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BIOLOGICAL STATE INDEX OF HUMAN GROUPS *

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INTRODUCTION

The following main factors condition the biological state and dynamics of human populations: The qualitative and quantitative characteristics of the hereditary material, the natural environment, and the totality of cultural phenomena.

These factors are interrelated and connected with the biological state of the population by way of feedback loops system. Because of the high complexity of this system there is, at present, no possibility to measure accurately the interrelations between its elements. This is due to the incompleteness of sources concerning the majority of historical stages of the species i.e. the prehistorical and early historical times as well as to the impossibility of experimentally isolating the various factors in order to examine their influence on the biological situation of the groups of human individuals.

The behaviour of the entire set of feedback loops can be described synthetically by performing a measurement of the biological state.

The measure of the biological state of a human population has to fulfil the following conditions: 1. It has to be directly adapted for an ecological and for genetic-evolutional interpretation. 2. It has to be of universal nature i.e. to be applicable with no essential modifications to prehistorical as well as contamporaneous populations. 3. It has to have strictly defined limits of variability, i.e. to express absolutely and not relatively the biological situation of the group.

The aim of this paper is to propose such a measure, which, in our opinion fulfils these postulates, and to illustrate the possibilities it provides for an interpretation of the results obtained when using it.

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MEASUREMENT OF SELECTIVE PRESSURE IN MAN, THE CONCEPT OF BIOLOGICAL POPULATION STATE

A good measure of the adaptation of a biological unit to its environmental conditions is to be found in its fitness, in the evolutional meaning of the word.

With regard to the investigation of human populations, Crow proposed in 1958 to calculate the so-called „total selection intensity index", which measures the maximum possible selective pressure within a given population (the total opportunity for selection) basing on demographic data. This index (I) is the sum of the index determining the selective pressures due to mortality (I_m) on the ground of the proportion of individuals deceased before achieving the limit of their reproductive age, and selection index due to differential fertility (I_f) — the ratio of the variance of offspring number and the squared mean offspring number in a complete family (one in which the parents live throughout their entire reproductive period).

However, in man, similarly as in all species in which the parent gives rise to more than one annual class of progeniture, there exists a serious difficulty with regard to the correct estimation of fertility and mortality contributing to total selective pressure. This difficulty is due to the mortality of sexually mature individuals during their reproductive period. The death of an individual before the end of this period, but after he or she has given birth to some children, has a selective significance which is not equivalent to the death of an individual before achieving puberty. Hence the use for I_m calculations, the proportion of persons dying previous to achieving puberty only leads to an underestimation of the part of mortality in the total selective pressure. On the other hand, using for calculations the proportion of all persons deceased before the end of reproductive period (e.g. under the age of 50) one makes overestimation.

Equally essential are the considerations of the intrapopulational fertility differences affecting the final offspring number in complete families (i.e. families in which both parents have achieved the age considered as the limit of normal reproductive period). Omitting problems of intragroup differentiation of cultural natality determinants, we can assume that in non-Malthusian populations the variance of the final birth number in complete families depends in fact on the biological diversity of parents. However in such populations the general amount of selective pressure measured by the index I_f is relatively small and its contribution to the general opportunity for selection is lower than in Malthusian populations (Spuhler 1962, Swedlund 1971). In populations applying a conscious, planned birth control, the result of fluctuations in the number of children, is almost entirely independent of the genetic endowment of the parents and therefore cannot be considered as a measure of the biological state. Hence it is difficult to estimate directly the fertility differentiation due to genetic diversity only and having an essential significance for a selection. Moreover the fertility measures are applicable solely with regard to contemporaneously living populations, or historic ones for which suitable written documents are available. Attempts undertaken to estabilish differential fertility in skeletal series by observations of the changes in pelvic bones of females (A n g e l 1969b) reuire a very good state of preservation of the entire material. This makes them practically inapplicable to the majority of finds, especially cremated bones.

A separate problem resides in the meaning of intragroup fertility differentiation for reproductive success of a population as a whole. The reproductive success of a population is expressed by the size of generations, sucessively following one another, and this size is influenced decisively by the total number of offspring of all the individuals independent of the differences between families. Obviously it depends also on mortality conditions.

In the last stage of anthropogenesis — from the advent of Homo sapiens to the forming of contemporaneous human groups — the evolution of culture is the main regulator of changes in the relationship between man and his environment. Culture induced manipulations, on selective forces, occured to a large extent, if not wholly, by action on the rate of threat to life, and on mortality, throughout most of human history.

In accordance with the above considerations, the concept of biological population state can be formulated in terms of adaptation.

The biological state of a population is adequate to the general size of selection pressures, acting through mortality on all its individuals.

A measure of biological state, thus understood, is provided by a quantity expressing what fraction of a given generation has a chance to participate fully in reproducing the next generation under given mortality conditions. This is a measure of the reproductive success possbility of the population as a whole or, equivalently, its average individual. The larger probability, in a given population, for complete reproduction of an average genotype, the better is the population's adaptation to the complexity of its environmental conditions. The biological state is thus an expression of adaptation, taken as the totality of biological and cultural characteristics making possible the reproductive success of a population though not necessarily causing it. With regard to man we can speak of the chance to reproduce only, as a good standard of biological situation, and not of the absolute reproduction intensity. This derives from man's ability, unique in the world of living beings, of conscious birth control. This birth control depends in a complicated way (feedback loops) on the ecological state of the group.

The notion of the ecological population state, however close, is not equivalent to the notion of biological state. The ecological state is described by the population's size, its sex and age structure, natural increase and migrations, as well as its technological and organisation systems. The ecological state is one of the main determinants of the biological state through interrelations between population and eco-cultural environment influencing — together with the genetic structure — the size and directions of selective pressures. The biological state is described exclusively by the data on population structure, whereas the description of the ecological state is based on data concerning the natural and cultural environment as well as the population. So we can expect groups to exist with similar biological state but markedly different ecological situations. The biological state thus reflects the degree of adaptation whereas the ecological state describes the ways by which the population achieves this adaptation. Studies of biological state of populations or their subgroups living in different eco-cultural systems can help to estimate the adaptive efficiency of these systems.

CONSTRUCTION OF THE BIOLOGICAL STATE INDEX

To describe a population's biological state, we use the index I_{bs} constructed on the basis of mortality structure and probability of not possessing the complete offspring number by individuals dying in successive age categories. The probability of not possessing complete progeniture for individuals generatively immature obviously equals 1; for older persons it diminishes with age and reaches the value 0 at an age corresponding to physiological cessation of reproductive capacity. To determine this probability in the population under investigation basing on age-specific fertility rates or on other equivalent data, we calculate the final cumulative number of births $-U_c$. This is the cumulative number of live births devolving on the average upon one individual living to the end of her (or his) reproductive capacity period. Basing on the same data we compute the cumulative number of births $-U_x$ — for individuals of age x. The probability of not possessing the complete number of births at age $x - s_x$ is equal to $1 - U_x : U_c$.

Having available the data bearing on the frequency of death at various ages — the d_x column of the life table — as well as the set of probabilities s_x, we can calculate the index of biological state according to the formula:

$$I_{bs} = 1 - \sum_{x=0}^{x=\omega} d_x s_x$$

where: d_x — the frequency of death at the age x; s_x — the probability of not possesing the complete number of births at the age x; ω — the age at death of the oldest member of the group.

It is easy to observe that the index is composed of two groups of data: the frequency of deaths of immature individuals (for whom, at $s_x=1$, the sum of products $d_x \cdot s_x$ equals the sum of values d_x) and weighted by probabilities $s_x<1$ mortality of adults. Thus I_{bs} can be written in the from

$$I_{bs}=1-(d_{0-14}+\sum_{x=14}^{x=\omega} d_x s_x)$$

where: d_{0-14} — frequency of deaths of progenitively immature individuals, when assumed puberty age is 14.

The sum $\sum_{x=14}^{x=\omega} d_x s_x$, computed for $\sum_{x=14}^{x=\omega} d_x=1$, and subtracted from unity is the potential gross reproduction rate (R_{pot}) expressing the natality possibilities in a population with given mortality conditions. The details of the construction of this coefficient as well as its application in paleobiological studies of human populations are discussed in a separate paper (Henneberg 1975).

The above mentioned components of the biological state index (i.e. d_{0-14} and R_{pot}) are very weakly correlated — the Pearson correlation coefficient, calculated for 32 groups, is − 0.13. Separate consideration of the contribution to the total quantity I_{bs} from subadults mortality and R_{pot} provides additional essential information as to the manner of action of selective pressures through mortality, completely excluding individuals from bearing children and relatively differentiating reproductive values. Such an approach to the subject allows, jointly with other informations, to interprete the cultural regulation of the biological state by control of the birth rate, protection of children, and life conditions of adults.

The values of I_{bs} can theoretically range from 0 to 1. Zero signifies a total lack of adaptation and impossibility to give life to the next generation; 1 signifies total adaptation (ideal adaptation) of the population, by excluding completely the operation of mortality as a selective factor on born individuals. Intermediate values inform about the possibility of complete reproduction of an average individual from a population living under given mortality conditions. The biological state index is of cognitive value similar to the life expectancy of a newborn (e_0^0 - parameter of the life table). An essential correction for the evolutional interpretation, introduced by I_{bs}, resides in the elimination of the influence on the results of differentiated subadults and old people mortality, and in the connection of the mortality and reproductive value of adults. For the investigations of early human populations the elimination of the influence on the final results of systematical errors in age estimations on skeletons of persons deceased after the age of 60, is also very important.

The index under consideration can be used fo rcontemporaneous populations as well as for prehistoric ones, yelding directly comparable results. In the case of prehistoric groups we assume the following set of s_x values (Henneberg 1975):

x	15 - 19	20 - 24	25 - 29	30 - 34	35 - 39	40 - 44	45 - ω years
s_x	.95	.75	.55	.35	.17	.05	.00

This is a set common to non-Malthusian populations in which irrespective of even quite considerable differences in intensity and number of births, the increment of relative, cumulative number of births with the parents' age, takes a very similar course. We assume, of course, that the prehistoric populations were non-Malthusian.

EXAMPLE OF APPLICATION OF THE INDEX AND INTERPRETATIVE POSSIBILITIES

We have computed indices of biological state for 22 human groups, beginning with the Neandertal and ending with contemporary Poland. Our estimates are based on numerical data from the literature (Acsádi and Nemeskéri 1970, Angel 1969a, Bach and Bach 1971, Ery 1967, Modrzewska 1958, Nicolaescu-Plopsor and Wolski 1972, Piontek 1975, Rocznik Demograficzny 1968, Schott 1964, Ullrich 1972, Vallois 1937).

According to Table 1 it follows that in the course of history improves the upper limit of adaptive possibilities rather than the biological state of all human populations — groups with a low adaptation level are always present. Taking into account values $d_{0\text{-}14}$ and R_{pot} we may ascertain that the improvement in the biological situation of adults is a long way in advance of the decline in children's mortality. From the joint analysis of the three parameters given in Table 1, the following obviously incomplete and rough picture of changes in biological state, can be derived. In the first stage, at low R_{pot} and considerable subadults mortality, the general biological state of the population is bad, less than 1/2 of individuals born having a chance of complete reproduction. In the second stage, there occurs an improvement in life conditions of the adults, the values R_{pot} are higher, increase in births number is possible. This, in turn, at essentially unchanged mortality conditions of children, involves a high frequency of deaths in the ages 0 - 14. Finally, the biological state of the population is bad, as it was in the first stage. However selective forces are to a higher degree directed

Tab. 1. R_0 and I_{bs}, estaimtions is some earlier human populations, I_{bs}, R_{pot} and d_{0-14} for modern Poland are given for comparison

Population	I_{bs}	R_{pot}	d_{0-14}	Source of mortality data
Neandertal	.26 - .32	.56	.38 - .40	Vallois, 1937, Acsádi, Nemeskéri 1970
Upper Paleolithic	.30	.49	.38	Vallois 1937
Mesolithic	.30	.42	.30	Vallois 1937
Maghreb type (epipaleolithic)	.35	.75	.53	Acsadi, Nemeskeri 1970
Nea Nikomedeia (Early Neolithic)	.23	.58	.58	Angel 1969
Volni (Neolithic)	.44	.69	.36	Acsádi, Neméskeri 1970
Germany, Neolithic	.48	.66	.27	Ullrich 1972
Alsónemedi (Copper Age)	.51	.80	.36	Acsádi, Nemeskéri, 1970
Grossbrembach (Early Bronze)	.32	.53	.42	Ullrich 1972
Lerna (Middle Bronze Age)	.30	.66	.56	Angel 1969
Sulęcin (Late Bronze Age)	.42	.64	.34	Piontek 1975
Intercisa-Brigetio (I - IV c. A.D.)	.43	.68	.36	Acsádi, Nemeskéri 1970
Valachians (IV c.A.D.)	.40	.56	.29	Nicolaescu, Wolski 1972
Keszthely-Dobogó (Late Roman Era)	.60	.83	.28	Acsádi Nemeskéri 1970
Sopronköhida IX c.A.D.)	.50	.93	.46	Acsádi Nemeskéri 1970
Ártánd (IX c.A.D.)	.58	.78	.26	Ery 1967
Espenfeld (XI - XII c.A.D.)	.31	.60	.49	Bach, Bach 1971
CzarnaWielka (XI - XII c.A.D.)	.44	.65	.32	Modrzewska 1958
Hungarian model (XI - XII c.A.D.)	.49	.80	.39	Acsádi, Nemeskéri 1970
Reckahn (XII - XIV c.A.D.)	.47	.66	.28	Schott 1964
Villages in parish Szczepanowo (Poland, middle of XIX c.A.D.)	.32	.79	.59	authors unpublished data
Poland 1960 - 1966	.94	.99	.05	Rocznik... 1968

against the traits and characteristics unfavourable for the developing organism than for the adult one.

This situation is most probably the result of cultural changes, because evolving culture, at a low degree of medical sciences, is able to transform mortality conditions of adults more rapidly and with greater efficiency than the conditions of children mortality.

In the third stage, specific to highly developped civilisation systems, R_{pot} approaches the ideal level (1), d_{0-14} drops very considerably, jointly leading to a high value of biological state index. Very weak operation of selection through the mortality factors as well as the necessity of introducing extensive, conscious birth control (on account of very high reproduction possibilities) counteracting selection through differential fertility, largely diminish the action of natural selection on man.

We are well aware that the data at our disposal were fragmentary. Nevertheless there arise some conclusions concerning the species-specificity of biological changes in the last stage of anthropogenesis. They are in accordance with the actual state of knowledge about man.

In the course of history, the upper limit of the ability of human populations to improve their biological state increased steadily, at an unchanged and constantly realised minimum. This increasing divergence of biological states led to an increase in interpopulational differences with regard to the mechanisms and range of intragroup variability. As a result, the way of regulation of intraspecies variability was also liable to changes. This variability in conditions of bad biological state, is maintained mainly due to interpopulational differences, at a low intragroup variability. A considerable improvement in biological state causes an increase in the significance of intrapopulational variability for the variability of the species. Marked interpopulational differences in the chances for reproductive success involve a transformation in the contributions from the gene pools of separate populations to the gene pool of the species. This composite mechanism of transformations moreover involves elements of cultural regulation of group size related with the improvement of biological state, as well as changes in direction and intensity of hybrydization due to numerous eco-cultural conditionings. The explanation of this mechanism is the key problem in the research of human groups histories and their contemporary differentiation.

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L'INDICE DE L'ÉTAT BIOLOGIQUE DES GROUPES HUMAINS

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L'état et la dynamicité des groupes humains dépendent de nombre de facturs reliés entre eux et constituant des ensembles complexes qui, à leur tour, forment un système de rapports en feed-back. L'évaluation de l'état biologique permet une description synthétique du comportement du système dans son ensemble. L'état biologique d'une population correspond au niveau total des pressions sélectives agissant par l'intermédiaire de la mortalité. Il exprime donc l'adaptation, comprise en tant qu'ensemble de caractères biologiques et culturels qui rendent possible le succès d'une reproduction satisfaisante de la population, bien que ces caractères n'en soient pas nécéssairement la cause. Pour ce qui est de l'homme, nous ne pouvons parler que d'une possibilité de reproduction, en tant que mesure adéquate de la situation biologique; ceci resulte de la capacité humaine de controler les naissances. Afin de mesurer l'état biologique, on se sert d'une unité exprimant quelle est la portion de la génération étudiée qui a des chances de participer pleinement a la reproduction de la génération suivante, dans des conditions de mortalité:

$$I_{bs}=1-\sum_{x=0}^{x=\omega} d_x \cdot s_x$$

pour lequel: d_x=fraction de la population décédant à l'âge de x ans, s_x=probabilité de n'obtenir qu'un nombre incomplet de naissances à l'âge x: calculée sous forme de rapport du nombre cumulé de naissances obtenues par un sujet à l'âge x au nombre cumulé de naissances obtenues au cours de toute la période de reproduction.

Ce coefficient peut étre également présenté sous une forme reliant le taux latent de la reproduction brute (R_{pot}) et qui exprime la possibilité de naissances dans les conditions de mortalité déterminées et la mortalité des sujets non-adultes:

$$I_{bs}=1-(d_{0-14}+\sum_{x=14}^{x=\omega} d_x \cdot s_x)$$

où d_{0-14}=fraction décès pour sujets non-adultes.

Bien qu'il en soit assez proche, le concept de l'état biologique n'est point identique au concept de l'état écologique d'une population. Ce dernier est déterminé par la dimension de la population par sa structure, son taux de natalité, ses migrations, ainsi que par son niveau technologique et son système d'organisation. L'état biologique ne s'appuie que sur les donnéss concernant la structure de la population — sa description ne tient pas compte de données touchant les conditions naturelles et culturelles de son existende. On peut donc s'attendre à ce qu'il existe des groupes humains dont l'état biologique sera similaire et qui, cependant, vivront dans des situations ecologiques fort diverses. L'état biologique est donc le reflet du degré d'adaptation d'une population aux conditions de l'existence, tandis que l'état écologique décrit les voies qui mènent à cette adaptation.

Les recherches sur l'état biologique de groupes humains vivant dans des systèmes écologiques et culturels différents peuvent contribuer à l'evaluation de l'efficacité de ces systèmes à l'adaptation. Dans le but d'illustrer l'explication de I_{bs}, on a présenté les résultats statistiques obtenus pour 22 groupes (T. 1); pour les populations préhistoriques on s'est servi de rangs s_x communs à toutes les populations non-malthusiennes.

Le présent article ne constitue qu'une communication préliminaire et les suggestions qui en résultent pour les recherches à venir pouvent être formulées comme suit:

1. la divergence entre états biologiques, croissant au cours de l'histoire humaine, mène à l'accroissement des différences entre populations concernant les mécanismes et l'extension de la variabilité des caractères morpho-fonctionnels à l'intérieur du groupe.

2. lorsque l'état biologique laisse à désirer, la variabilité à l'intérieur de l'espece se maintient surtout grâce à des divergences des valeurs moyennes entre les populations particulières la différenciation à l'intérieur du groupe demeurant réduite.

3. Une amelioration visible de l'état biologique provoque un accroissement de la variabilité à l'intérieur de la population et de son importance pour la variabilité de la classe tout entière.

WSKAŹNIK STANU BIOLOGICZNEGO GRUP LUDZKICH

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Stan i dynamika grup ludzkich warunkowane są licznymi czynnikami wchodzącymi ze sobą w złożone zależności tworzące system sprzężeń zwrotnych. Ze względu na znaczne skomplikowanie tego systemu nie mamy obecnie możliwości zmierzenia zależności pomiędzy jego pojedynczymi elementami. Zachowanie się całego systemu można opisać syntetycznie poprzez ocenę stanu biologicznego. Stan biologiczny jest więc wyrazem adaptacji, rozumianej jako całość biologicznych i kulturowych charakterystyk umożliwiających sukces reprodukcyjny populacji, chociaż niekoniecznie go wywołujących. W odniesieniu do człowieka możemy bowiem mówić jedynie o szansie na zreprodukowanie się, jako dobrym mierniku sytuacji biologicznej; wynika to ze zdolności do świadomej kontroli urodzeń. Miarą stanu biologicznego jest wielkość wyrażająca jaka frakcja danego pokolenia ma szansę uczestniczyć w pełni w reprodukcji następnego pokolenia, w danych warunkach wymieralności

$$I_{bs}=1-\sum_{x=0}^{x=\omega} d_x\cdot s_x$$

gdzie: d_x — frakcja osobników wymierających w wieku x lat, s_x — prawdopodobieństwo nie posiadania kompletnej liczby urodzeń w wieku x, obliczane jako stosunek skumulowanej liczby urodzeń osiągniętych przez osobnika w wieku x do skumulowanej liczby urodzeń w całym okresie reprodukcyjnym.

Wskaźnik ten można również przedstawić w innej formie wiążącej potencjalny współczynnik reprodukcji brutto (R_{pot}) (wyrażający możliwości urodzeń w danych warunkach wymieralności) i wymieralność osobników niedorosłych

$$I_{bs}=1-(d_{0-14}+\sum_{x=14}^{x=\omega} d_x\cdot s_x)$$

gdzie: d_{0-14} — frakcja wymierających niedorosłych

Pojęcie stanu biologicznego jakkolwiek bliskie, nie jest jednoznaczne z pojęciem stanu ekologicznego. Stan ekologiczny jest determinowany wielkością populacji, jej strukturą, przyrostem naturalnym, migracjami oraz technologią i systemem organizacji. Stan biologiczny jest oparty wyłącznie na danych o strukturze populacji — jego opis nie wymaga danych o naturalnych i kulturowych uwarunkowaniach populacji. Tak więc można oczekiwać, że będą istniały grupy ludzkie o podobnym stanie biologicznym w wyraźnie różnych sytuacjach ekologicznych. Stan biologiczny odzwierciedla więc stopień adaptacji, podczas gdy stan ekologiczny opisuje drogi jakimi populacja osiąga tę adaptację.

Badania stanu biologicznego grup ludzkich żyjących w różnych systemach ekologiczno-kulturowych mogą przyczynić się do oceny efektywności adaptacyjnej tych systemów. Dla zilustrowania możliwości zastosowania I_{bs} przedstawiono wyniki obliczeń dla 22 grup ludzkich (tab. 1); dla populacji pradziejowych stosowano szeregi s_x wspólne dla wszystkich populacji niemaltuzjańskich.

Niniejsza praca ma charakter wstępnego doniesienia, a sugestie dotyczące dalszych badań wynikające z naszych rozważań można przedstawić w formie następujących wniosków:

1. Wzrastająca w historii człowieka dywergencja stanów biologicznych prowadzi do wzrostu międzypopulacyjnych różnic dotyczących mechanizmów i zakresu zmienności wewnątrzgrupowej w cechach morfofunkcjonalnych.
2. W warunkach złego stanu biologicznego zmienność wewnątrzgatunkowa jest utrzymywana głównie poprzez międzypopulacyjne różnice wartości przeciętnych przy małym zróżnicowaniu wewnątrzgrupowym.
3. Wyraźna poprawa stanu biologicznego wywołuje wzrost zmienności wewnątrzgrupowej i jej znaczenia dla zmienności całego gatunku.