur length to stature at 26.7%, which maintains stability across sex and ethnic groups. When tested on the remains of Vietnam era soldiers, South African Blacks, and one Akka pygmy, the ratio performed better than the traditional Trotter and Gleser equations. However, the appropriate regression equations for the South African Black population worked better than the ratio in the tribal Blacks. Applications of the ratio method to fossil hominids provided more satisfactory results than population specific regression formulae.

The most recent attempt at stature estimation was McHenry's (1991b) report on a much larger fossil sample of 31 Plio-Pleistocene hominids. McHenry used femoral lengths to estimate stature by employing the femur/stature ratio (Feldesman, et. al., 1989,1990). He found strong sexual dimorphism in *A. afarensis* and *Homo habilis* and moderate dimorphism in the other species. The robust australopithecine forms were also quite small; their robustness is confined to their masticatory specializations. Lastly,

McHenry points out that the secular trend of increasing human height through time may have begun in early *Homo* and *H. erectus*.

Although methods for stature estimation have improved over the decades, it is clear from the various studies described above that stature estimation is an ongoing area of research. Some investigators prefer the Model I regression techniques, while others consistently support the Model II formulae. Numerous studies try to account for these differences by reporting results from both techniques and including reference samples that are closer to the mean of the population being studied. However, as Jungers' (1988c) study points out, we cannot be sure which estimator will work best with fossil remains. An innovative approach is to incorporate both human and non-human primate reference samples. Thus, the fossil hominid whose allometry may differ from modern human's may be better estimated.

Studies in Weight Estimation

The most common variable used to describe body size is body mass or weight. Ford and Corruccini (1985) point out some of the difficulties that may be present when using body mass as a variable including: individual variation, health of the animal, the tendency of captive animals in the reference sample to be overweight and interobserver error. Smith (1993b,c) recognizes problems that occur with transformation bias in equations used in mass estimation. It is important to recognize that body weight estimations and functional morphological interpretations are not separable. When using

modern species as a reference sample, one must be sure of a similar relationship between body parts and mass between the reference sample and the individuals being estimated. Grand (1990) notes a difference in how mass is viewed by paleontologists and anatomists. Paleontologists generally disregard the individual variability that may be present in components making up body mass, while anatomists focus on examining the variability in separate tissue and organ components. As a functional morphologist, Grand (1990) examines mass as a composite character made up of numerous components that may differ in animals with different locomotor patterns. The largest body tissues: skin, muscle, bone and adipose are the most important aspects of weight and Grand demonstrates that the proportion of these tissues varies in animals with different locomotion. This is clearly relevant when examining extant hominoids who show a multitude of postural and locomotor specializations, including knuckle-walking, terrestrial bipedalism and a size range of approximately 5 kg - 200 kg (Jungers, 1988b). Jungers (1988b) has also shown that when body weight is accounted for overall limb proportions are correlated to locomotor adaptations.

Despite all of this, mass has the advantage of not being dependent on shape (Hills and Wood, 1984) and it can be used for comparisons across taxonomic lines (Jungers, 1984). As a representative of body size, mass has been shown to be correlated with numerous metabolic and physiological variables (Schmid-Nielson, 1977, 1984) and ecological variables (Fleagle, 1978, Roberts, 1953). Because of these factors, mass is considered the best single indicator of size of an organism and a good reference for

comparing an animal to components of itself, other animals and the environment (Martin, 1990; Smith, 1985, 1993a; Steudel, 1985).

It would seem that mass should be straightforward and easy to measure. However, mass cannot be measured directly from fossil remains and estimates must be reconstructed from bones and teeth. Estimates of volumes are thus derived from linear measures, which introduce errors (Martin, 1990). Studies vary in their degree of precision because of these errors and also because different body parts, different reference samples and different regression models are used (Damuth and MacFadden, 1990; Scott, 1983). When deriving estimates for a fossil species, researchers must choose an extant species that exhibits a similar relation between body parts and mass. Thus, broad functional and morphological groups must be identified that may or may not follow along traditional taxonomic lines (Damuth and MacFadden, 1990; see also: Grand, 1990).

Primate paleontologists and paleoanthropologists traditionally link body mass to tooth size (McHenry, 1984a, 1992a; Wolpoff, 1973), brain size/degree of encephalization (McHenry, 1975, 1976, 1988, 1992a) and size variability/sexual dimorphism (Jungers, 1988a; Leigh, 1992; McHenry, 1986b, 1988, 1991a,c; Plavcan and vanSchaik, 1997). Numerous skeletal elements are used to estimate body mass across the primate order. Teeth are commonly used because of their durability in fossil assemblages and high correlation with weight (Blumenberg, 1984; Conroy, 1987; Fleagle, 1978; Fleagle and Kay, 1985; Gingerich, 1977; Gingerich, et al., 1982; Kay and Simons, 1980; Wolpoff, 1973). All of these studies show how body weight estimates have been used for comparative relationships with other variables, but little emphasis was placed on the

methodological problems in body weight estimation. Hylander (1985) notes that primates (including humans) do not transmit body weight through their skulls or teeth. Thus there is no biomechanical reason to expect a relationship between dental or cranial variables and body weight. It would be better to estimate body mass from weight bearing portions of the skeleton. Some better alternatives emphasized in other studies include: diameters or circumferences of diaphyses (Aiello, 1981; McHenry, 1975, 1976, 1988; Rightmire, 1986), limb lengths (Scott, 1983), cross-sectional measures (Ruff, 1988, 1990) and joint surface measures (Alexander 1980a,b; Jungers, 1988a,b, 1990b; McHenry, 1976; Rightmire, 1986). Smith (1993a) warns against the use of a strict biomechanical approach. This type of approach does not explain the scaling of numerous factors, i.e. basal metabolic rate, brain size, home range size, gestational length, longevity, population density and others. These traits are related to other structures in the system and to components of the organism.

Despite the problems inherent in body weight estimation, its importance cannot be overemphasized. The use of estimated body weights in comparisons across taxonomic lines, life history analyses and ecological, metabolic and biomechanical studies keep body weight estimation an important area of investigation that is highly dependent on reliable, repeatable estimates.

Allometry

General Principles

No estimations of body size are complete without a consideration of scale. A change in size, whether for a bridge, brick house, or an animal, involves a change in scale. Scaling " ...deals with the structural and functional consequences of changes in size or scale among otherwise similar organisms" (Schmidt-Nielsen, 1984:7). Schmidt-Nielsen (1984) discusses the basics of scaling, which will be summarized here.

Geometrically similar bodies have the same proportions and are referred to as isometric. Thus, three-dimensional bodies, no matter what shape, which are isometric will follow the rules of geometric similarity. These rules state that the surface area changes with the second power of linear dimensions and the volume changes with the third power of linear dimensions. Therefore, surface area and volume do not increase in the same proportions, but the surface area increases in proportion to the 2/3 power of the volume.

Isometry is seldom found in biological organisms, even when they have the same organization. Nonisometric scaling is referred to as allometric and many features scale allometrically with body size. Allometric scales are found in the general form:

$$y = ax^b$$

Taking the log results in:

$$\log y = \log a + b \log x$$

The use of log scales results in a straight regression line, which allows for easier graphical representation and comparison (Jungers, et al., 1995; Smith, 1980). The slope, *b*, can be either positive or negative, depending on the function being considered. A slope of 0 indicates that some feature or quantity is not changing with changes in size. A slope of 1.0 represents simple proportionality where as size increases, some feature (e.g. blood volume) also increases in the same proportion. However, as body mass increases, some features (e.g. the skeleton) increase out of proportion at a faster rate than mass, resulting in a slope greater than 1.0. If a feature (e.g. metabolic rate) increases out of proportion with body mass, but at a slower rate, the slope is positive, but less than 1.0. A slope that is negative indicates a feature or quantity that is decreasing with increasing body size (e.g. heart rate). Graphical depictions of these concepts are shown in Figure 5.

The term *a* in the above equation is the proportionality coefficient or the intercept at unity. When comparing two or more regression lines, if the slopes are equal, the proportionality coefficients can be compared to answer different research questions. For example, the slope addresses the question: How does blood volume change with respect to increasing body size? The proportionality coefficient, *a*, asks which organism has a higher blood volume when the slopes are equal (i.e. when blood volumes change in the identical way for different organisms).

Fossil Allometry

Because biological organisms frequently display allometric scaling, many researchers focus on the scaling relationships between varying structures and body size

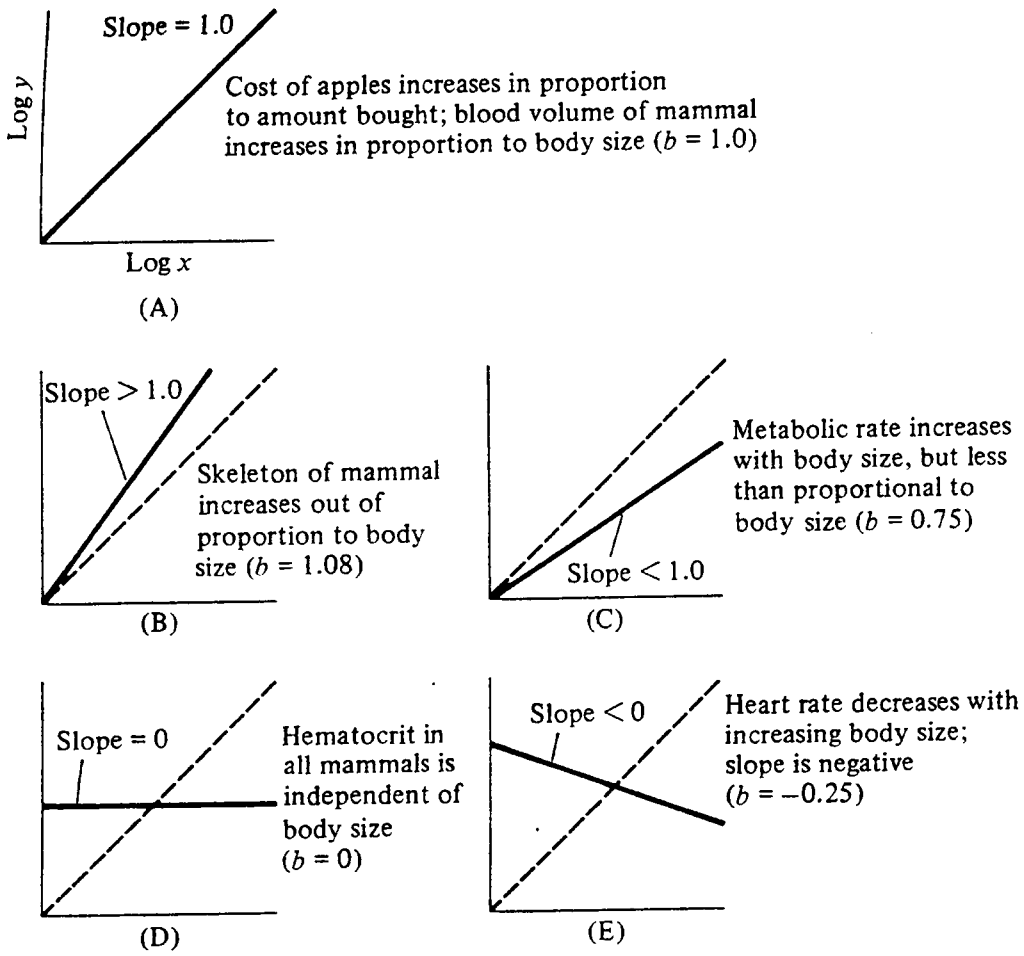

Figure 5. Logarithmic plots of regression lines with different exponents have different slopes depending on the value of *b*. The slope (b) may indicate proportionality (fully drawn line), but can deviate in a regular way from proportionality (dotted line). *Source*: Adapted from Schmidt-Nielsen K (1984) Scaling. Why is Animal Size so Important? Cambridge: Cambridge University Press.

(see Jungers, 1985a and references therein). At issue here is how the variation in global (overall) size and local size influences stature reconstructions. The use of cross species reference samples and fossils with unclear allometries complicates stature estimation. Differing body proportions bias stature estimates and directly impact locomotor interpretations (Jungers, 1984). Numerous researchers have investigated postcranial size scaling in fossil hominids especially in relation to bipedality (Corruccini and McHenry, 1978; Jungers, 1988b, 1990a; McHenry, 1978, 1982, 1986a, 1986b, 1992b; McHenry and Corruccini, 1976; Ruff, 1988) as well as in other fossil primates with varying locomotor patterns (Jungers, 1978, 1984, 1985b; Jungers and Cole, 1992; Ruff, 1988; Shea, 1992, 1995). Leg proportions affect stature reconstructions more than humeral differences in bipeds, but both femoral and humeral dimensions affect locomotion in quadrupeds.

The work presented here uses several members of the Hominoidea that show differing scaling relationships between stature and limb proportions. It is well known that gorillas and chimpanzees scale differently from modern humans by having shorter legs and longer arms (Schultz, 1930, 1936, 1937, 1956, 1973). However, the scaling of fossil hominid limb proportions is not as easily understood and has been debated for over two decades.

Prior to the discovery of the 40% complete *Australopithecus afarensis* specimen "Lucy" (A.L. 288-1) (Johanson, 1976; Johanson and Taieb, 1976), few fossil hominid remains of a similar evolutionary stage showed associated upper and lower limb bones. This lack of associated postcrania did not allow for extensive exploration of allometry. With the discovery of Lucy in 1974, investigators began discussing the proportionality of

her limb bones in relation to other human and non-human primates (Feldesman and Lundy, 1988; Feldesman et al., 1989, 1990; Johanson and Edey, 1980; Jungers, 1982; Jungers and Stern, 1983; McHenry, 1978; Wolpoff, 1983a,b; Wolpoff and Lovejoy, 1975).

One of the first studies reporting on Lucy's limb proportions was Wolpoff and Lovejoy (1975) who stated that australopithecine postcrania were identical to *Homo sapiens* in form and proportion. These findings were not supported by the work of McHenry (1978) and Johanson and Edey (1981) who find that Lucy's hindlimbs were relatively short and her forelimbs relatively long compared to modern humans of similar body weight. McHenry (1978) did not report any ape like similarities in limb proportions for Lucy.

Jungers (1982) reported a close similarity in relative humerus length between Lucy and *Homo sapiens*, but hindlimbs that were relatively shorter than modern humans. This results in an intermediate humerofemoral index (85.1) for Lucy when she is compared to humans and great apes. Jungers conclusions are challenged by Wolpoff (1983a,b) who asserts that Lucy's legs are appropriately sized for an individual of her body size (weight). Wolpoff also criticizes Jungers' use of pongids in comparisons, stating that they are irrelevant with regard to early hominid locomotion. In a reply, Jungers and Stern (1983) use new data and analysis in support of Jungers' (1982) earlier work. Jungers and Stern compare Lucy to the short-statured modern human pygmies and reaffirm that Lucy's femur is significantly shorter than expected for modern humans of similar body weight and similar to small bodied African apes. However, Lucy's arms

were similar to the modern human pygmies. Jungers and Stern feel that the evidence up to this point favors their conclusions that Lucy's femur is small and her arms appropriately sized for a human of similar body weight. The reduced femur suggests to the authors that Lucy's pattern of bipedality differs substantially from modern humans by a reduced stride length with higher peak velocity resulting in increased energy expenditure. Later hindlimb elongation would have been bioenergetically beneficial.

Feldesman and Lundy (1988) take a new approach to the dilemma by considering whether Lucy's femur is short for her stature (previous studies emphasized her weight). Using Schmid's (1986) anatomically reconstructed estimate for Lucy's stature, Feldesman and Lundy find that Lucy's femur has the same relative proportion to stature as in most human populations, including human pygmies. Thus, although Lucy's legs are disproportionate for her body weight, they are in proportion with her stature.

The Nariokotome *Homo erectus* skeleton (KNM-WT 15000) found in 1984 at Lake Turkana, Kenya represents the virtually complete remains of a 11-12 year old boy (Brown et al., 1985; Leakey and Walker, 1985). The find is significant for many reasons, providing insights into growth and body size as well as providing the first examples of numerous skeletal elements not previously known for *Homo erectus.* The skeleton is extensively documented in Walker and Leakey's (1993) edited volume, "*The Nariokotome Homo erectus Skeleton*". Ruff and Walker (1993) provide an analysis of body size and shape, including stature reconstructions for the specimen. Their analysis suggests that "The Boy's" general postcranial proportions are well within the range for modern humans and outside the range of nonhuman hominoids. However, the authors

proceed to examine intralimb proportions and find that WT 15000's are hyper-tropical in proportion when compared to living tropical and subtropical male samples. They argue that this is not a racial or ethnic affiliation, but is based on thermoregulatory principles. Ruff and Walker base their stature estimates on all long bones with an emphasis placed on the lower limb bones. They use modern reference samples from native tropical populations including South African Bantus and Ugandan samples. American Blacks were considered unacceptable reference samples because American Blacks were as different from African Blacks as they were from American Whites. This is likely due to genetic admixture and/or environmental effects.

Summary

This chapter has reviewed the pertinent literature in the field of stature estimation, weight estimation and fossil allometry. It is clear that authors favor different regression models when attempting stature estimates. The chosen reference samples upon which the parameters derive also vary. Any attempts to discuss the stature of fossil hominids automatically involve a discussion of the allometric differences between the fossils and any reference sample chosen.

The next section, Chapter 4, deals with the sample materials and statistics used for analysis in this thesis.

Chapter 4

Materials and Methods

Nature of the Samples

This study incorporates three skeletal samples. The first is a large modern human sample (N=2,209) composed of individuals derived from three sources: 1) the Terry Anatomical collection, 2) World War II dead collected by Mildred Trotter, and 3) Forensic Data Bank material from the University of Tennessee. Data from the Terry and Trotter collections were transferred from punch cards into a personal computer by Lee Meadows Jantz (Jantz, 1996) and combined with the Forensic Data Bank material.

The second sample is a small (N=19) sample of human pygmies from west Africa, and the third sample is represented by a collection of African great apes (N=85). Two well-known hominid fossils are also examined. Measurements recorded on all of the individuals in the samples include maximum femur length and maximum humerus length, while stature is known for the reference samples and estimated for the fossil hominids.

Large Modern Human Sample

As mentioned above, the composition of the large modern human sample derives from three separate collections. The Terry Anatomical collection, housed at the National Museum of Natural History, Smithsonian Institution, Washington D.C., was started by

Robert Terry and continued by Mildred Trotter. It is a large cadaver collection from the early 1900s composed of 1,737 American "White" and "Black" individuals of known age, sex, stature, "race" and cause of death (Terry, 1940). For this study, 853 individuals from the Terry collection were used. Table 1 provides the racial and sex composition of the sample used here. Stature in the Terry collection is cadaver stature, where the cadaver is measured in a vertical position with the feet flat on a board. These measurements were taken by Terry (1940). Terry also notes that although most individuals in the collection suffered from poor health, the reported statures are accurate. The Terry long bone measurements were taken by Trotter and are extensively documented by Jantz (1996). Table 2 shows the simple statistics for the long bone and stature variables in the Terry collection.

The second component of the large human sample comes from the data collected by Mildred Trotter on over 1,200 repatriated American war dead from World War II. Trotter examined the individuals while working at the Central Identification Laboratory, where the remains were processed following the war (Stewart, 1979). The portion of the collection used in the present research is composed of 1,197 male individuals of both European and African ancestry (see Table 3). Almost all geographic areas of the United States are represented (Jantz, 1996). The long bone measurements were recorded after the death of the individual during processing of the remains at the Central Identification Laboratory. Stature is that reported upon the individual's induction into the armed forces under standard military guidelines (Trotter and Gleser, 1952). Simple statistics describing the World War II sample are shown in Table 4.

Table 1: Composition of the Terry Anatomical collection (N=853).

	White	Black
Male	255	358
Female	63	177

Table 2: Variance/Covariance matrix and other simple statistics for the Terry Anatomical collection.

	Stature	Humerus	Femur
Stature	8081.2	1698.4	2470.4
Humerus	1698.4	486.4	607.7
Femur	2470.4	607.7	949.1
Average	1687.8	326.7	458.2
St. Dev.	89.9	22.1	30.8

Table 3: Composition of the Trotter W.W.II collection (N=1,197).

	White	Black
Males	1,111	86

Table 4: Variance/Covariance matrix and other simple statistics for the Trotter W.W.II collection.

	Stature	Humerus	Femur
Stature	3948.0	743.2	1221.8
Humerus	743.2	257.6	309.5
Femur	1221.8	309.5	558.0
Average	1740.3	336.3	473.9
St. Dev.	62.8	16.1	23.6

The Forensic Data Bank (FDB) is the third constituent of the large modern human sample. The FDB is a computerized databank housed at the Forensic Anthropology Center, Department of Anthropology, University of Tennessee, Knoxville (Moore-Jansen, et al., 1994). The databank is the product of collaboration by numerous researchers in an effort to report the results of their skeletal data collection from forensic cases, anatomical specimens and donated skeletons. A total of 159 individuals from this collection were used in this study. The sex and racial composition of the sample is described in Table 5. FDB statures are listed as cadaver stature and "Forensic stature", which come from various sources (Moore-Jansen, et al., 1994; Ousley, 1995). Both the Terry and FDB cadaver statures were corrected for age related stature loss and cadaver stature by subtracting 2.5 cm as described in Trotter and Gleser (1951). Simple statistics pertaining to the FDB collection are reported in Table 6.

Human Pygmy Sample

The human pygmy sample comes from a West African skeletal collection. It is represented by 11 males and 8 females. One female individual is missing a humerus. This individual is not used in multivariate calculations, however, she was included in the univariate analysis based on the femur. All long bone measurements were taken by William Jungers of S.U.N.Y. Stony Brook. Stature derives from Fully's (1956) anatomical method for calculating both living stature and skeletal height. Feldesman and Lundy (1988:586) provide an English translation of the Fully (1956) method:

"Fully's method...sums the basi-bregmatic height of the skull,

Table 5: Composition of the Forensic Data Bank collection (N=159).

	White	Black
Male	81	21
Female	39	18

Table 6: Variance/Covariance matrix and simple statistics for the Forensic Data Bank collection.

	Stature	Humerus	Femur
Stature	10077.1	1847.9	2564.1
Humerus	1847.9	514.3	598.6
Femur	2564.1	598.6	914.7
Average	1725.0	329.0	464.9
St. Dev.	100.4	22.7	30.2

> the anterior heights of each vertebra from C1 to S1, the bicondylar lengths of the femur and tibia, and the articulated height of talus and calcaneus. This sum yields total skeletal height."

A correction factor to account for soft tissue is found in Fully and Pineau (1960).

> "This adds 10cm to skeletal heights under 153.5cm, 10.5cm for heights between 153.6 and 165.4cm, and 11.5cm for heights exceeding 165.4cm" (Feldesman and Lundy, 1988:586).

The computed skeletal stature was found to deviate from actual living stature by less than 2 cm (Fully and Pineau, 1960). Statures for most of the pygmy sample were derived by Marquer (1972), while one female pygmy specimen was taken from Flower (1889). Average statures, long bone lengths and other simple statistics for the pygmy sample with all individuals represented (n=19) are reported in Table 7. This sample was used in the univariate analysis section of this paper. Table 8 shows the simple statistics for the smaller (n=18) pygmy sample that was used in the multivariate analysis.

African Great Ape Sample

The great ape sample is represented by 85 mature, wild-shot individuals including: 35 *Gorilla gorilla*, 42 *Pan troglodytes* and 8 *Pan paniscus* (Table 9) housed at the Terverun Museum in Belgium and the Powell-Cotton Museum in England. Only adult individuals were included in the study as evidenced by fusion of the epiphyses of

Table 7: Variance/Covariance matrix and simple statistics for the complete human pygmy sample (N=19).

	Stature	Humerus	Femur
Stature	6202.5	1140.9	1478.5
Humerus	1140.9	230.4	294.9
Femur	1478.5	294.9	446.8
Average	1404.8	276.5	376.6
St. Dev.	78.8	15.2	21.1

Table 8: Variance/Covariance matrix and simple statistics for the human pygmies used in the multivariate analysis (N=18).

	Stature	Humerus	Femur
Stature	6566.8	1140.9	1564.1
Humerus	1140.9	230.4	295.8
Femur	1564.1	295.8	469.5
Average	1405.0	276.5	377.0
St. Dev.	81.0	15.2	21.7

Table 9: Composition of the great ape sample (N=85).

	Male	Female	Total
Gorilla	16	19	35
P. troglodytes	11	31	42
P. paniscus	4	4	8

the long bones. These data were used in an earlier study by Wood (1979). However, Jungers remeasured the maximum femur length, maximum humerus length and other long bone lengths not utilized in the current study. Measurements of body length (stature) for the ape sample came from field reports. Cousins (1972) illustrates the method used for the measurement of body length on *Pan troglodytes* and *Gorilla* specimens in the field. The apes were measured from crown to heel with the hips and knees clearly extended. The data on external body length for the pygmy chimpanzees comes from Coolidge and Shea (1982) where the animals were reportedly measured from top of head to heel. Simple statistics for the combined ape sample are included in Table 10 while Tables 11-13 show the simple statistics for each ape species.

Fossil Specimens

Two well-preserved fossil specimens were used in the present study. The first represents the *Australopithecus afarensis* fossil hominid, A.L. 288-1, popularly known as "Lucy" (Johansen and Edey, 1981). A.L. 288-1 is the remains of a 40% complete adult, probable female australopithecine, recovered during the 1973 and 1974 field seasons at the Hadar Formation, Ethiopia (Johansen, 1976; Johansen, et al., 1982; Johansen and White, 1979). The specimen dates to the Pliocene, approximately 3.0-3.5 mya. Maximum femur length and maximum humerus length are reported in Jungers (1982). The actual stature of the A.L. 288-1 specimen is based on Schmid's (1986) anatomical reconstruction of 105.0cm (1050mm). Table 14 shows the values used for these remains.

Table 10: Variance/Covariance matrix and simple statistics for the combined ape sample (N=85).

	Stature	Humerus	Femur
Stature	27329.5	9465.6	5301.0
Humerus	9465.6	3795.4	1999.1
Femur	5301.0	1999.1	1185.6
Average	1312.4	343.1	314.0
St.Dev.	165.3	61.6	34.4

Table 11: Variance/Covariance matrix and other simple statistics for the Gorillas (n=35).

	Stature	Humerus	Femur
Stature	19068.2	4327.4	3716.9
Humerus	4327.4	1232.8	1021.1
Femur	3716.9	1021.1	920.2
Average	1466.9	410.1	345.5
St. Dev.	138.1	35.1	30.3

Table 12: Variance/Covariance matrix and other simple statistics for the common chimpanzees (*Pan troglodytes*) (n=42).

	Stature	Humerus	Femur
Stature	4070.8	466.4	594.7
Humerus	466.4	168.9	157.6
Femur	594.7	157.6	191.1
Average	1214.0	298.4	291.7
St. Dev.	63.8	13.0	13.8

Table 13: Variance/Covariance matrix and other simple statistics for the pygmy chimpanzee sample (*Pan paniscus*) (n=8).

	Stature	Humerus	Femur
Stature	5066.2	1099.7	839.9
Humerus	1099.7	260.1	205.2
Femur	839.9	205.2	212.6
Average	1153.3	285.1	293.5
St. Dev.	71.2	16.1	14.6

Table 14: Long bone and stature values for A.L. 288-1, "Lucy" (in mm).

Stature[1]	Humerus[2]	Femur[2]
1050	239	281

1. from: Schmid (1986)
2. from: Jungers (1982)

"The Boy" (KNM-WT 15000) represents the remains of a single individual, nearly 80% complete found at Nariokotome in the Turkana Basin, Kenya. The specimen was discovered by Kamoya Kimeu in 1984 and dates to 1.6 mya (Brown, et al., 1985; Leakey and Walker, 1985; Walker and Leakey, 1993a). The individual has been assigned to the taxon *Homo erectus* and the age at death has been estimated at 11-12 years (Walker and Leakey, 1993a,b).

The edited volume *The Nariokotome Homo erectus Skeleton* (Walker and Leakey, 1993a) provides detailed descriptions of the find. Longbones were measured for actual length at time of death in order to provide estimates of juvenile stature. Adult stature was also projected. Some reconstructions were necessary. The left humerus was not recovered. The right humerus measures 301.2 mm long. However, by accounting for the missing superior epiphysis, the humerus is estimated at 319.0 mm long. The left femur suffered some postmortem distortion of the distal epiphyses. Without reconstruction, the femur measures 430.3 mm in total length. Allowance for crushing and distortion provides an estimate of 432.0 mm for maximum length of the left femur (Table 15). The right femur suffered more serious damage with missing proximal epiphyses and could not be used in the analysis (Walker and Leakey, 1993b). Reconstructed limb lengths were used in the present study.

Ruff and Walker (1993) outline the procedure used to estimate the stature of KNM-WT 15000. Anatomical reconstruction was not considered due to The Boy's juvenile status. In comparisons of intralimb proportions, Ruff and Walker find that The Boy's limbs are "hyper-tropical" in proportion. They tend toward the extremes of living

Table 15: Actual and reconstructed long bone lengths for WT 15000 (in mm).

	Humerus	Femur
Actual	301.2	430.3
Reconstructed*	319.0	432.0

*signifies values used in the present analysis

populations in lower latitudes. This proportionality difference affects the choice of reference sample upon which to base the stature estimations. The reference samples need to be representative of tropical populations with similar body proportions as WT 15000. Using various long bone lengths and combinations with African Black reference samples as a reference, Ruff and Walker (1993) used Model I and Model II regressions to estimate "The Boy's" height at death. The average estimate is 160.0cm. The estimates derived in this dissertation are compared to Ruff and Walker's average estimate of 160.0cm.

Statistics for Estimation and Analysis

In this section, I first present an analysis of the five regression methods and their performance in stature estimation. Here the five models are tested for their ability to estimate stature in situations of extreme extrapolation from the mean of the reference sample, and where there are potential allometric differences in limb proportions. The models are tested twice: 1) a univariate procedure, using only the femur values to predict stature, and 2) a multivariate procedure, using both the humerus and femur measurements to estimate stature. For both univariate and multivariate tests, parameters from the large human sample are used to predict stature in the great ape sample and the great ape parameters are used to estimate stature in the large human sample. Two measures are used to determine which of five regression models provides the best estimate of stature in the target sample: the root mean squared error (RMSE) and the bias. The RMSE is the

square root of the average squared term of the predicted values around their true values. A better estimator is indicated by a low RMSE value.

The bias is the mean of the predictions for stature minus the actual mean for stature. The bias allows for an understanding of how well the predictor performs, i.e. how close the estimates came on average to the actual value. When an estimate is unbiased, the RMSE measures the efficiency of the estimator. However, the RMSE includes terms for both bias and prediction uncertainty making it less informative when an estimator is biased.

The second section of the work presented here involves the prediction of stature for the two fossil hominids discussed previously: A.L. 288-1 and WT 15000. This analysis involves examining both the choice of regression model and the choice of reference sample. All five statistical estimators are used to predict stature in the hominids with both univariate and multivariate models. In the first case, A.L. 288-1, the regression parameters are drawn from the pygmy human sample and the great ape sample. The great apes test the ability of the models to predict stature when allometric differences are present. The human pygmy sample has the same proportions to stature as other, taller modern human groups. However, they extend the range of variation down to the lower extremes of height for modern humans. Thus, they are used to demonstrate the model's ability to account for extrapolation away from the mean.

The five models are finally tested with estimating stature for the Nariokotome Boy. Since Ruff and Walker (1993) show "The Boy" to be similar to modern tropical human limb and stature proportions, the regression parameters are drawn from the large

modern human sample for each of the five models based on both univariate and multivariate analyses.

Chapter 5

Results

This chapter is divided into two main sections corresponding to the two major goals of the study. The first section presents the results of the analysis of the five regression methods and their ability to estimate stature in challenging situations. These situations involve estimating stature in specimens where there is extreme extrapolation away from the mean of the reference sample and where allometric differences in limb proportions exist between the target sample and the reference sample. The univariate and multivariate analyses are also separated for clarity.

The second set of results reports on the ability of the five techniques to correctly estimate stature in the two fossil hominid cases from univariate data derived from the femur and multivariate data derived from the femur and humerus. Associated with this analysis is the choice of correct reference sample upon which to derive the regression parameters.

The Five Estimators: How Well Do They Perform?

Univariate Analyses

Table 16 provides the slope and y-intercept values derived from both the large human reference sample and great ape reference sample for all five models. Table 17

Table 16: Regression parameters based on the univariate analyses for each of the five models for the large modern human sample (N=2,209) and the great ape sample (N=85). Also included are the conditional standard deviations for the human sample, which do not incorporate a bias term.

	Human	Sample	Cond. Std.Dev.	Great Ape	Sample
	y-intercept	slope		y-intercept	slope
Inverse	545.2775	2.5122	34.98	-91.6667	4.4710
Classical	163.3462	3.3297	46.38	-306.6453	5.1556
RMA	367.7388	2.8922	40.28	-195.3293	4.8011
Ratio	0.0000	3.6793	51.27	0.0000	4.1791
MA	205.1319	3.2402	45.13	-297.6589	5.1270

Table 17: RMSE and bias for the five models derived from 2,209 humans and applied to *Pan* and *Gorilla* femur data (univariate case).

	Pan (n=50)		*Gorilla* (n=35)	
	RMSE (mm)	Bias (mm)	RMSE (mm)	Bias (mm)
Inverse	91	+74	94	-54
Classical	86	-68	167	-153
RMA	52	+8	123	-100
MA	74	-53	157	-142
Ratio	140	-130	206	-196

shows the values for the root mean squared error (RMSE) and the bias for each regression model when the large human sample is used as the reference sample and the chimpanzees and gorillas are the target samples. For the *Pan* sample, the reduced major axis model has the lowest RMSE indicating that the reduced major axis is the optimal indicator of body length from femur length in the chimpanzee sample. The bias for this model is minimal. The reduced major axis on average overestimates chimpanzee body length by only 8 mm. However, the major axis, classical, and ratio estimators underestimate body length by 68 to 130 mm. The inverse calibration method overestimated the actual value, in this case by an average of 74 mm.

In the *Gorilla* sample, the inverse calibration of body length on femur length by standard least squares regression provides the lowest RMSE. The bias shows that all five estimators underestimate gorilla body length by 54 to 196 mm.

The examination of RMSE and bias for these five estimators in the two genera does not provide a clear preference for a body length estimator. The Model I technique of least squares regression by inverse calibration is preferred for the gorilla sample. However, the Model II reduced major axis is favored in the *Pan* sample. The body length/femur length ratio performs poorly in both samples.

The next set of results addresses the question of how well the estimators performed when estimating stature in the large human sample with parameters derived from the great ape sample. Table 18 shows the RMSE and bias values for each of the five models. The five estimators performed rather poorly when estimating stature in the

Table 18: RMSE and bias for the five models derived from 85 African great apes and applied to the large human sample in the univariate case.

	RMSE (mm)	Bias (mm)
Inverse	286	+278
Classical	392	+383
RMA	337	+329
MA	388	+379
Ratio	241	+234

humans. All RMSE values are high with the ratio model as the "best" estimator with an RMSE of 241. The bias shows all five models overestimated stature in the human sample from a minimum of 234 mm with the ratio model to a maximum of 383 mm with the classical model.

Multivariate Analyses

Tables 19 and 20 show the values for the y-intercepts and slopes derived from the large human sample and the great ape sample based on the multivariate data of the humerus and femur. The root mean squared error and the bias derived from the human reference sample are reported in Table 21 for *Pan* and *Gorilla*. The results for the multivariate data set are different from those reported earlier with the univariate data. Examination of Table 21 shows that for the combined chimpanzee sample, the long bone/body length ratio and the classical calibration estimator are tied for having the lowest RMSE at 62 mm. However, the bias for these two models varies slightly. The classical estimator overestimates chimpanzee height by 39 mm, while the ratio model overestimates chimpanzee body length by 37 mm. The major axis performed exceedingly poorly in this example. The reported values for the gorilla sample demonstrate that the classical estimator has the lowest RMSE and the smallest bias, only overestimating gorilla body length by 60 mm. Both of the Model II regressions, reduced major axis and major axis perform poorly with the gorillas.

Turning now to using the ape sample to predict stature in the large human sample, a similar table is shown in Table 22. Again, the classical model shows the lowest RMSE

Table 19: Regression parameters based on the multivariate analyses for each of the five models for the large human sample (N=2,209). Slope 1 is for humerus and slope 2 is for femur. Also included are the conditional standard deviations, which do not incorporate a bias term.

	y-intercept	slope (1)	Slope (2)	Cond. Std.Dev.
Inverse	495.5982	1.0395	1.8796	34.21
Classical	129.6196	1.3505	2.4419	44.44
RMA	446.8894	-4.1722	5.6881	65.82
Ratio	0.0000	1.8855	2.3392	47.95
MA	2200.9399	-79.4012	55.4033	795.75

Table 20: Regression parameters based on the multivariate analyses for each of the five models for the African great ape sample (N=85). Slope 1 is for humerus and slope 2 is for femur.

	y-intercept	slope (1)	slope (2)
Inverse	139.8680	1.2424	2.3762
Classical	-3.2592	1.3941	2.6663
RMA	-7558.2901	-33.7497	65.1239
Ratio	0.0000	0.8704	3.2281
MA	-1632.6558	-6.1187	16.0636

Table 21: RMSE and bias for the five models derived from 2,209 humans and applied to *Pan* and *Gorilla* in the multivariate (humerus and femur) case.

	Pan (n=50)		*Gorilla* (n=35)	
	RMSE (mm)	Bias (mm)	RMSE (mm)	Bias (mm)
Inverse	156	+148	124	+104
Classical	62	+39	85	+60
RMA	284	-332	775	-766
MA	6386	-6347	12759	-12687
Ratio	62	+37	130	+115

Table 22: RMSE and bias for the five models derived from 85 African great apes and applied to the large human sample in the multivariate case.

	RMSE (mm)	Bias (mm)
Inverse	71	-56
Classical	50	-14
RMA	10018	+9941
MA	2141	+2121
Ratio	94	+78

at 50 and the bias indicates that humans are underestimated by a minimal value of 14 mm. Of the other estimators, only the Model II equations had exceedingly high RMSE values and large biases. The examination of RMSE and bias in these two situations, the prediction of human stature from the ape estimates and the prediction of ape stature from human estimates shows a clear preference for the classical calibration model. Classical calibration performs well in these situations of extrapolation to larger or smaller individuals than were used in the reference sample.

Estimating Stature in the Fossil Hominids

A.L. 288-1, Lucy

The actual stature for Lucy is based on the anatomical reconstruction by Schmid (1986) of 105.0 cm. This estimate is used for comparison so that the regression estimates derived in this work may be compared to an estimate derived by other non-statistical means. Reconstructing the stature of this particular fossil hominid is difficult because no modern analog exists for comparison. Therefore, the choice of reference sample is critical. As discussed previously in this work, Lucy's limb proportions are argued to be different from those of modern human groups and different from the apes. Her height is also out of the range of modern humans making extrapolation a significant factor to consider in choosing a reference sample. Here, I have chosen to use the great apes as a reference sample and the modern human pygmies as a reference sample. Both the apes and the human pygmies may have allometric differences in limb proportions to height

when compared to Lucy. However, both are of shorter stature and limit the amount of extrapolation necessary for stature prediction. The great ape regression parameters were presented previously and Tables 23 and 24 report on the regression parameters for the modern human pygmy group with both the univariate and multivariate data. Table 25 presents the univariate estimates of stature based on the femur alone for Lucy using each of the five regression models. The choice of regression model varies depending upon which reference sample is used. When using a human pygmy reference sample, the reduced major axis and the long bone/body length ratio methods both provide very close estimates of stature, differing by no more than 2 mm. Overall, none of the estimators are "bad". All are within a five cm range, and all slightly underestimate Lucy's stature. However, a different picture develops when viewing the estimates derived from the great ape reference sample. Here, all of the estimators overestimate Lucy's stature by a minimum of slightly over 9 cm. The two best, which are also very close in their estimates are the classical calibration model at 114.2 cm and the major axis model at 114.3 cm.

Table 26 presents the multivariate estimates for Lucy based on the combined humerus and femur measurements. Combining long bones from the upper and lower limbs complicates matters, due to varying allometries between humerus/stature versus femur/stature. Examination of Table 26 shows that when the human pygmies are used as the reference sample, all five estimators overestimate Lucy's stature. The classical calibration model provides the closest estimate at 113.3 cm. With the great ape reference sample, the classical model is again favored, with an even better estimate of 107.9 cm. With both samples, the Model II regressions, major axis and reduced major axis

Table 23: Regression parameters based on univariate (femur) data derived from the modern human pygmy reference sample (N=19).

	y-intercept	slope
Inverse	158.7579	3.3090
Classical	-174.9645	4.1952
RMA	1.7840	3.7258
Ratio	0.0000	3.7305
MA	-152.2343	4.1348

Table 24: Regression parameters based on the multivariate data derived from the modern human pygmy reference sample (N=18). Slope 1 is for humerus and slope 2 is for femur.

	y-intercept	slope (1)	slope (2)
Inverse	11.3469	3.5307	1.1072
Classical	-183.8933	4.0254	1.2623
RMA	-73.1888	6.0617	-0.5248
Ratio	0.0000	3.5605	1.1154
MA	-187.5300	10.2598	-3.3006

Table 25: Stature estimates for the A.L. 288-1 "Lucy" fossil hominid based on univariate data from femur length. Actual stature for Lucy is 105.0 cm.

	Pygmy reference	Ape reference
Inverse	108.9	116.5
Classical	100.4	114.2*
RMA	104.9*	115.4
Ratio	104.8	117.4
MA	101.0	114.3

* signifies closest to actual value

Table 26: Stature estimates for the A.L. 288-1 "Lucy" fossil hominid based on multivariate data from humerus and femur length. Actual stature for Lucy is 105.0 cm.

	Pygmy reference	Ape reference
Inverse	116.6	110.5
Classical	113.3*	107.9*
RMA	122.8	267.5
Ratio	116.4	111.5
MA	133.7	141.9

* signifies closest to actual value

performed the worst and were unable to compensate for the differing allometries present between the target specimen and the reference samples. The two reference samples used in the multivariate analyses provide over a five cm difference in estimation between the best estimators. Graphical depictions of the allometric differences between the samples assist in understanding the situation. Figure 6 is a plot of the humerofemoral index of all specimens in the reference sample and Lucy. This plot shows Lucy at the far left of the graph. She is out of range of stature for the gorillas and for the human pygmies. Thus, the use of either of these groups as a reference sample will require some extrapolation. Lucy's stature is barely in the lower end of the range of chimpanzees. However, Lucy's humerofemoral index can be seen to be between the pygmies and the chimpanzees. This suggests a better reference sample might include both *Pan* and human pygmies combined or *Pan* alone without *Gorilla*.

Although the humerofemoral index shows an allometric difference between Lucy and the reference samples, it does not provide detail about where these differences lie. The next graph assists in this interpretation. Figure 7 has humerus over stature on the horizontal axis and femur over stature on the vertical axis. This shows that Lucy's femoral allometry is aligned with that of modern pygmy humans (which scale similarly to other taller modern human groups). However, Lucy is not similar to the ape femoral allometry. There is also a substantial difference between the chimpanzees and the gorillas. This suggests that these samples should not be combined when calculating stature. Lucy's humerus falls in between the pygmy humans and the chimpanzees suggesting that there are allometric differences, i.e. Lucy's arms are long for her height,

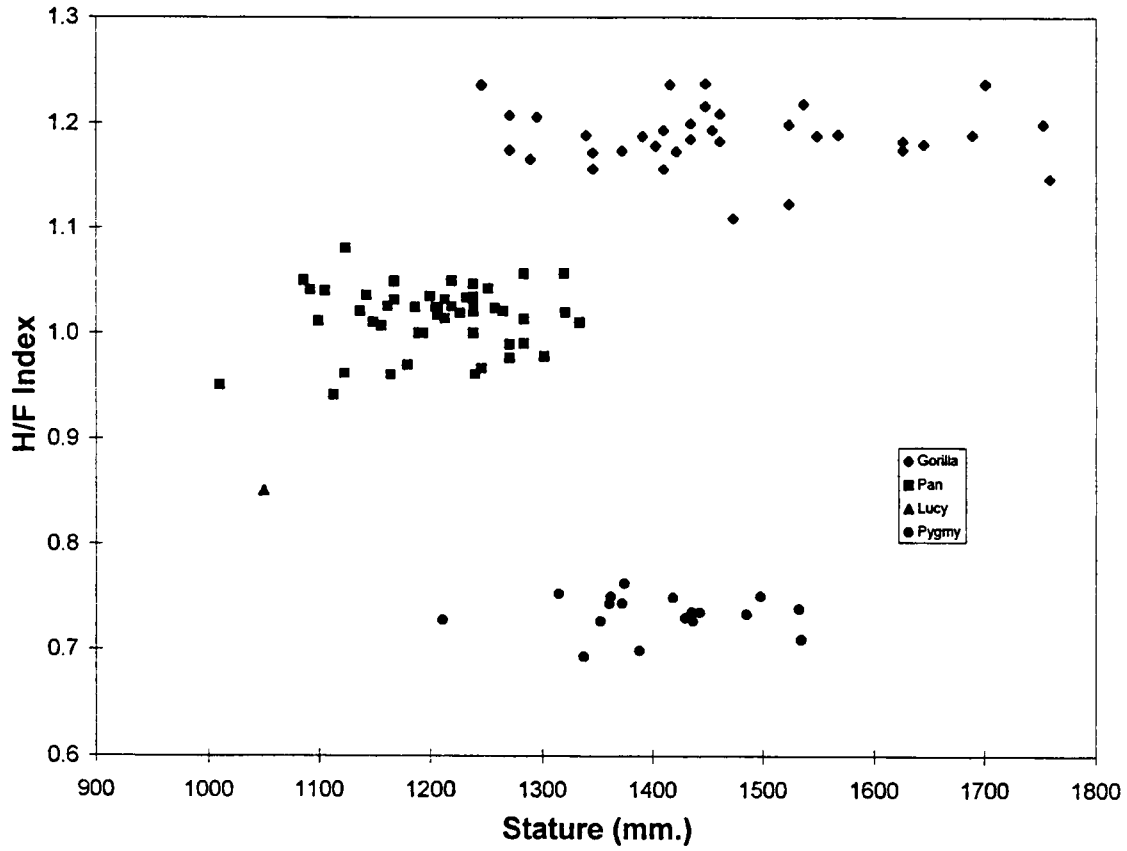

Figure 6: A plot of the humerofemoral index of all specimens in the reference sample and Lucy.

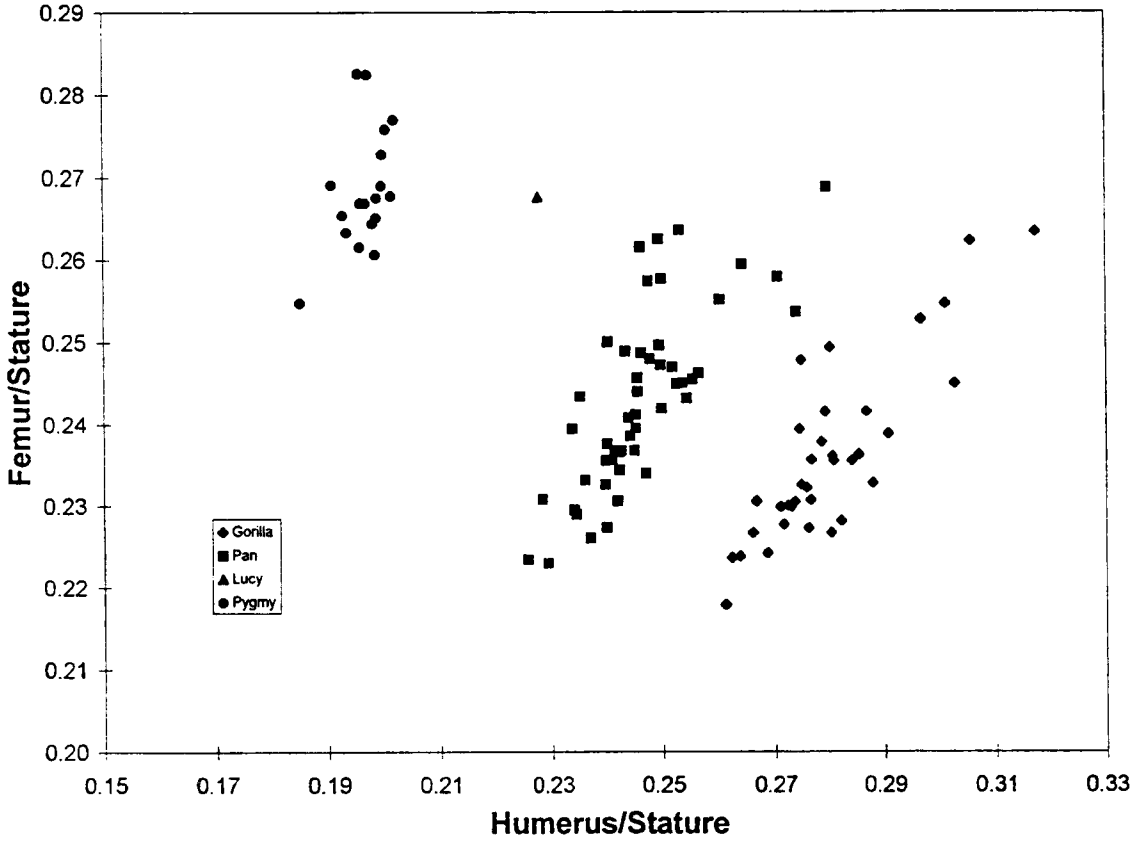

Figure 7: A plot of humerus/stature by femur/stature for all specimens in the reference sample and Lucy.

but her legs are in proportion with modern humans as suggested by Feldesman and coworkers (1989).

When considering a multivariate model for stature estimation, these allometric differences can influence the outcome. Since Lucy falls between the human pygmies and chimpanzees, it is interesting to examine stature estimates derived from a combined pygmy human and chimpanzee reference sample as well as stature estimates derived from the chimpanzees alone. Since no differences in limb proportions are noted between the bonobos and the common chimpanzees, they are treated as one group, *Pan*. Although *P. paniscus* and *P. troglodytes* are distinct in many ways, compared to other hominoids, the differences in their postcranial anatomy are not great and the two species are more similar to each other than to any other hominoids (McHenry, 1984). Table 27 shows the regression parameters derived from the chimpanzee sample for the multivariate data set. Table 28 reports the stature estimates derived from the multivariate chimpanzee sample. The inverse calibration model and the ratio model came the closest to estimating Lucy's stature with the multivariate chimpanzee data. The Model II regressions performed exceedingly poorly, giving negative estimates for stature with these data. Interestingly the Model II regressions perform similarly to the Model I regressions and the ratio model when the univariate data is used from the chimpanzee sample. Tables 29 and 30 show the regression parameters and stature estimates derived from the univariate chimpanzee data. Here, the classical model and major axis come closest to Lucy's reconstructed stature.

Lastly, Table 31 shows the regression parameters derived from the combined Pygmy/*Pan* sample. Table 32 reports the estimates derived for Lucy from the combined

Table 27: Regression parameters based on the multivariate analyses for each of the five models for the chimpanzee sample (N=50). Slope 1 is for humerus and slope 2 is for femur.

	y-intercept	slope (1)	Slope (2)
Inverse	161.3940	2.2090	1.3303
Classical	-940.1110	4.5422	2.7355
RMA	190.4481	35.7408	-32.7879
Ratio	0.0000	2.4598	1.6286
MA	479.3143	67.3378	-65.8329

Table 28: Stature estimates for the A.L.288-1 "Lucy" fossil hominid based on multivariate data from humerus and femur length using the chimpanzee reference sample. Actual stature for Lucy is 105.0 cm.

	Chimpanzees
Inverse	106.3
Classical	91.4
RMA	-48.1
Ratio	104.6*
MA	-192.6

*signifies closest to actual value

Table 29: Regression parameters based on the univariate analyses for each of the five models for the chimpanzee reference sample (N=50).

	y-intercept	Slope
Inverse	281.5312	3.1600
Classical	-1041.4412	7.6907
RMA	-235.2424	4.9297
Ratio	0.0000	4.1241
MA	-987.9298	7.5074

Table 30: Stature estimates for the A.L. 288-1 "Lucy" fossil hominid based on univariate data from the chimpanzee reference sample. Actual stature for Lucy is 105.0 cm.

	Chimpanzees
Inverse	116.9
Classical	112.0*
RMA	115.0
Ratio	115.9
MA	112.2

*signifies closest to actual value

Table 31: Regression parameters based on the multivariate anaylses for each of the five models for the combined Pygmy/*Pan* sample (N=68). Slope 1 is for humerus and slope 2 is for femur.

	y-intercept	slope (1)	slope (2)
Inverse	76.2727	1.2480	2.6007
Classical	-149.3914	1.4865	3.0976
RMA	-72.7728	1.4912	2.8496
Ratio	0.0000	1.4555	2.6512
MA	-683.8284	3.3576	3.0655

Table 32: Stature estimates for the A.L. 288-1 "Lucy" fossil hominid based on multivariate data from humerus and femur length using the combined Pygmy/*Pan* reference sample. Actual stature for Lucy is 105.0 cm.

	Pygmy/*Pan*
Inverse	110.5
Classical	107.6* (+2.6)
RMA	108.4
Ratio	109.3
MA	102.5* (-2.4)

* signifies closest to actual value

Pygmy/*Pan* sample. The classical model and major axis model come the closest to predicting Lucy's actual stature. The classical model overestimates Lucy's stature by 2.6 cm and the major axis underestimates Lucy's stature by 2.4 cm. Interestingly, both Model II regressions, especially the major axis, worked much better with this combined sample than it did with the separate samples viewed previously. Since the classical model was favored with the pygmy sample alone, the total ape sample and was very close with the combined Pygmy/*Pan* sample, it can be recommended here for estimating Lucy's stature with multivariate models. The results from the multivariate analyses are encouraging because one estimator was preferred in most cases over all others. Stature estimations based on the univariate data can also be computed from the combined Pygmy/*Pan* reference sample. Table 33 shows the regression parameters for the combined sample and Table 34 shows the estimated values for Lucy's stature based on the univariate data. In this scenario, all five estimators overestimate Lucy's stature by at least 7.2 cm. The femur length/stature ratio model provides the closest estimate at 112.2 cm. This model was also favored with the pygmy reference sample alone, but not with the ape reference sample. Considering that Lucy's femur scales isometrically with stature as in modern humans, the performance of the ratio model is not surprising.

WT 15000, The Nariokotome Boy

For this target specimen, only the large modern human sample was used here to generate parameters for prediction since the allometry of The Boy is easily understood and recognized as similar to modern humans. Walker and Leakey's (1993b) estimate of

Table 33: Regression parameters based on the univariate analyses for each of the five models on the combined Pgymy/*Pan* reference sample (N=69).

	y-intercept	slope
Inverse	471.1314	2.5004
Classical	287.9467	3.0814
RMA	384.3189	2.7757
Ratio	0.0000	3.9947
MA	309.4108	3.0133

Table 34: Stature estimates for the A.L. 288-1 "Lucy" fossil hominid based on univariate data from the combined Pygmy/*Pan* reference sample. Actual stature for Lucy is 105.0 cm.

	Pygmy/*Pan*
Inverse	117.3
Classical	115.3
RMA	116.4
Ratio	112.2*
MA	115.6

*signifies closest to actual value

160.0 cm derived from South African Black reference samples of similar body proportions was used for comparison. Table 35 provides the univariate and multivariate estimates for the Nariokotome Boy for each of the five models. In the univariate model, the classical estimator provides a very close estimate of 160.2 cm. This is followed closely by the major axis model at 160.5 cm. All of the models performed reasonably well. Upon examination of the multivariate results, the long bone/stature ratio model just barely outperforms the classical calibration model estimating The Boy's stature at 161.2 cm and 161.5 cm, respectively. Again all of the models were good predictors except for the major axis, which this time, provided a very poor estimate. No extrapolation away from the mean is necessary with this reference sample and no marked allometric differences are present between humerus and stature or femur and stature. Table 35 also reports the standard error of the estimates for each of the five models. Doubling the standard error gives the 95% confidence interval around each estimate. Examination of the standard errors shows that in almost all cases, the models 95% confidence interval encloses the "actual" value for stature for "The Boy".

A plot of the Nariokotome Boy with the modern human sample seen in Figure 8 verifies the use of this sample as a reference sample. The Boy's proportions fit well into the modern humans. This graph shows the first ten convex hulls for the large modern human sample. The first convex hull is constructed by enclosing all of the outermost points by "connecting the dots". The second hull encloses the next set of outermost points. The remaining hulls are constructed similarly as if one was peeling an onion. The Boy is indicated by the small dot within the innermost hull. The use of a standard

Table 35: Stature estimates and standard errors for the WT 15000 specimen, The Nariokotome Boy, based on the large modern human reference sample. Stature estimate for comparison is 160.0 cm.

	Univariate	Std. error	Multivariate	Std. error
Inverse	163.1	3.57	163.9	3.54
Classical	160.2*	4.64	161.5	4.44
RMA	161.7	4.03	157.3	6.59
Ratio	158.9	5.13	161.2*	4.80
MA	160.5	4.51	80.6	79.58

*signifies closest values to actual

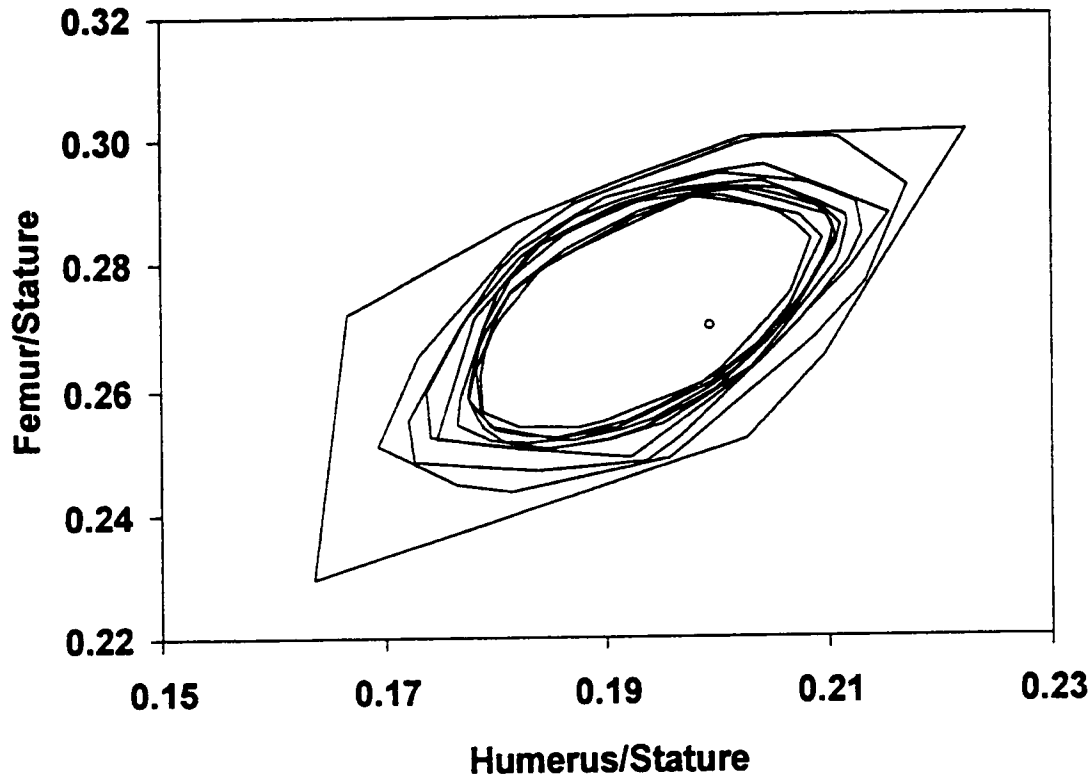

Figure 8: A plot of the *Homo erectus* specimen, WT 15000, the Nariokotome Boy, with the large modern human sample. The modern humans are represented by the first ten convex hulls. The Boy is indicated by the dot within the innermost hull.

scatterplot graph here completely obliterates The Boy's position in relation to the modern humans because of the sheer number of cases in the modern human sample (over 2,000). The Boy is within the 37th hull, which includes 58.14% of the points. Although Ruff and Walker (1993b) argue that The Boy has hyper-tropical limb proportions, this refers to the distal limb segments. Figure 8 shows that when femur and stature are examined, WT 15000 fits well into the range of variation presented by the modern humans.

Summary

This chapter has presented the results of two lines of analyses. Presented first were the results of the five regression techniques and their ability to estimate stature in situations of differing allometries and extrapolation away from the mean. In univariate analyses, when the large modern human sample was used to estimate stature in the great apes, both the reduced major axis and the least squares regression by inverse calibration had the lowest RMSE values in the chimpanzees and the gorillas, respectively. However, the long bone/stature ratio method worked best for predicting human stature from the great apes. The multivariate analyses showed quite different results. When applied to *Pan* and *Gorilla*, the human parameters worked best with the classical calibration model. This estimator was also favored when the great ape parameters estimated stature in the large human sample.

The second section of this chapter presented the results of estimating stature in fossil hominids. Stature estimation in the A.L.288-1 fossil hominid remains problematic

because of her unique allometry, which has no known analog among extant taxa. In the univariate analyses based on all four reference samples (pygmies, great apes, chimpanzees, and the combined Pygmy/*Pan* sample) four out of the five regression models were favored depending on the reference sample used. The ratio model did provide the closest estimates on two occasions: with the combined Pygmy/*Pan* sample and with the pygmy reference sample. However, the variable results do not allow for a clear choice of preferred estimator overall. When the multivariate results for Lucy are examined, the scenario is a little clearer. The classical calibration model gives the best results from three of the reference samples making the choice of statistical estimator slightly easier. However, the closest multivariate estimate overall was with the ratio estimator and the chimpanzee reference sample.

Finally, estimating stature in the Nariokotome Boy fossil hominid was more straightforward than in Lucy. The Boy's femoral limb proportions are shown to be well within modern human ranges making the choice of reference sample clear. The classical estimator was favored with the univariate data while both the ratio and classical estimators worked well with the multivariate data. However, these choices are based on how close the estimates came to a published regression estimate. The standard errors show us that all five models incorporated the "actual" stature within their 95% confidence intervals.

Overall, the choice of statistical estimator remains unclear with univariate models while the multivariate models seem to work best with the classical calibration estimator. A discussion of the significance of these results follows in the next chapter.

Chapter 6

Discussion and Conclusions

This study focused on the performance of five regression estimators (inverse calibration, classical calibration, reduced major axis, major axis and the zero-intercept ratio model) and their ability to estimate stature in various situations. The estimators were tested in rigorous situations in the first half of the study, including the model's ability to compensate for extrapolation away from the mean of the reference sample and substantially different allometric proportions in limb length to body length ratios. Obviously, chimpanzees and gorillas scale differently than modern humans. It is unlikely that any researcher today would not recognize the problems inherent in applying regression formulae across species lines. However, the fossil record seldom provides complete or nearly complete specimens upon which allometry can be understood. Thus, when estimating stature in fossil remains, we may not have the luxury of knowing that allometries differ between reference samples and the target samples consisting of isolated/commingled bones. In these situations, the choice of regression estimator and reference population becomes critical. The use of the Terry, Trotter and Forensic Data Bank collections here is for instructive purposes for modeling a "worst-case" scenario.

The examination of RMSE and bias for the five estimators gives conflicting results for the univariate data. The RMA, inverse calibration and ratio methods are all favored. The choice of statistical estimator is not clear for these data. However, the multivariate data sets unanimously favored the classical estimator. Classical calibration

performed best when extrapolating to individuals above the mean stature in the reference sample and below the mean stature in the reference sample. Classical calibration also compensated for the differing allometric proportions in humerus/stature and femur/stature ratios. The Model I least squares techniques are thought to be better for prediction (Smith, 1994), while the Model II techniques are better for estimating functional relationships (Martin and Barbour, 1989; Rayner, 1985; Ricker, 1973). The poor performance of the major axis is likely due to the assumption of equal error variances for the humerus, femur and stature variables. The reduced major axis has been shown to be a compromise between the classical and inverse estimators (Hens, et al., 1998). The RMA allows for further extrapolation relative to the inverse calibrator, but not to the extent of the classical estimator. The inverse calibrator has widespread usage in the modern forensic literature and performs well in situations where an individual case comes from the same distribution as the reference sample (Konigsberg, et al., 1998). However, with the data presented here, inverse calibration performed very poorly because estimating stature in the target samples required significant extrapolation away from the mean. The zero-intercept ratio model has been shown to be a special case of the classical calibration model where limb length(s) scale isometrically with stature (Hens, et al., 1998; Konigsberg, 1997; Konigsberg, et al., 1998). Because of this, it is difficult to recommend the ratio model over the classical calibration model in any scenario.

Examination of the results of the fossil hominid stature estimations also show conflicting results with univariate data and a somewhat clearer choice for the classical

estimator in the multivariate cases. Table 36 shows the models favored with each reference sample for the A.L.288-1 specimen. This table also reports how close the estimators came to Lucy's actual stature. The variable results for the univariate data do not allow for a clear choice of estimator. However, the use of the pygmy reference sample with the univariate data allowed for very close estimates of stature for Lucy compared to anatomical reconstruction. The RMA and ratio models were only off by one and two millimeters respectively. The ratio model works well here because Lucy's femora scale with stature in the same proportions as the modern pygmy humans. However, the multivariate situation is quite different. Here, Lucy's femur is in proportion to the human pygmies, but her humerus is in between human pygmies and chimpanzees. The chimpanzee reference sample provided the closest estimations to published reconstructed values for Lucy, differing by only 4 mm with the ratio model. The classical method performed best with the other three reference samples. Thus, in most cases, the classical estimator maximized the useful range around the mean stature and compensated for the differences in scaling proportions. Owing that the ratio estimator defaults to the classical estimator in situations where extrapolation away from the mean is minimized (Hens, et al., 1998; Konigsberg, 1997), in most situations the classical calibration estimator would be preferred for multivariate data.

The Nariokotome Boy's allometry is similar to modern humans in both humerus and femur proportions. Where allometry is similar, little or no extrapolation is necessary. The univariate data supported both the classical model and the major axis method. The

Table 36: Summary of results of stature estimation on the A.L. 288-1 fossil hominid. The value in parentheses indicates how close each of the estimators came (in cm) to the published reconstructed estimate.

	Univariate	Multivariate
Pygmy	RMA (-.1)	Classical (+8.3)
	Ratio (-.2)	
Total Ape	Classical (+9.2)	Classical (+2.9)
	Major Axis (+9.3)	
Chimpanzees	Classical (+7.0)	Ratio (-0.4)
	Major Axis (+7.2)	
Pygmy/*Pan*	Ratio (+7.2)	Classical (+2.6)
		Major Axis (-2.4)

multivariate data supported the classical model and the ratio model. As expected, the ratio model worked well in this situation because The Boy's limbs scale isometrically with

stature. However, if a model is chosen based on how close the estimate came to the published value in Euclidean distance, then the classical model worked well with both data sets it is recommended here for estimating stature in the Nariokotome Boy. In most cases, the differences in stature estimates were minimal. The standard errors for almost all models were very low and most models incorporated the "actual" stature of WT 15000 in their 95% confidence intervals. Thus, the choice of one model over another remains unresolved.

Summary

Two problems facing stature estimation in fossil hominid remains are the choice of regression estimator and the choice of reference sample. These problems are slowly being resolved with comparative work. For univariate data, the choice of regression estimator is unclear. Various models are favored depending on the reference sample used. Different reference samples have differing allometries and may require extrapolation. It is clear that with univariate data based on femur length, Lucy's stature is best estimated using a human pygmy reference sample because her femoral proportions scale similarly with human pygmies. The Nariokotome Boy poses few such problems.

His limb proportions are well within modern human ranges, making the large modern human sample an appropriate reference sample.

The multivariate data, based on femoral and humeral measurements, would seem to pose sufficient problems for stature estimation. However, in almost all situations, the classical model performed substantially better than the other four models by providing the closest estimate of stature to published values. Classical calibration better accommodated both extrapolation and differing allometries. Examination of the fossil hominids shows that Lucy's humeri are in between the chimpanzees and human pygmies, and the combined Pygmy/*Pan* reference sample worked well. This combined sample is composed of 18 human pygmies and 50 chimpanzees. Thus, the chimpanzees are lending more "weight" to the analysis. The effect that the greater number of chimpanzees has on the combined sample is examined with the performance of the chimpanzee sample alone. The chimpanzees provided the closest estimate of Lucy's stature with multivariate models, in terms of Euclidean distance.

Lastly, the multivariate analysis of stature in the Nariokotome Boy shows that this hominid fits well with the modern human ranges for femur and humerus proportions to stature and that his stature is best estimated with the large modern human sample.

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Vita

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