QUANTITATIVE GENETICS OF SEXUAL DIMORPHISM IN HUMAN BODY SIZE

ALAN R. ROGERS
Department of Anthropology, University of Utah, Salt Lake City, UT 84112 USA

AND

ARINDAM MUKHERJEE
Department of Anthropology, Penn State University, University Park, PA 16802 USA

Abstract.—A classical data set is used to predict the effect of selection on sexual dimorphism and on the population means of three characters—stature, span, and cubit—in humans. Given selection of equal intensity, the population means of stature and of cubit should respond more than 60 times as fast as dimorphism in these characters. The population mean of span should also respond far more rapidly than dimorphism, but no numerical estimate of the ratio of these rates was possible. These results imply that sexual dimorphism in these characters can evolve only very slowly. Consequently, hypotheses about the causes of sexual dimorphism cannot be tested by comparing the dimorphism of different human societies. It has been suggested that primate sexual dimorphism may be an allometric response to selection for larger body size. We show that such selection can indeed generate sexual dimorphism, but that this effect is too weak to account for the observed relationship between dimorphism and body size in primates.

Key words.—Anthropometrics, genetic constraints, natural selection, sexual dimorphism, sexual selection.

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On average, men are larger than women. In length measurements, this difference amounts to about 10%, and is relatively constant across human societies (see Fig. 1). Several causes for this dimorphism have been suggested. To evaluate these alternative hypotheses, relationships have been sought between the dimorphism of human populations and several other variables. In this paper we show that these studies provide only the weakest of tests of the alternative hypotheses. Sexual dimorphism evolves so slowly that we cannot expect a close fit between it and the ecological or social circumstances of local populations.

Several hypotheses have been proposed to account for sexual dimorphism in body size. The first, which we owe to Charles Darwin (1872 p. 325), is that of sexual selection. In polygynous species, males must compete for mates, and successful males produce large numbers of offspring. Thus, selection for competitive ability in males is strong. If large males are successful competitors, then selection should tend to increase the size of males in polygynous species. Thus, males of polygynous species should be larger than their mates. In monogamous species, the reward for competitive ability will be more similar in the two sexes, so sexual dimorphism should be less pronounced. Figure 2 shows that this is indeed the case among primate species. This argument has been refined, extended, and applied to diverse taxa by several recent authors (Trivers, 1978; Alexander et al., 1979; Trinkhaus, 1980; Clutton-Brock, 1985). It leads us to expect polygynous human societies to exhibit greater sexual dimorphism than do monogamous societies. However, there are few human societies where the sexes are as nearly equal in size as is typical of monogamous primates. Several authors have compared the dimorphism of polygynous and monogamous human societies. Alexander et al. (1979) find a weak relationship, after distinguishing societies where monogamy is "ecological" from those where it is "socially imposed." Gaulin and Boster (unpubl. data) confirm this result, and go on to report an intriguing puzzle. Populations with socially imposed monogamy are more dimorphic than those with resource defense polygyny. As Gaulin and Boster observe, it is difficult to see how sexual selection could produce this pattern. Elsewhere (Gaulin and Boster, 1985), these authors argue that most of the variation in human sexual dimorphism is

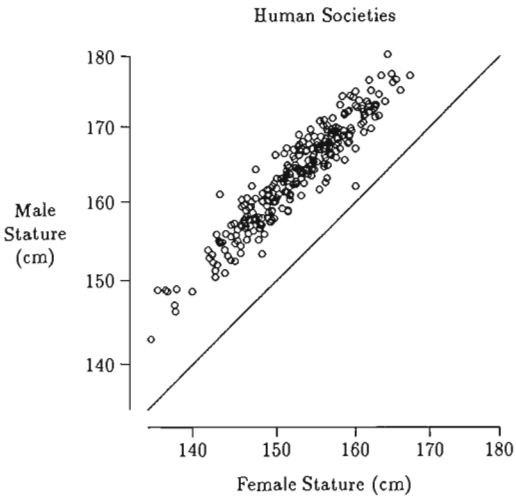

FIG. 1. Sexual dimorphism in stature among human societies. Data were provided by P. Gray.

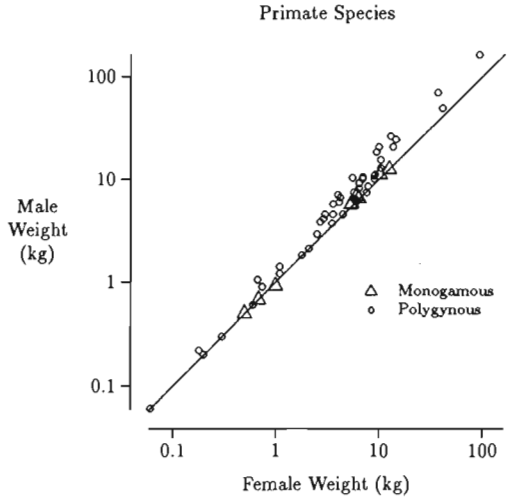

FIG. 2. Sexual dimorphism in body weight among primate species. Data are from Gaulin and Sailer (1984).

sampling error. In short, the relationship between dimorphism and mating system in human societies is puzzling, and seems to make little adaptive sense. We will argue that this is to be expected, in view of the time scale on which sexual dimorphism evolves.

Darwin also recognized (1872 p. 254) that sex differences could arise under natural selection if the two sexes differ in "habits of life." However, he doubted that this could account for the sex difference in human body size since, as he put it, "the women in all barbarous nations are compelled to work at least as hard as the men (Darwin, 1872 p. 325)." Darwin's skepticism notwithstanding, Wolpoff (1976), and Frayer (1980) have recently championed a modern version of this hypothesis. They observe that, in modern foraging societies, hunting is typically done by males, gathering by females. If large body size is useful in hunting, but less so in gathering, then the traditional division of labor would favor larger body size in males than in females. It has been suggested that this hypothesis has two implications: (a) In archeological data, dimorphism should decline as hunting becomes less important, and (b) modern hunting populations should be more dimorphic than other modern populations. Empirical support for this hypothesis is weak. Ruff (1987) finds the predicted difference in a study of the cross-sectional shape of the long bones, but the effect does not show up in the studies of length measurements. Indeed, Wolfe and Gray (1982) find a difference that is the reverse of that predicted. We suggest below that these findings are not unexpected, in view of the rate at which sexual dimorphism in length measurements evolves.

A third hypothesis, proposed by Leutenegger, Cheverud, and Dow (Leutenegger and Cheverud, 1982; Cheverud et al., 1985, 1986), holds that the increased sexual dimorphism in polygynous primates is an incidental effect of selection for larger body size. It suggests, in effect, that genes that make females large make males even larger. This conclusion has been criticized elsewhere (Gaulin and Sailer, 1984; Clutton-Brock, 1985; Ely and Kurland, 1989), and we offer an additional critique below.

To evaluate these hypotheses, we need a theory that can tell us how male and female body sizes will change in response to natural selection. This problem is complicated by the fact that homologous characters in males and females typically show high genetic correlations (Lande, 1980 p. 300), suggesting that many genes may have very similar effects in both sexes. Thus, selection for increased stature in males may increase the stature of both sexes, and have little effect on sexual dimorphism. In this paper, we use Lande's (1980) model of sexual dimorphism to study the data published by Pear-

son and Lee (1903). These data include observations on three characters—stature, span, and cubit—from about 1,100 families.

THEORY

Lande's Model

Let

$$z_\delta = \begin{matrix}\text{male stature}\\ \text{male span}\\ \text{male cubit}\end{matrix}\begin{pmatrix} z_{\delta 1}\\ z_{\delta 2}\\ z_{\delta 3}\end{pmatrix} \quad \text{and}$$

$$z_\varphi = \begin{matrix}\text{female stature}\\ \text{female span}\\ \text{female cubit}\end{matrix}\begin{pmatrix} z_{\varphi 1}\\ z_{\varphi 2}\\ z_{\varphi 3}\end{pmatrix}.$$

In males, we can observe only z_δ, and in females, only z_φ. In this respect, these characters resemble milk yield in dairy cows, and egg production in chickens.

The matrix of phenotypic covariances among male characters is denoted by $\mathbf{P}_\delta$, and that among female characters is $\mathbf{P}_\varphi$. The corresponding additive genetic covariance matrices are denoted by $\mathbf{G}_\delta$ and $\mathbf{G}_\varphi$. The matrix of additive genetic covariances of male with female characters is $\mathbf{B}$. These matrices determine how selection on one character will affect the others.

Let $z = (z_\delta, z_\varphi)^T$ denote the column vector of all six variables, $\bar{z}$ its mean in some generation, and $\bar{z}'$ the mean in the following generation. Here and below, the superscript ^{T} denotes matrix transposition. The change, $\Delta\bar{z} = \bar{z}' - \bar{z}$, caused by one generation of selection is (Lande, 1980)

$$\Delta\bar{z} = \mathbf{G}\mathbf{P}^{-1}s, \tag{1}$$

where s is the "selection differential," a vector whose ith entry is the difference between the mean values of character i before and after selection, and where

$$\mathbf{G} = \frac{1}{2}\begin{pmatrix}\mathbf{G}_\delta & \mathbf{B}\\ \mathbf{B}^T & \mathbf{G}_\varphi\end{pmatrix}, \quad \text{and}$$

$$\mathbf{P} = \begin{pmatrix}\mathbf{P}_\delta & 0\\ 0 & \mathbf{P}_\varphi\end{pmatrix}. \tag{2}$$

(The notation used here differs slightly from that of Lande (1980). His ½**G** is equivalent to our **G**.)

The Intensity of Selection

In Equation 1, the quantity $\beta = \mathbf{P}^{-1}s$ is called the *selection gradient,* and is one measure of the strength of selection. For comparisons, it is useful to reexpress the selection gradient in units of phenotypic standard deviations. Thus, we measure the strength of selection by the *standardized selection gradient* (Lande and Arnold, 1983 p. 1219),

$$\beta' = \mathbf{D}\mathbf{P}^{-1}s,$$

where $\mathbf{D}$ is a diagonal matrix whose diagonal entries are the phenotypic standard deviations, the square roots of the diagonal entries of $\mathbf{P}$. The standardized selection gradient is a multivariate analog of what is generally called the *intensity* of selection in univariate models (Falconer, 1981 p. 175). Equation 1 now becomes

$$\Delta z = \mathbf{G}\mathbf{D}^{-1}\beta'. \tag{3}$$

Thus, for a given intensity of selection the response is proportional to $\mathbf{G}\mathbf{D}^{-1}$. If selection acts only on the ith character, so that all the entries of β' are zero except the ith, then the response of the ith character is

$$\Delta z_i = \beta'_i g_{ii}/\sqrt{p_{ii}}, \tag{4}$$

where g_{ii} and p_{ii} are the ith diagonal entries of $\mathbf{G}$ and $\mathbf{P}$, respectively, and β'_i is the ith entry of β'. We use this formula below to compare the response of each character to a given intensity of selection.

Sexual Dimorphism and the Population Mean

We measure sexual dimorphism by the difference between male and female characters, and denote the vector of such differences by $u = \bar{z}_\delta - \bar{z}_\varphi$. The population mean is the average of mean male and mean female character values, $v = (\bar{z}_\delta + \bar{z}_\varphi)/2$. Selection on one of these vectors may produce a correlated response in the other. To allow for this effect, we study the evolution of $\tilde{z} = (u^T v^T)^T$, a vector whose first three entries measure dimorphism, and whose last three entries contain the population means of the three characters. To derive a recursion for $\tilde{z}$, note that

$$\mathbf{C}\bar{z} = \tilde{\bar{z}}, \quad \text{where} \quad \mathbf{C} = \begin{pmatrix}\mathbf{I} & -\mathbf{I}\\ \mathbf{I}/2 & \mathbf{I}/2\end{pmatrix}.$$

Now multiply both sides of (1) by **C** to obtain

$$\begin{aligned}\Delta\tilde{\bar{z}} &= \mathbf{C}\Delta\bar{z} \\ &= \mathbf{CGP}^{-1}s \\ &= [\mathbf{CGC}^T] \\ &\quad \cdot[(\mathbf{C}^T)^{-1}\mathbf{P}^{-1}\mathbf{C}^{-1}][\mathbf{C}s] \\ &= \tilde{\mathbf{G}}\tilde{\mathbf{P}}^{-1}\tilde{s}, \end{aligned} \tag{5}$$

where $\tilde{\mathbf{G}}$ and $\tilde{\mathbf{P}}$ are as defined by Equations 6–8 below.

Equation 5 shows that the vector $\tilde{\bar{z}}$ obeys Equation 1, after replacing s with $\tilde{s} = \mathbf{C}s$, $\mathbf{G}$ with $\tilde{\mathbf{G}}$, and $\mathbf{P}$ with $\tilde{\mathbf{P}}$. Sexual dimorphism (u) and the population mean (v) evolve independently of each other only if the off-diagonal blocks of $\tilde{\mathbf{G}}$ are zero. Equation 7 shows that, in general, this condition will not hold, and selection acting on the population mean will produce a correlated response in sexual dimorphism (Cheverud et al., 1985). By analogy with Equations 3–4 we can also write

$$\Delta\tilde{z} = \tilde{\mathbf{G}}\tilde{\mathbf{D}}^{-1}\tilde{\beta}' \tag{9}$$

$$\Delta\tilde{z}_i = \tilde{\beta}_i'\tilde{g}_{ii}/\sqrt{\tilde{p}_{ii}} \tag{10}$$

where $\tilde{\beta}' = \mathbf{C}\beta'$ gives, in its first three entries, the intensity of selection on dimorphism, and in it last three, the intensity of selection on the population means.

Data Analysis

The Data

In 1903, Pearson and Lee published the results of what was then the most extensive study ever of the inheritance of human physical characteristics. These data occupy a distinguished position in the history of population genetics, since they were the basis of R. A. Fisher's (1918) famous demonstration that the principles of Mendelian inheritance could account continuous characters. Pearson and Lee (1903) collected data on stature, span, and cubit (forearm length), from about 1,100 families. Their published data include (a) the mean and standard deviation of each character, within each of four categories of individuals: husbands, wives, adult sons, and adult daughters, (b) standard deviations of each variable within each category, (c) correlations of each variable between each pair of categories of individual, and (d) the "cross-correlations" of each pair of variables between each pair of categories of individual. The mean values in Table 1 illustrate both the excess of male values over females values, and a tendency for offspring to be larger than their parents.

TABLE 1. Means of males and females. The first four columns contain the mean values of the three characters in husbands, sons, wives, and daughters, respectively. The last column contains the ratios of the sum of the two values for males to the sum of the two values for females. Source: Pearson and Lee (1903).

Character	Husbands	Sons	Wives	Daughters	$\frac{h+s}{w+d}$
Stature	67.68	68.65	62.48	63.87	1.08
Span	68.67	69.94	61.80	63.40	1.11
Cubit	18.31	18.52	16.51	16.75	1.11

Estimation of $\mathbf{G}$, $\mathbf{P}$, $\tilde{\mathbf{G}}$, *and* $\tilde{\mathbf{P}}$

For each category of individual, and each pair of categories, Pearson and Lee (1903) provide a 3 × 3 correlation matrix. For example, the correlation matrix for husbands and sons is

$$\mathbf{R}_{hs} = \begin{array}{c} \\ z_{\delta 1} \\ z_{\delta 2} \\ z_{\delta 3} \end{array} \begin{array}{c} \begin{array}{ccc} z_{\delta 1} & z_{\delta 2} & z_{\delta 3} \end{array} \\ \begin{pmatrix} 0.514 & 0.418 & 0.370 \\ 0.399 & 0.454 & 0.399 \\ 0.355 & 0.400 & 0.421 \end{pmatrix} \end{array},$$

a matrix whose ijth entry is the correlation

$$\tilde{\mathbf{G}} = \mathbf{CGC}^T \tag{6}$$

$$= \left(\begin{array}{c|c} \mathbf{G}_\delta + \mathbf{G}_\varphi - \mathbf{B}^T - \mathbf{B} & (\mathbf{G}_\delta - \mathbf{G}_\varphi + \mathbf{B} - \mathbf{B}^T)/2 \\ \hline (\mathbf{G}_\delta - \mathbf{G}_\varphi + \mathbf{B}^T - \mathbf{B})/2 & (\mathbf{G}_\delta + \mathbf{G}_\varphi + \mathbf{B} + \mathbf{B}^T)/4 \end{array}\right), \tag{7}$$

$$\tilde{\mathbf{P}} = \mathbf{CPC}^T$$

$$= \left(\begin{array}{c|c} \mathbf{P}_\delta + \mathbf{P}_\varphi & (\mathbf{P}_\delta - \mathbf{P}_\varphi)/2 \\ \hline (\mathbf{P}_\delta - \mathbf{P}_\varphi)/2 & (\mathbf{P}_\delta + \mathbf{P}_\varphi)/4 \end{array}\right). \tag{8}$$

of character $z_{\delta i}$ in fathers with character $z_{\delta j}$ in sons. The 12 correlation matrices for pairs of biological relatives are denoted as

$$\begin{array}{l} \\ \text{Husband} \\ \text{Son} \\ \text{Wife} \\ \text{Daughter} \end{array} \begin{array}{c} \begin{array}{cccc} \text{Husband} & \text{Son} & \text{Wife} & \text{Daughter} \end{array} \\ \begin{pmatrix} & \mathbf{R}_{hs} & & \mathbf{R}_{hd} \\ \mathbf{R}_{sh} & \mathbf{R}_{ss} & \mathbf{R}_{sw} & \mathbf{R}_{sd} \\ & \mathbf{R}_{ws} & & \mathbf{R}_{wd} \\ \mathbf{R}_{dh} & \mathbf{R}_{ds} & \mathbf{R}_{dw} & \mathbf{R}_{dd} \end{pmatrix} \end{array}.$$

There are also four matrices of correlations within categories. These are denoted, using a single subscript, by $\mathbf{R}_h$, $\mathbf{R}_s$, $\mathbf{R}_w$, and $\mathbf{R}_d$, for husbands, sons, wives, and daughters, respectively. In addition to correlation matrices, we also define four vectors of means (z_h, z_s, z_w, and z_d), and four matrices ($\mathbf{S}_h$, $\mathbf{S}_s$, $\mathbf{S}_w$, and $\mathbf{S}_d$) containing standard deviations in their diagonal entries and zeroes in their off-diagonal entries, using the same subscripts to distinguish categories of individual.

The model we are using assumes the standard deviation to be independent of the mean. In these data, however, the standard deviation is roughly proportional to the mean. If the original data were available, we could correct this problem by analyzing the logarithms of the variables instead of the variables themselves. Unfortunately, this is not possible because the published data are grouped into nonlogarithmic size categories. Instead, we use the "delta method" (Bulmer, 1980 pp. 82–83) to approximate the logarithmic transformation. The means and covariances of the transformed variables (say x and y) are approximately $E\{\log x\} \approx \log \bar{x} - \mathrm{Var}\{x\}/2\bar{x}^2$ and $\mathrm{Cov}\{\log x, \log y\} \approx \mathrm{Cov}\{x, y\}/\bar{x}\bar{y}$. These approximations are accurate when the standard deviations of the raw data are small compared to the means. In these data, the raw standard deviations were all between 4% and 5% of the means.

There is also a secular trend in these data: the offspring are larger than their parents. The transformation just discussed removed the effect of this trend on the standard deviations, and to remove it from the means, we simply ignored the offspring means, estimating the male and female mean vectors as $\hat{z}_\delta = z_h$ and $\hat{z}_\varphi = z_w$, respectively.

The next step is to convert the various correlations into covariances by multiplying each correlation by the product of the two relevant standard deviations. For example, the phenotypic covariance matrix between husbands and sons is $\mathbf{P}_{hs} = \mathbf{S}_h\mathbf{R}_{hs}\mathbf{S}_s$. Since all the biological relationships in these data have a coefficient of relationship of 0.5, we can obtain the additive genetic covariance matrix for each pair of relatives by multiplying the phenotypic covariance matrix by 2. Thus, $\mathbf{G}_{hs} = 2\mathbf{P}_{hs}$, $\mathbf{G}_{hd} = 2\mathbf{P}_{hd}$, and so forth, assuming that environmental effects on different individuals are uncorrelated. The covariances among siblings ($\mathbf{P}_{ss}$, $\mathbf{P}_{dd}$, and $\mathbf{P}_{sd}$) provide only a biased estimate of the additive variance, since their values are inflated by any dominance variance that may be present. The entries in these matrices are, on average, between 10 and 25 percent larger than the corresponding entries of the parent-offspring covariance matrices, suggesting that dominance variance is substantial in these data. Therefore, covariances between siblings were ignored in estimating $\mathbf{G}$.

The various matrices of interest were estimated as follows.

$$\begin{aligned} \hat{\mathbf{P}}_\delta &= (\mathbf{P}_h + \mathbf{P}_s)/2 \\ \hat{\mathbf{P}}_\varphi &= (\mathbf{P}_w + \mathbf{P}_d)/2 \\ \hat{\mathbf{G}}_\delta &= 2\mathbf{P}_{hs} \\ \hat{\mathbf{G}}_\varphi &= 2\mathbf{P}_{wd} \\ \hat{\mathbf{B}} &= \mathbf{P}_{hd} + \mathbf{P}_{sw} \end{aligned}$$

Finally, $\mathbf{G}$ and $\mathbf{P}$ were estimated using Equation 2, and the resulting estimates were symmetrized by averaging each matrix with its transpose. The resulting estimates are shown in Equations 11–12. We now apply Equations 6 and 8 to obtain $\tilde{\tilde{\mathbf{G}}}$ and $\tilde{\tilde{\mathbf{P}}}$, shown in Equations 13–14. The upper left quadrant of each matrix contains the variances and covariances of dimorphism (the differences between male and female characters). Similarly, the lower right quadrant refers to the population means, and the off-diagonal quadrants contain covariances between dimorphism and the population means. Since the entries of the off-diagonal quadrant of $\tilde{\tilde{\mathbf{G}}}$ are not zero, selection on the mean will produce a correlated response in dimorphism.

$$\hat{\mathbf{G}} = \left(\begin{array}{ccc|ccc} 0.809 & 0.731 & 0.758 & 0.789 & 0.741 & 0.723 \\ 0.731 & 0.923 & 0.949 & 0.741 & 0.943 & 0.897 \\ 0.758 & 0.949 & 1.168 & 0.771 & 0.896 & 1.161 \\ \hline 0.789 & 0.741 & 0.771 & 0.793 & 0.740 & 0.741 \\ 0.741 & 0.943 & 0.896 & 0.740 & 0.953 & 0.894 \\ 0.723 & 0.897 & 1.161 & 0.741 & 0.894 & 1.191 \end{array}\right) /1000 \tag{11}$$

$$\hat{\mathbf{P}} = \left(\begin{array}{ccc|ccc} 1.575 & 1.418 & 1.386 & 0 & 0 & 0 \\ 1.418 & 2.034 & 1.793 & 0 & 0 & 0 \\ 1.386 & 1.793 & 2.775 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 1.567 & 1.442 & 1.390 \\ 0 & 0 & 0 & 1.442 & 2.109 & 1.773 \\ 0 & 0 & 0 & 1.390 & 1.773 & 2.832 \end{array}\right) /1000 \tag{12}$$

$$\hat{\tilde{\mathbf{G}}} = \left(\begin{array}{ccc|ccc} 0.025 & -0.011 & 0.005 & 0.008 & -0.004 & -0.015 \\ -0.011 & -0.011 & 0.050 & -0.005 & -0.015 & 0.028 \\ 0.005 & 0.050 & 0.038 & 0.032 & 0.027 & -0.012 \\ \hline 0.008 & -0.005 & 0.032 & 0.795 & 0.738 & 0.748 \\ -0.004 & -0.015 & 0.027 & 0.738 & 0.941 & 0.909 \\ -0.015 & 0.028 & -0.012 & 0.748 & 0.909 & 1.170 \end{array}\right) /1000 \tag{13}$$

$$\hat{\tilde{\mathbf{P}}} = \left(\begin{array}{ccc|ccc} 3.141 & 2.860 & 2.775 & 0.004 & -0.012 & -0.002 \\ 2.860 & 4.143 & 3.566 & -0.012 & -0.037 & 0.010 \\ 2.775 & 3.566 & 5.607 & -0.002 & 0.010 & -0.029 \\ \hline 0.004 & -0.012 & -0.002 & 0.785 & 0.715 & 0.694 \\ -0.012 & -0.037 & 0.010 & 0.715 & 1.036 & 0.892 \\ -0.002 & 0.010 & -0.029 & 0.694 & 0.892 & 1.402 \end{array}\right) /1000 \tag{14}$$

Response Ratios

The values in the upper left quadrant of $\hat{\tilde{\mathbf{G}}}$ are much smaller than those in the lower right quadrant. This implies that sexual dimorphism will respond to selection more slowly than will the population mean. We can make this statement more precise using Equation 10. Suppose that selection acts only on dimorphism in stature, so that $\tilde{\beta}'_2 = \tilde{\beta}'_3 = \cdots = \tilde{\beta}'_6 = 0$. Then Equation 10 tells us that the response of stature will be $\Delta\tilde{z}_1 = \tilde{\beta}'_1 \times 0.000025/\sqrt{0.003141} = \tilde{\beta}'_1 \times 0.000439$. Similarly, if selection acts only on the population mean stature, the response in this character is $\Delta\tilde{z}_4 = \tilde{\beta}'_4 \times 0.000795/\sqrt{0.000785} = \tilde{\beta}'_4 \times 0.028362$. For equal intensities of selection, the latter response is $0.028362/0.000439 = 64.6$ times as large as the former. Thus, the population mean responds to selection about 65 times as fast as does sexual dimorphism. This response ratio is included in Table 2 along with that of cubit. The population mean of both of these characters responds more than 60 times as fast as dimorphism.

No sensible estimate of the response ratio for span could be made because $\hat{\tilde{\mathbf{G}}}$ contains a negative estimate of $\tilde{g}_{22}$, the additive genetic variance of dimorphism in span. It is impossible for a variance to be negative, so the true value of $\tilde{g}_{22}$ must be positive. However, it is not surprising that our estimate is negative. Any unbiased estimator of a parameter whose lower bound is zero must occasionally take negative values (Kendall and Stuart, 1979 p. 5). Our negative estimate of $\tilde{g}_{22}$ implies only that the true value of the parameter is probably near zero, and thus that dimorphism in stature evolves far

TABLE 2. Heritabilities and response ratios. Shown are h^2_s, the heritability of the characters in males, h^2_v, the heritability of the character in females, and "response ratio," the ratio of response in the population mean to response in sexual dimorphism when the intensity of selection (β'_i) is held constant. No numerical estimate of the response ratio of span could be made for reasons that are discussed in the text.

Character	h^2_s	h^2_v	Response ratio
Stature	0.5140	0.5059	65
Span	0.4538	0.4519	***
Cubit	0.4210	0.4206	61

more slowly than the population mean, in qualitative agreement with the numerical results obtained for the other two characters.

Are Sex Differences a Correlated Response to Selection on the Mean?

Cheverud, Dow, and Leutenegger (Leutenegger and Cheverud, 1982; Cheverud et al., 1985, 1986) point out that sex differences in body size may be generated even when the selection pressures acting on males and females are identical. If the heritability of male characters exceeds that of female characters, they say, then male body size might respond to selection faster than that of females. Thus, sexual dimorphism can result from selection for larger body size. Gaulin and Sailer (1984) are skeptical of this suggestion. They point out that since the growth and development of males appears to respond more to environmental influences than does that of females, the heritability of male characters should be lower, not higher. This seems plausible, yet the male heritabilities listed in Table 2 slightly exceed those of female characters. These excesses are slight, however, and of doubtful statistical significance.

Let us address this issue more directly, using Equation 9 to study the effect of selection for increased body size, and assuming that the selection pressures acting on each sex are identical. For example, suppose that the standardized selection gradient is $\tilde{\beta}' = (0, 0, 0, 1, 1, 1)^T$. This says that selection is acting to increase the population mean of all three characters, but has no direct effect on dimorphism. Substituting into Equation 9 gives $\Delta\tilde{z} = (-0.00023, 0.00011, 0.00168, 0.07128, 0.07986, 0.08620)^T$, where the first three entries give the response in sexual dimorphism, and the last three the response in the population mean. The responses of dimorphism in stature, span, and cubit are -0.3%, 0.1%, and 2.0%, respectively, of the responses in the corresponding population means. Thus, for each unit of increase in the population mean of cubit, the correlated in response in dimorphism should be 0.02 units. The correlated responses in the other two characters should be an order of magnitude smaller.

How does this compare to the relationship between dimorphism and weight among primates? Using the data in Figure 2, we find that the linear regression of log(male weight/female weight) against log female weight is equal to 0.0672. Thus, for each unit of increase in female weight there is, on average, an increase of 0.0672 units in sexual dimorphism. This effect is three times greater than that predicted for dimorphism in cubit, and many times greater than those predicted for the other two characters. Thus, it seems unlikely that dimorphism in primates has evolved as a correlated response to selection for increased body size, as Leutenegger, Cheverud, and Dow have suggested.

It might be objected that we are comparing apples with oranges here, since our quantitative genetic estimates refer to length variables, whereas the primate data are for body weight. However, weight scales with the cube of length, so our results on length variables are roughly comparable with weight$^{1/3}$. Replacing the variable "weight" with "weight$^{1/3}$" has not the slightest effect on the regression coefficient in the preceding paragraph, since the exponents cancel in the course of the analysis. Thus, our comparison seems sensible.

On the other hand, we have not shown that the human **G** matrix is typical of primates in general, and we cannot claim great accuracy for our estimate of **G**. Thus, it remains possible that the genetic covariances between dimorphism and the population mean are often stronger than our data suggest. If so, the Leutenegger-Cheverud-Dow effect may have been important in the evolution of primate sexual dimorphism. The

data of Pearson and Lee, however, provide no support for this hypothesis.

Discussion and Conclusions

The additive genetic covariances between male and female length measurements are extremely high, suggesting that genes for such characters tend to affect males and females in the same way. The result is that the mean of the two sexes responds to selection many times faster than does sexual dimorphism. For example, if selection took 100 years to produce a one inch change in human stature, it might well take 6,000 years to accomplish an equivalent change in sexual dimorphism, assuming that it operated with equal force in the two cases. The slow response of sexual dimorphism implies that it can track environmental changes only slowly. We should not expect sexual dimorphism to be well adapted to environmental factors that vary at even moderate rates.

This raises several questions. If sexual dimorphism is indeed shaped by sexual selection, then how strongly should it be associated with, say polygyny? On the other hand, if sexual dimorphism is shaped by sex differences in subsistence activities, then what sort of relationship should be expected between the economy of a population and its sexual dimorphism? Unfortunately, neither of these questions can yet be answered. To answer the first, we would need to know how the mating system has varied over time, and also how the strength and direction of selection (i.e., the value of β') are affected by the mating system. An answer to the second question would require analogous knowledge of the history and selective effects of changes in the sexual division of labor. Lacking this knowledge, we can only observe that sexual dimorphism will respond to natural selection far more slowly than will overall size.

Still, it seems clear that mating systems in some societies have changed far too rapidly to be tracked by natural selection. For example, many of today's monogamous Mormons are descended from polygynous great grandparents who were descended from monogamous ancestors a few generations back. If such changes have been common in human history, then the relationship between dimorphism and system of mating in modern human societies will tell us little. This relationship may be weak or absent even if human sexual dimorphism has been shaped by sexual selection.

Similar comments apply to the Wolfpoff-Frayer hypothesis, which proposes that large body size is an adaptation that helps men hunt game. This hypothesis does not imply, as is often assumed, that modern hunting populations should be more sexually dimorphic than modern farming populations. Modern farmers are descended from hunters, and many modern hunters probably have farmers among their recent ancestors (Lathrap, 1968; Cashdan, 1986). Since sexual dimorphism evolves only slowly, there need be no relationship between these variables even if the Wolpoff-Frayer hypothesis is correct.

Finally, Leutenegger, Cheverud, and Dow were right in arguing that selection for larger mean body size could generate changes in sexual dimorphism. Our estimates imply that selection for greater overall size would generate some sexual dimorphism as a correlated response. However, this response seems far too weak to account for the observed relationship between dimorphism and body size in primates.

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