

Fertility, offspring survival, and adaptive value as related to morphological traits – methodological and interpretation problems

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ABSTRACT A great deal of research has been carried out in order to find a relationship between somatic traits and fertility, offspring survival rate and adaptive value. However, the results of these studies lack consistency. The reason behind these discrepancies is the use of inadequate statistical methods and the application of unreliable principles of interpretation. The purpose of this paper is to indicate the methods of data analysis and result interpretation, which permit optimum utilisation of the information contained in a given sample and make it possible to draw the correct conclusions.

KEY WORDS fertility, offspring survival, adaptive value, curve fitting

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Introduction

An individual's fitness and its constituents: fertility and offspring survival rate have been a subject of anthropologists' interest for many reasons. One of the most important ones is the fact that the adaptive value, differentiated with regard to the values of specified traits, can bring about intergenerational changes of the distribution (genotype values) of these traits, or in other words their evolution. This holds true irrespective of the degree to which the relationship of fitness with phenotype traits is biologically or culturally conditioned. The search for

such relationships is very difficult, since in contemporary populations, and in the highly developed populations in particular, opportunity for natural selection through differential survival rate is weak, while the intensity of natural selection through differential fertility is considerably lower than the opportunity for selection expressed by the intrapopulation differentiation of fertility [LASKER & THOMAS 1976; WOLAŃSKI & HENNEBERG 1990]. Despite these difficulties, the purpose of a considerable number of studies has been to find a relationship between somatic traits and fertility, survival rate and adaptive value.

In this analysis I will take into account only the most common morphological traits such as body height, body weight and body built indices (Quetelet index, body mass index (BMI) and ponderal index). It turns out that the results of studies conducted by various researchers are frequently very different and the authors frequently draw different conclusions about the type of selection exerting an effect on a given trait. I believe that a considerable proportion of these discrepancies result from the use of inadequate analytical methods and employment of unreliable principles of inference. Therefore, the purpose of this paper is to carry out a critical analysis of statistical methods of data processing and of the ways of inference with regard to the biological significance of the relationships found. Developing of methodological standards of research on relationships between morphological traits and fitness and establishing reliable principles of interpretation of results of such research would be instrumental in better utilisation of the information contained in a sample, in obtaining of at least partial comparability of results of different studies and in drawing correct conclusions from the data available.

Literature review

Table 1 specifies the results of research on the relationship between fertility, survival rate and adaptive value, and morphological features such as body height, body weight, birth body weight, BMI, Quetelet index and ponderal index. The column with the head "Adaptive trait" specifies the trait or traits under research that can be treated as a measure or a constituent of adaptive value.

Some types of relationships shown in the Table 1 are uncontroversial. The relationship between survival rate and birth body weight is curvilinear with the maximum value obtained for the body weight several hundred grams in excess of the mean value [KARN & PENROSE 1951; FRACCARO 1956; BATTAGLIA *et al.* 1966; ELLIS 1973]. Furthermore, taller women seem to have fewer miscarriages, stillbirths and more rarely require surgical interventions during labour [BAIRD 1949, 1952; BRESLER 1962].

The relationship between the survival rate of offspring and body height is not that clear-cut. Majority of the studies indicate a positive relationship between these traits [CONTERIO & CAVALLISFORZA 1960; FURUSHO 1964; MARTORELL 1981; JURYNEC 1986; DZIEWIĘCKI 1994]. DZIEWIĘCKI [1994] observed also a higher survival rate among children of women with greater body mass and higher BMI and Quetelet index. However, two other studies [FRISANCHO *et al.* 1973; DEVI *et al.* 1985] indicated a negative relationship between offspring survival rate and parental body height. The results obtained by FRISANCHO *et al.* [1973] used to be explained with a low economic status and malnutrition of the population under study (the Peruvian Andes) – shorter individuals have smaller nutritional requirements and as a result they exhibit higher survival rate in difficult living conditions. A similar explanation can be applied to the results obtained by DEVI *et al.* [1985] who studied a social class in India living under very poor conditions. Accordingly, one can venture the following generalisation: in populations that do not suffer malnutrition and have access to medical care at a decent level

Table 1. List of results of researches on relationships between fertility and survival rate, and some morphological traits

Author	Sample	Morphological trait	Adaptive trait	Relation
GALTON [1886]	unknown	H♀	NL	-
DAVENPORT [1923]	USA, 506 couples	BMI	NL	+
FRASSETO [1934]	Italy, 1,450 families	BMI	NL	+
BAIRD [1949, 1952]	Scotland ♀	H♀	MC, SB	-
KARN, PENROSE [1951]	USA, 13,370 newborns	BW	PSUR	⊂
FRACCARO [1956]	Italy, 5,486 newborns	BW	PSUR	⊂
CLARK, SPUHLER [1959]	USA, unmarried: 97 ♀, 43 ♂ married: 227 ♀, 187 ♂	W♂ H, W♀	NLB	+ 0
CONTERIO, CAVALLI-SFORZA [1960]	Italy, recruits	H♂	NL SUR (0-13)	⊂ +
BRESLER [1962]	USA, 272 ♀	H♀	NP, MC SB	0 -
FURUSHO [1964]	Japan, villages, 533 families	H	NLB SUR (0-20)	- +
BATTAGLIA <i>et al.</i> [1966]	USA, 68,343 newborns	BW	NL PSUR	0 ⊂
DAMON, THOMAS [1967]	USA, 2,631 ♂	H, W, PI♂	NLB	0
ELLIS [1973]	USA, 8,382 newborns	BW	PSUR	⊂
FRISANCHO <i>et al.</i> [1973]	Peruvian Andes, 145 families	H♀	SUR (0-19) MC, SB	- 0
MITTON [1975]	reanalysis of data of Clark & Spuhler [1959]	H♂ H♀	NLB	⊂ 0
reanalysis of data of Damon & Thomas [1967]		H♂		⊂
VETTA [1975]	reanalysis of data of Damon & Thomas [1967]	H♂, W♂	NLB	⊂
LASKER, THOMAS [1976]	Mexico, 480 families	H, W	NLB, NS, SSUR	0
BAILEY, GARN [1979]	USA, 4,829 ♀	H, PI♀ W♀	NLB	- 0
MUELLER [1979]	Colombian Andes, 366 ♀, 338 ♂	FAT BONE	NL	+ ⊂
SZEMIK [1980]	Poland, 241 city, 250 village ♀	H♀	NP	-
MARTORELL <i>et al.</i> [1981]	Guatemala, 380 ♀	H♀	NP SUR (0-1, -2, -5), NL	0 +
MUELLER <i>et al.</i> [1981]	Mexico, 159 ♂, 121 ♀	H, W, BMI	NL	0
SCOTT, BAJEMA [1982]	USA, 621 ♂, 610 ♀	H, W♂ W♀, BMI W, BMI♀ (sa=12)	NLB	0 + -
BRUSH <i>et al.</i> [1983]	New Guinea, 150 ♀	H♀ W♀	NLB, NL	⊂ +
GOLDSTEIN, KOBLYANSKY [1984]	USA, 305 Mexican families	H, W	NL	⊂
DEVI <i>et al.</i> [1985]	India, 291 families	H♀	NP, SUR (0-1), NL	-
JURYNEC [1986]	Poland, 2569 recruits	H♂	SSUR	+
SZEMIK, WOLAŃSKI [1989]	Poland, 277 families	H, W♂	NP	-
DZIEWIĘCKI [1994]	Poland, 935 ♀	H♂, (W, BMI, Q)♀ (W, BMI, Q)♀	SUR NL	+ +
DZIEWIĘCKI [1998]	Poland, 277 families	H, (W, BMI, Q)♂ H♀	NL NL	- ⊂
PAWŁOWSKI <i>et al.</i> [2000]	Poland, 3201 ♂	H♂	NL	+

Abbreviations: H – height, W – weight, BW – birth weight, BMI – body mass index, Q – Quetelet index, PI – ponderal index, FAT – fat component, BONE – bone component, sa – skeletal age, NP – number of pregnancies, NLB – number of live-born offspring, NL – number of living offspring, NS – number of siblings, SUR (0-x) – offspring survival in first x years of life, PSUR – perinatal survival, SSUR – sibling survival, MC – miscarriages, SB – stillbirths, + – positive relation, - – negative relation, 0 – no relation, ⊂ – reversed-U-shape relation.

Table 2. List of researches grouped by results obtained, on relation between fertility and morphological traits

	Height	Weight	BMI	Quetelet index	ponderal index
number of live-born offspring					
+		Clark, Spuhler [1959] ♂ Scott, Bajema [1982] ♀ Brush <i>et al.</i> [1983] ♀	Scott, Bajema [1982] ♀		
-	Furusho [1964] Bailey, Garn [1979] ♀ Szemik [1980] ♀ (NP) Devi <i>et al.</i> [1985] ♀ (NP) Szemik, Wolański [1989] ♂ (NP)	Szemik, Wolański [1989] ♂ (NP)			Bailey, Garn [1979] ♀
∩	Conterio, Cavalli-Sforza [1960] ♀ Mitton [1975] ♂ Vetta [1975] ♂ Brush <i>et al.</i> [1983] ♀ Goldstein, Kobylansky [1984]	Vetta [1975] ♂ Goldstein, Kobylansky [1984]			
0	Clark, Spuhler [1959] Damon, Thomas [1967] ♂ Lasker, Thomas [1976] Martorell <i>et al.</i> [1981] ♀ (NP) Mueller [1981] Scott, Bajema [1982]	Clark, Spuhler [1959] ♀ Lasker, Thomas [1976] Bailey, Garn [1979] ♀ Mueller [1981] Scott, Bajema [1982] ♂	Mueller [1981]		Damon, Thomas [1967] ♂
number of living offspring					
+	Martorell <i>et al.</i> [1981] ♀ Pawłowski <i>et al.</i> [2000] ♂	Mueller [1979] Brush <i>et al.</i> [1983] ♀ Dziewięcki [1994] ♀	Davenport [1923] Frassetto [1934] Dziewięcki [1994] ♀	Dziewięcki [1994] ♀	
-	Galton [1886] Devi <i>et al.</i> [1985] ♀ Dziewięcki [1994]	Dziewięcki [1994] ♂	Dziewięcki [1994] ♂	Dziewięcki [1994] ♂	
∩	Mueller [1979] Brush <i>et al.</i> [1983] ♀ Dziewięcki [1998]				
0	Furusho [1964]				

offspring survival is positively correlated with the body height of the parents. In populations, which do not satisfy these requirements low body height has adaptive value, which means it increases the chances of survival.

In the results regarding the relationship between fertility, body weight and body built indices such as Quetelet index, BMI or ponderal index we have to do with a total chaos (at least that is the first impression). Table 2 contains a list of research projects by the results obtained with regard to the relationship between fertility and morphological traits. However, there is no uniform understanding of the notion of fertility among the authors. Some of them use the notion in reference to the number of offspring alive at the time of the study, others understand it as the number of live births, and still others as the number of past pregnancies. In Table 2, I separated the number of births from the number of offspring, including the studies referring to the number of pregnancies to the former group and marking them with the "NP" symbol. Individual columns in the table refer to particular morphological traits and the lines refer to a type of relationship between fertility and a given morphological trait. These are: positive relationship (+), negative (-), curvilinear (∩) or no relationship (0).

Results referring to a relationship between broadly understood fertility and body built are scarce. They suggest that for both sexes sturdier individuals, that is persons with higher BMI and Quetelet index values, but with lower values of ponderal index are characterised by higher fertility. An inverse relationship was observed only by DZIEWIĘCKI [1994] in men.

A large proportion of studies resulted in finding no relationship between fertility and body weight. However, the studies that did reveal the existence of such a relationship usually indicated its positive character, which means that individuals with higher weight have more numerous offspring delivered, or alive at the time of the study. Results obtained by SZEMIK & WOLAŃSKI [1989] and DZIEWIĘCKI [1994] for men are an exception to this rule, both of them show a negative relationship. Two studies [VETTA 1975; GOLDSTEIN & KOBLYANSKY 1984] indicated a curvilinear relationship, but the analysis of Vetta's results (Table 3) proves that in fact it is a positive relationship, only it is better described by a curve than by a straight line. A curvilinear relationship neither excludes directional selection nor does it indicate the existence of stabilising selection, however one can often come across such hasty conclusions in the literature [SZEMIK 1989].

Table 3. Mean number of children of individuals in a given body weight category and the number of individuals within a given category [VETTA 1975]

parental body weight	< 49	50-59	60-69	70-79	> 80
number of children	2.55	2.62	2.69	2.76	2.61
number of individuals	31	426	767	243	44

There is no certainty whether fertility indeed decreases when parental body weight exceeds 73 kilograms or whether it only grows slower (then also the relationship would be of curvilinear character). The last category contains only a small number of individuals, hence the error of the mean from the sample may be high. Assuming that variance of fertility is 1, error of the mean for this category will equal $1/\sqrt{44} \approx 0.15$ child.

From among morphological traits body height is the one, which is most frequently studied with regard to its relationship with fertility and adaptive value. For this reason my further discussion of the relationship between fertility, survival rate and adaptive value, and morphological traits will be conducted with the use of this very trait's example.

The final results of a research and their interpretation are composed of many determinants and all of them may be responsible for the discrepancies present in the results of research by different authors. Let us distinguish three stages at which particular determinants appear: data collection stage, data analysis stage and the stage of the interpretation of results. Methodological and interpretation analysis of the research on the relationships under discussion may be carried out in the three following steps corresponding to the above mentioned stages.

Data collection stage

Human populations are differentiated with regard to a great number of traits and due to this fact research results may be determined by a characteristics of a given population under study. Part of the studies performed concern poor, malnourished populations living in very bad conditions [MUELLER 1979; MARTORELL *et al.* 1981; BRUSH *et al.* 1983; DEVI *et al.* 1985], other works refer to populations with medium (for instance Poland) or high (for instance the USA) living standards. Part of studies concern rural populations, while others deal with urban ones. In statistical terms a male population is different than a female population. It is an important distinction, since it frequently happens that a given research detects a relationship only for one of the

sexes. However, no systematic difference between sexes is observable. The same is true of the pairs: rural areas – urban areas and low – high living standard (still, we remember that the living standard had an effect on the nature of the relationship between offspring survival rate and body height).

In this stage we should include issues related to the subjects' age. Firstly, for fertility analysis a sample of individuals at post-reproductive age would be most suitable. Only a small proportion of studies satisfies this requirement [DAMON & THOMAS 1967; BAILEY & GARN 1979; SCOTT & BAJEMA 1982; DZIEWIĘCKI 1998]. Secondly, if we are interested in reproductive success (fitness), we should take into account only adult offspring. The number of non-adult offspring may be an indicator of fertility rather than fitness, if we have to do with differentiated survival rate at a later age.¹ This condition too is satisfied only by a minor proportion of the studies [FURUSHO 1964].

The stage of data collection involves also data elimination. DAMON & THOMAS [1967] rejected childless males, DZIEWIĘCKI [1998] excluded childless females, while PAWŁOWSKI *et al.* [2000] excluded males with body height from beyond the range $\bar{x} \pm 2S$.

Data analysis stage

The principal element of this stage is the statistical analysis of the material collected. The three following statistical methods: the Student's t-test, analysis of

¹ The number of offspring surviving till the adult age is not an accurate measure of fitness either. This is so because differentiated survival rate can occur also at a later age, and furthermore the number of offspring may correlate negatively with the number of these offspring's offspring.

variance and analysis of regression are the most popular methods used in the checking of the presence and identifying of the nature of the relationship between body height and fertility and adaptive value. Analysis of variance and the Student's t-test require categorisation of variables, which entails a loss of information. Student's t-test in particular is here a tool of low precision, since it requires two categories. As a result the entire range of variation of the trait needs to be split into two parts; the mean value or the median can serve as a criterion of the split, or two extreme with regard to the percentile value groups can be distinguished [BAILEY & GARN 1979; SZEMIK 1980; DEVI *et al.* 1985; SZEMIK & WOLAŃSKI 1989]. Furthermore, the application of this method makes it impossible to find a curvilinear relationship.

Analysis of variance admits any number of categories, which is its advantage compared to the Student's t-test. Another benefit resulting from the use of this method is the possibility of simultaneous consideration of more than two variables (there are only two variables: grouping one and dependent one in Student's t-test). This can be done by taking more than one independent variables [CLARK & SPUHLER 1959; DZIEWIĘCKI 1994] or by inclusion of a covariate [PAWŁOWSKI *et al.* 2000]. These additional variables are usually: age, economic status, education level and the like.

However, analysis of variance is not free from disadvantages. Rejection of the hypothesis about the equality of k means makes it impossible to determine the type of relationship between the traits under study. Conclusions about a linear, whether positive or negative, or non-linear relationship are then drawn fol-

lowing a "visual inspection", looking at the mean values in particular categories or at the corresponding charts. The same criticism applies also to the Duncan's test used by DZIEWIĘCKI [1998].

Occasionally, the analysis of variance is employed in a rather unexpected manner. CLARK & SPUHLER [1959] used morphological traits as dependent variables and the number of offspring delivered as an independent variable – just the reverse of what is suggested by the assumption on the effect of morphological traits on fertility. Not only did they exhibit lack of intuition but also made it impossible to detect a potential curvilinear relationship between fertility and morphological traits. Also LASKER & THOMAS [1976] treated morphological traits as dependent variables. They used the Student's t-test to compare the mean values of these traits in groups with fertility above the average level with the mean values in groups with fertility below the average level (in order to detect directional selection). They also employed Snedecor's F-test to compare the variance of these traits in those groups (in order to detect stabilising or disruptive selection).

In my opinion analysis of regression is the best of the three methods. We do not lose information due to grouping, we can investigate relationships between a chosen trait and many other traits simultaneously, adding to the regression equation components with squares or cubes of variables we may test curvilinear relationships, and using relevant Snedecor's F-tests we may check whether a parabola, for instance, represents the relationship under study better than a straight line or whether the introduction of a new variable to the regression equation signifi-

cantly increases its predictive power. The components of regression equation may contain both biological variables (morphological traits, age) and environmental ones (economic status, educational status).

Regression analysis is the most commonly used method researching the relationship between the traits characterising reproductive success and somatic traits. However, it is not always a multivariate analysis. Only in certain cases does it contain square or cubic components [VETTA 1975; MUELLER 1979; SCOTT & BAJEMA 1982; BRUSH *et al.* 1983]. It happens that curvilinear relationships are investigated with an ordinary linear equation [MITTON 1975]. This is possible due to proper data transformation. If we replace the values of a morphological trait with absolute values of the deviations of these values from the mean, a positive regression coefficient will indicate a U-shaped relationship, while a negative coefficient will mean a relationship in the shape of a reversed letter U.

In exceptional cases χ^2 test is used. It was used, for instance, by BRESLER [1962] who studied an effect of female body height on the frequency of miscarriages. The same author used also a similar, accurate Fisher's test to estimate the influence of female stature on the risk of stillbirth.

MUELLER [1979] used the principal components method in his study. This method distinguishing a small number of factors contained in a large number of input variables permits to reduce the multitude of input data and to make use of correlation of many variables, but it does not allow to investigate the relationships between these traits and fertility or fitness. Mueller found these relationships using regression analysis.

Result interpretation stage

At this stage the three following issues seem to be crucial for the correct understanding of the results obtained: determination of a type of relationship between fertility or reproductive success and body height (or any other somatic trait), establishing of an empirical basis of this relationship and recognition of its biological (and other) significance.

The determination of a type of relationship based on the results of the statistical analyses used is a process of relatively the least complexity. Conventionally, statistical decisions are taken at a significance level $p = 0.05$ and all the works reviewed have stuck to that canon. Let us add that significant results were often obtained at the level $p = 0.1$. Those results were rated as insignificant but it is worth remembering that for samples of 100 individuals' size for each sex (which was the case in a few studies) obtaining of a significant relationship for traits weakly correlated with each other may be difficult.

It is also interesting to know whether the methods used make it possible to correctly identify a relationship present if not in a population then at least in a sample. Results obtained by several researchers indicate a curvilinear relationship for fertility, but, as I have said earlier, in many studies no methods of analysis enabling the discovery of such a relationship were used. If we exclude these studies from our review we will obtain a considerable consistency in the literature on the relations between fertility and fitness and body height. In one case only curvilinear relationship between the traits under discussion was not found [SCOTT & BAJEMA 1982]. In all other studies the results revealed the relationship in the

shape of a reversed letter U [CONTERIO & CAVALLI-SFORZA 1960; MITTON 1975; VETTA 1975; MUELLER 1979; BRUSH *et al.* 1983; GOLDSTEIN & KOBLYANSKY 1984; DZIEWIĘCKI 1998]. Usually this was achieved by means of the regression analysis with squares or cubes of variables, but Mitton used the normal analysis of regression for transformed data, and Dzięwiecki with a “naked eye” read the shape of the relationship based on the mean values of several categories having had earlier rejected a hypothesis on the equality of these means on the basis of the Duncan’s test.

It is understandable that if to data containing curvilinear relations we apply statistical methods that do not detect such relationships we can obtain any result: no relationship, positive relationship or negative relationship. In this way this great discrepancy in the results of researches on the relationship between fertility and fitness and body height can be easily explained. Therefore, one can presume that fertility and adaptive value depend curvilinearly on body height, with their maximum values concurring with the medium values of height.

In empirical sciences, including also anthropology, it is not enough to find the presence of a statistically significant correlation between certain traits. Finding the causes of this correlation is of fundamental significance, as is discovering whether one trait exerts an effect on the other one (and if so, what is the direction of the influence), or whether some additional factor influences both these traits at the same time resulting in a correlation between them. In the literature under review one can come across the reasoning which admits two possibilities.

Firstly, a morphological trait may be a cause of higher fertility or fitness. Then the relationship discovered is to have a genetic origin, since the value of the morphological trait is genetically determined. Secondly, environmental factors such as economic standard or educational status may have effect on both the traits, which have been discovered to be correlated. In this way a statistical relationship is created between traits that do not exert an effect on each other.

Such an equation between the genetic – environmental dichotomy and the causal – non-causal dichotomy is incorrect. If a morphological trait determines fertility, then the environmental component of this trait’s variance is likely to influence fertility in the same way as its genetic component does. In such a case we would have to do with a causal interaction between the correlated traits, triggered by environmental factors. On the other hand, as a result of pleiotropic effect of genes, a genetically determined correlation between the traits under discussion will occur with the absence of any interactions between these traits.

In spite of that the problem of genetic or environmental causes of the correlations under discussion is, as it will be shown further, of great biological importance. For this reason I will now devote some attention to the methods of their differentiation. In literature one may come across two such methods. One of them was used by CLARK & SPUHLER [1959] and by MUELLER [1979], and it employs the following criterion: if a given morphological trait exhibits high heritability, its relationship with fertility has a genetic origin, if heritability is low, the relationship is determined by environmental factors. I believe I do not need

to prove the limitations of this reasoning, especially in a situation when the coefficient of heritability is close to 0.5.

The other method consists in investigating a relation between a morphological trait and fertility (or fitness) with simultaneous monitoring of environmental variables. Specifically, one may use two-way analysis of variance with the level of environmental factor as the other grouping variable, next to the morphological trait [BAILEY & GARN 1979; DZIEWIĘCKI 1994], multivariate analysis of regression with environmental factors attached as additional independent variables [SCOTT & BAJEMA 1982], coefficient of partial correlation with exclusion of the environmental variable [MUELLER 1979], or the simplest statistical methods (for instance Student's t-test), but applied to parts of the sample homogenous with regard to a given environmental characteristic [BAILEY & GARN 1979].

The results obtained are divergent. BAILEY & GARN [1979] and DZIEWIĘCKI [1994] found that variables such as income per person, educational status or place of residence (urban area – rural area) explain relations between morphological traits and fertility (though in Dzięwiecki relationships for body weight, Quetelet index and BMI in women were still significant). In turn, in the studies by MUELLER [1979] and SCOTT & BAJEMA [1982] these variables did not have any effect on the relationships mentioned. Thus, we cannot say anything definite about the role of environmental factors in the creation of correlations between fertility and reproductive success and morphological traits (body height in particular).

If, as it has already been mentioned, the genetic – environmental factors di-

chotomy does not translate into the causal – non-causal factors division, then even if the results regarding the former issue were clear-cut, still we would not know what is the causal background of the observed relationships. Little has been done so far in the matter of experimental examination of these causes, so we can only make presumptions about them. There have been attempts to provide a causal explanation to the above mentioned negative relationship between offspring survival rate and parental stature in poor populations (shorter persons have smaller nutritional needs and hence they bear malnutrition better), and a non-causal elucidation to the positive relation between these traits in highly developed populations (a high living standard enhances both body height and survival rate). As to a higher fertility of individuals with higher weight and stronger built the literature often supplies a non-causal environmental explanation, since it is known that representatives of the wealthier social strata have on average less children and they are also characterised by slimmer physique. In turn, BRUSH and associates [1983] put forth a non-causal genetic hypothesis saying that the organism has a genetically determined efficiency in building body tissue which has an effect on body mass and on fertility. I have not come across any attempt of causal explanation of these relationships, in which body weight would be a cause and the number of offspring a result. On the other hand, SCOTT & BAJEMA [1982] give a causal explanation of the issue but with the reverse direction of influence. They found a positive relationship in women between the actual BMI and the number of offspring and a negative one between the BMI at the

skeletal age of 12 years and the number of offspring. The authors' conclusion is that the positive relationship between the actual BMI and the number of offspring is a consequence of weight gain as a result of each past pregnancy.

With regard to body height, the literature offers only environmental explanations of its relationship with fertility or number of offspring. There may, however, exist an intrapopulation variance of the energy distribution manner. Some individuals will use a greater proportion of energy for growth and smaller part of it for reproduction, others – on the contrary [ELLISON 1981]. If we agree that the dependency of fertility on body height is curvilinear, this hypothesis explains the relationship only within the scope of higher values of body height. The relationship within the remaining part of the scope must result from other factors. PAWŁOWSKI *et al.* [2000] explain the observed positive relationship between the number of offspring and body height with sexual selection (taller persons are regarded as more attractive ones). It is true that this relationship has not occurred in other studies, but sexual selection may be responsible for the relation observed in the lower scope of body height in the case of curvilinear relationship.

So much for genetic and environmental as well as causal and non-causal factors responsible for the observed relationships between fertility and fitness. The last issue within the stage of result interpretation is recognition of the biological significance of the relationships under discussion. In my opinion, two principal questions arise in reference to this matter: firstly, whether a given dependency of fitness on a morphological

trait entails intergenerational changes in the gene pool, and secondly, whether this dependency results in intergenerational changes in the phenotype distribution of this trait.

If a given relationship cannot be explained with an influence of environmental factors and as a result we presume it is of genetic origin, its influence on the change of the gene pool and on phenotype distribution is obvious. We only need to determine the type of this influence. If, on the other hand, the dependency of reproductive success on a morphological trait can be explained with some environmental characteristic (let us assume it is the level of income per person) the situation becomes more complex. One would be justified to think that there should be no intergenerational changes to this trait, but it is not necessarily the case. Firstly, economic differentiation can have some genetic basis, if certain genes predispose an individual to achieve financial success. Then these genes would be decreasing their share in the population, since economic standard correlates negatively with fertility. Together with the change of the frequency of genes determining income, mean values of the phenotype traits, which are affected by the level of income would also change. In this situation modifications would take place both in the gene pool and in the trait's phenotype distribution. Secondly, cultural inheriting may result in intergenerational transfer of morphological traits through nutritional habits, and the like. In this way, for instance, culturally transmitted high BMI (obesity) may cause a spread of obesity owing to the fact that it is related to greater fertility. In this case we would have to do with intergenerational changes

in phenotype distribution of a trait but no changes in the gene pool.

Let us come back to a situation where the relationship between a morphological trait and fitness has a genetic background. Here a question arises about the type of selection affecting this trait: whether it is stabilising, directional or disruptive selection. No studies have reported the occurrence of the last type, so I will ignore it in my further discussion of the topic. As far as the two former types are concerned I need to correct a certain error common in the literature. In the majority of the studies in which the authors found curvilinear relationships the conclusion was that the morphological trait was under the influence of stabilising selection. Similar reasoning is presented by SZEMIK [1989] in a review article. However, such conclusions are incorrect. Even in the case of a curvilinear relationship the mean value of a given trait may be distinctly different from the value maximising reproductive success (VETTA [1975] found that the optimum body weight value amounts to 73.56 kg, while the mean value equals 63.5 kg), which indicates the presence of directional selection.

Concerning my earlier remarks on the necessity of testing of curvilinear relationship between fitness and body height and the current comments referring to researchers' hasty conclusions about the existence of stabilising selection, I suggest the use of the following statistical methods, which will help in the solving of these problems. Let us assume that we have calculated the following regression equation:

$$(1) \quad Y = b_0 + b_1X$$

where Y is reproductive success, X is

body height (or other somatic trait), and b_1 and b_0 are estimated parameters. Further, let us assume that we have calculated the following square regression equation:

$$(2) \quad Y = b_0 + b_1X + b_2X^2$$

Depending on whether equation (2) fits the line to empirical points better than equation (1) the relationship between fitness and body height will be recognised as straight linear or curvilinear (parabolic) one. In order to find out whether a parabola fits the data better than a straight line we need to calculate the following statistics [DRAPER & SMITH 1973: p. 88]

$$(3) \quad F = (S_2 - S_1)/s^2$$

where S_2 and S_1 are sums of the squares of variable Y in regression for equations (2) and (1), respectively:

$$(4) \quad S = \sum_{i=1}^n (\hat{y}_i - \bar{y})^2$$

and s^2 is residual variance of variable Y obtained for equation (2):

$$(5) \quad s^2 = \frac{1}{n-3} \sum_{i=1}^n (y_i - \hat{y}_i)^2$$

(\hat{y}_i is a predicted value of variable Y of i -element). We compare the F value obtained with the table value of Snedecor's F -distribution for one and $n-3$ degrees of freedom and for a selected α . If the value computed is not statistically significant, it means that the parabola does not fit better than the straight line. Therefore, inferring a relationship between fitness and body height we will base our reason-

ning on equation (1). Now we need to check the sign in front of coefficient b_1 and to find out whether the correlation between X and Y is significant at all². Having done that we can say whether the relationship between fitness and body height is positive, negative or non-existent.

If on the other hand, value F calculated from equation (3) proves to be statistically significant, this will mean that a parabola will reflect the distribution of empirical points better than a straight line. In such an event one should find a relation between the mean value of body height and that one of its values, which ensures the highest fitness. Equation (2) produces the best fitted parabola, whose vertex can fall to any value of trait X more or less different from the mean value. In order to make sure that the value that maximises fitness does not overlap with the mean value X -a we should find the best parabola with the vertex corresponding to the mean value and to find out whether it fits the empirical points significantly worse than the parabola without this limitation. We know that co-ordinate x of the parabola vertex is expressed with the formula $-b_1/2b_2$. This co-ordinate is to be equal with the mean, hence $b_1 = -2b_2\bar{x}$, and the regression equation will be:

$$(6) \quad Y = b_0 - (2b_2\bar{x})X + b_2X^2$$

Only two parameters b_0 and b_2 need to be estimated here. Let us note that if we

² Significance of the coefficient of correlation from sample r can be tested easily, if we know that the following statistics has the Student's t-distribution with $n - 2$ degrees of freedom [GREŇ 1987: p. 458]

$$t = \frac{r}{\sqrt{1-r^2}} \sqrt{n-2}.$$

standardise variable X , the second part of the equation will disappear and it will assume the form $Y = b_0 + b_2X^2$. Now we should use equation (3) again, this time replacing S_1 with the sum of squares of variable Y in regression for equation (6). If value F calculated in this manner proves to be higher than the table value (calculated in the same way as previously) then we can say that the mean value of trait X is not a value that maximises fitness, which means this trait is affected by directional and not by stabilising selection. The thesis about the stabilising character of selection with regard to this trait may be upheld only if the value F obtained is lower than the table value (upon prior proving that a parabola reflects the relationship between reproductive success and a given trait better than a straight line).

Unfortunately, none of the studies under review involved such investigation, so it cannot be stated whether body height is subject to stabilising or directional selection.

Summary

Dissimilarity of results of research on the relationship between fertility and adaptive value and morphological traits inspires a search for the reasons of these discrepancies and for research solutions that would ensure an optimum utilisation of the information contained in the sample as well as a correctness of conclusions.

The numerous comments presented in this paper may be recapitulated as follows:

1. In the search for the relationships under discussion researchers should use analysis of regression, as it does not lose information in the process of categorisation and enables an efficient formation of

the regression equation including any number of variables as well as their powers.

2. In each case one should check the data for the existence of a curvilinear relationship, since a considerable proportion of discrepancies in research results stems from the fact that a straight line is fitted to the non-linear distribution of empirical points.

3. If a curvilinear relationship is discovered one should wait with drawing a conclusion about the stabilising effect of natural selection till the moment when it is proved that the parabola with vertex coordinate x equal to the mean value of the morphological trait does not fit with empirical data significantly worse than the parabola best fitting with these data. Otherwise, one should speak of directional selection.

References

- BAILEY S.M., S.M. GARN, 1979, *Socioeconomic interaction with physique and fertility*, Hum. Biol., **51**, 317-333
- BAIRD D., 1949, *Social factors in obstetrics*, Lancet, **1**, 1070-1083
- BAIRD D., 1952, *The cause and prevention of difficult labor*, Am. J. Obst. Gynecol., **63**, 1200-1212
- BATTAGLIA F.C., T.M. FRAZIER, A.E. HELLEGERS, 1966, *Birth weight, gestational age, and pregnancy outcome, with special reference to high-birth-weight-low gestational age infant*, Pediatrics, **37**, 417-422
- BRESLER J.B., 1962, *Maternal height and the prevalence of stillbirths*, Am. J. Phys. Anthropol., **20**, 515-517
- BRUSH G., A.J. BOYCE, G.A. HARRISON, 1983, *Associations between anthropometric variables and reproductive performance in Papua New Guinea highland population*, Ann. Hum. Biol., **10**, 223-234
- CLARK P.J., J.N. SPUHLER, 1959, *Differential fertility in relation to body dimensions*, Hum. Biol., **31**, 121-137
- CONTERIO F., L.L. CAVALLI-SFORZA, 1960, *Selezione per caratteri quantitativi nell'uomo*, Atti Assoc. Genet. Ital., **5**, 295-304
- DAMON A., R.B. THOMAS, 1967, *Fertility and physique – height, weight, and ponderal index*, Hum. Biol., **39**, 5-13
- DAVENPORT C.B., 1923, *Body built and its inheritance*, Carnegie Institution of Washington, D.C.
- DEVI M.R., J.R. KUMARI, C.R. SRIKUMARI, 1985, *Fertility and mortality differences in relation to maternal body size*, Ann. Hum. Biol., **12**, 479-484
- DRAPER N.R., H. SMITH, 1973, *Analiza regresji stosowana*, PWN, Warszawa
- DZIEWIĘCKI C., 1994, *Zróżnicowanie płodności populacji ludzkich w Polsce*, Studies in Human Ecology, Suppl. **1**, 5-88
- DZIEWIĘCKI C., 1998, *Związki pomiędzy płodnością kobiet a ich cechami morfologicznymi*, Studies in Human Ecology, Suppl. **2**, 271-282
- ELLIS W.S., 1973, *Mortality and birth weight in Philadelphia Blacks: An example of stabilizing selection*, Am. J. Phys. Anthropol., **38**, 145-150
- ELLISON P.T., 1981, *Morbidity, mortality and menarche*, Hum. Biol., **53**, 635-643
- FACCARO M., 1956, *A contribution to the study of birth weight based on an Italian sample*, Ann. Hum. Gen., **20**, 282-297
- FRASSETTO F., 1934, *I principali caratteri antropologici e costituzionalistici studiate i 1450 genitore prolifici della regione Emiliana*, [in]: Proceedings of the International Congress for Studies on Population, Rome 1931
- FRISANCHO A.R., J. SANCHEZ, D. PALLARDEL, L. YANEZ, 1973, *Adaptive significance of small body size under poor socio-economic conditions in Southern Peru*, Am. J. Phys. Anthropol., **39**, 255-261
- FURUSHO T., 1964, *Relationship between the stature of parents and the mortality of their children*, Jap. J. Hum. Gen., **9**, 18-34
- GALTON F., 1886, *Family likeness in stature*, Proc. Roy. Soc., London, **40-42**, 73
- GOLDSTEIN M.S., E. KOBLYANSKY, 1984, *Anthropometric traits, balanced selection and fertility*, Hum. Biol., **56**, 35-46
- GREŃ J., 1987, *Statystyka matematyczna. Podręcznik programowany*, Warszawa
- JURYNEC R., 1986, *Wpływ selekcji negatywnej na średnią wysokość ciała w populacji – ujęcie ekologiczne*, Przegląd Antropologiczny, **52**, 113-127

- KARN M.N., L.S. PENROSE, 1951, *Birth weight and gestational time in relation to maternal age, parity and infant survival*, An. Eugenics, **161**, 147-164
- LASKER G.W., R. THOMAS, 1976, *Relationship between reproductive fitness and anthropometric dimensions, in a Mexican population*, Hum. Biol., **48**, 775-791
- MARTORELL R., H.L. DELGADO, V. VALVERDE, R.E. KLEIN, 1981, *Maternal stature, fertility and infant mortality*, Hum. Biol., **53**, 303-312
- MITTON J.B., 1975, *Fertility differentials in modern societies resulting in normalizing selection for height*, Hum. Biol., **47**, 189-200
- MUELLER W.H., 1979, *Fertility and physique in malnourished population*, Hum. Biol., **51**, 153-166
- MUELLER W.H., G.W. LASKER, F.G. EVANS, 1981, *Anthropometric measurements and Darwinian fitness*, J. Biosoc. Sc., **13**, 309-316
- PAWŁOWSKI B., R.I.M. DUNBAR, A. LIPOWICZ, 2000, *Tall men have more reproductive success*, Nature, **403**, 156
- SCOTT E., C.J. BAJEMA, 1982, *Height, weight and fertility among the participants of the third Harvard growth study*, Human Biology, **54**, 501-516
- SZEMIK M., 1980, *Wiek dojrzewania a niektóre właściwości kobiet w okresie reprodukcji ze szczególnym uwzględnieniem płodności i proporcji płci ich potomstwa*, Doctoral thesis, Warszawa
- SZEMIK M., 1989, *Studies of factors determining fertility in contemporary population (attempt at synthesis)*, Studies in Human Ecology, **8**, 221-238
- SZEMIK M., N. WOLAŃSKI, 1989, *Fertility and offspring survival, related to parental biological traits in Polish rural populations*, Studies in Human Ecology, **8**, 239-266
- VETTA A., 1975, *Fertility, physique and intensity of selection*, Hum. Biol., **43**, 283-293
- WOLAŃSKI N., M. HENNEBERG, 1990, *Natural selection in recent man: an interpretative problem*, Studies in Human Ecology, **9**, 275-293

Streszczenie

Dostosowanie osobnika do środowiska oraz składająca się nań płodność i przeżywalność potomstwa są przedmiotem zainteresowania antropologów z wielu powodów. Jednym z najważniejszych jest to, że zróżnicowane ze względu na wartości określonych cech dostosowanie może powodować międzypokoleniowe zmiany rozkładu wartości genotypowych tych cech czyli ich ewolucję. Mimo, że we współczesnych populacjach ludzkich poszukiwanie takich związków jest bardzo trudne, przeprowadzono sporo badań, w których poszukiwano związków cech somatycznych z płodnością, przeżywalnością i wartością dostosowawczą.

W niniejszej analizie ograniczyłem się do najpopularniejszych cech morfologicznych: wysokości ciała, masy ciała i wskaźników budowy ciała (Queteleta, BMI, ponderal index). Jak się okazało prace różnych badaczy często znacznie różnią się pod względem otrzymanych wyników oraz wyciągniętych wniosków o typie doboru działającego na daną cechę. Rozbieżności te w niemałym stopniu wynikają ze stosowania nie zawsze najlepszych metod analizy oraz posługiwania się zawodnymi regułami wnioskowania. Celem pracy była więc krytyczna analiza statystycznych metod opracowywania danych i sposobów wyciągania wniosków co do biologicznego znaczenia znalezionych zależności oraz wskazanie takich metod analizy danych i interpretacji wyników, które pozwalają na optymalne wykorzystanie informacji zawartej w próbie oraz na wyciąganie trafnych wniosków. Najważniejsze uwagi wyrażone w tej pracy można ująć w następujących punktach:

1. Do poszukiwania omawianych zależności warto używać analizy regresji, która nie traci informacji na kategoryzację i pozwala na wygodne tworzenie równania regresji z dowolną ilością zmiennych a także ich potęgami.

2. W każdym przypadku należy testować istnienie związku krzywoliniowego, ponieważ istotna część rozbieżności wyników badań wynika z dopasowywania linii prostej do nielinowego rozkładu punktów empirycznych.

3. W przypadku odkrycia zależności krzywoliniowej należy wstrzymać się z wnioskiem o stabilizującym działaniu doboru naturalnego do momentu wykazania, że parabola o współrzędnej x wierzchołka równej wartości średniej cechy morfologicznej nie pasuje do danych empirycznych w sposób istotnie gorszy niż parabola najlepiej do tych danych pasująca. W przeciwnym wypadku należałoby mówić o doborze kierunkowym.