

The Correlations Between Anthropobiological and Climatic Variables in Sub-Saharan Africa: Revised Estimates

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ABSTRACT

The coefficients of correlation between 30 anthropobiological and five climatic variables are recomputed in data from sub-Saharan African populations. Changes in the value and/or statistical significance of a number of coefficients are observed. The coefficients suggest that the *M*, *O*, *R₀* and *r* alleles are probably independent of climate in sub-Saharan Africa. An explanation of the apparent association of *B*, *R₁* and *R₂* frequencies with climate is proposed in terms of a sensitivity of lethal agents or of their intermediary hosts to climate, by analogy with the *Hb^s* case. Fingerprint patterns and some metric variables, like head length, are found to be independent of climate. The relevance of Bergmann's rule in the interpretation of body measurement from sub-Saharan Africa is discussed.

Following publication (Hiernaux, 1968) of the values of the coefficients of correlation between six climatic variables and the means or frequencies of 36 anthropobiological characteristics from a set of selected data on 460 populations of sub-Saharan Africa, a systematic and comprehensive collection has been made from the literature of further data (Hiernaux 1976, Table 1). They fulfil the conditions: (a) the samples must be of at least 40 adult male subjects for anthropometry, 50 subjects for dermatoglyphics and 100 subjects for blood traits; (b) they must represent well-defined sub-Saharan African ethnic groups within which no gross heterogeneity is suspected; (c) the techniques must be explicitly uniform.

The amount of fresh information so collected appeared large enough to justify a revision of the results of at least one of the lines of the 1968 analysis: that based on the correlations between anthropology and climate.

MATERIALS AND METHODS

The new biological data are of three kinds: (a) means of frequencies in one of the 460 populations, made available after the 1968 compilation, (b) data on populations absent from the 1968 list of 460 populations, and (c)

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data on G6PD deficiency and on transferrin variants, for which no correlation with climatic variables was computed in 1968.

Five climatic variables have been considered: mean annual rainfall, mean humidity mixing ratio of the wettest month, mean humidity mixing ratio of the driest month, mean daily maximum temperature of the hottest month, and mean daily minimum temperature of the coldest month (abbreviated as Pluv., Hum. +, Hum. -, Temp. +, Temp. -, respectively). All were read in the Climatological Atlas of Africa (Jackson, 1961).

The anthropobiological variables considered are: the frequencies of the A, B, and O alleles of the ABO blood groups, of the R_0 , R_1 , R_2 , and r alleles of the Rh blood groups (with the R_0^u variant grouped with r because a majority of the publications do not distinguish between these two alleles), of the M allele of the MN blood groups, of the Hb^s and Hb^c alleles of the hemoglobin locus where they are present, and of the three main dermatoglyphic fingerprint patterns (arches, loops and whorls), and the means of the following measurements: body weight, stature, sitting height, upper limb length, biacromial and biiliac diameters, transverse and sagittal thoracic diameters, calf circumference, head length and breadth, bizygomatic diameter, total face height, and nose height and width.

After a logarithmic transformation of the mean annual rainfall, the correlation coefficient r has been computed between each of the five climatic variables and each of the 31 anthropobiological attributes on the new total sets of populations.

RESULTS

Table 1 gives the two sets of correlation coefficients: those computed in 1968 on n_1 populations and those re-computed for this paper on N populations. In the recomputation, no significant positive correlation becomes significantly negative, nor vice-versa. The only changes are in the statistical significance of the coefficients, or in the sign of non-significant coefficients.

In the ABO system, only one of the two previously significant correlations with climate remains significant: a positive correlation of B with Temp. +. It retains its value of 0.24. In the Rh system, R_0 and r continue to be independent of climate. The correlation of R_1 with humidity is weakened and that with Temp. - loses its significance. R_2 remains significantly correlated with Temp. +, but by a lower value. In the MN system, only one of the two previously significant coefficients retains its significance: that of M with Hum. +, but it falls from -0.57 to -0.34 .

In the set of populations in which the Hb^s allele is present, that

Table 1

Coefficients of Correlation between 5 climatic Variables and 31 anthropological Variables (computed by Hiernaux, 1968 on n_1 Populations, and in this Paper on N Populations.)

Biological Variable	n_1	N	Pluv.	Hum. +	Hum. -	Temp. +	Temp. -
ABO system							
A	184		-.10	-.16*	-.03	-.08	-.13
		214	-.07	-.11	-.03	-.08	-.11
B	184		.00	+.10	-.09	+.24**	+.06
		214	+.04	+.10	-.11	+.24**	+.05
O	184		+.07	+.04	+.07	-.09	+.05
		214	+.03	+.02	+.06	-.09	-.02
Rh system							
R_0	37		+.13	+.16	-.01	+.15	+.16
		49	+.18	+.28	+.06	+.16	+.28
R_1	37		-.44**	-.45**	-.43**	+.09	-.55**
		58	-.46**	-.28*	-.19	+.18	-.24
R_2	37		+.09	-.12	+.20	-.51**	-.08
		59	+.15	-.07	-.04	-.42**	-.22
$r + R_0$	39		+.18	+.23	+.25	-.19	+.26
		49	+.21	+.10	+.09	-.25	+.09
MN system							
M	42		-.29	-.57**	-.21	-.16	-.52**
		67	-.24	-.34**	-.09	-.04	-.19
Hemoglobins							
Hb^s (all)	188		+.15*	+.10	+.16*	+.03	+.23**
		219	+.20**	+.14*	+.19**	-.01	+.23**

Biological Variable	n ₁	N	Pluv.	Hum. +	Hum. -	Temp. +	Temp. -
<i>Hb</i> ^a (where present)	169		+ .05	.00	+ .11	+ .06	+ .15
		194	+ .10	+ .05	+ .17*	+ .04	+ .19**
<i>Hb</i> ^b (all)	47		- .24	+ .21	- .37**	+ .50**	+ .11
		58	- .08	+ .20	- .17	+ .25	+ .21
<i>Hb</i> ^c (where present)	34		- .09	+ .17	- .28	+ .35*	+ .10
		38	- .03	+ .18	- .18	+ .27	+ .17
G 6 P D							
Deficients (all)	26		+ .41*	+ .57**	+ .49*	- .09	+ .42*
Deficients (where present)	19		+ .31	+ .50*	+ .44	.00	+ .35
Transferrin							
<i>Tf</i> ^d	0	26	+ .25	+ .25	+ .16	+ .34	+ .29
Dermatoglyphics							
Arches	54		+ .03	- .02	+ .02	+ .08	+ .01
		72	+ .12	+ .12	- .03	+ .14	+ .11
Loops	54		+ .08	- .08	+ .03	- .01	+ .04
		72	+ .03	- .16	- .04	- .15	- .12
Whorls	54		- .10	+ .09	+ .03	- .04	- .05
		72	- .08	+ .11	+ .12	+ .08	+ .06
Anthropometry							
Weight	63		- .09	+ .20	- .07	+ .19	+ .11
		78	- .02	+ .12	- .14	+ .25*	+ .08
Stature	312		- .26**	+ .15**	- .35**	+ .45**	+ .06
		330	- .26**	+ .13*	- .35**	+ .44**	+ .05
sitting height	87		- .18	+ .40**	- .40**	+ .57**	+ .33**
		107	- .13	+ .35**	- .32**	+ .50**	+ .31**

upper limb length	58		- .25	+ .05	- .38**	+ .39**	+ .14
		67	- .24	+ .06	- .41**	+ .38*	+ .15
biacromial	106		+ .55**	+ .19	+ .07	+ .02	+ .36**
		126	+ .45**	+ .16	+ .02	+ .04	+ .31**
biiliac	62		- .35**	+ .14	+ .01	+ .21	+ .15
		81	- .43**	- .04	- .14	+ .15	- .04
transv. thoracic	37		- .50**	- .24	- .33*	+ .24	- .21
		44	- .44**	- .24	- .29	+ .07	- .26
sagittal thoracic	36		.00	- .02	- .12	+ .04	- .18
		43	- .10	- .13	- .12	- .08	- .14
calf circumf.	32		+ .27	+ .38*	+ .13	+ .01	+ .19
		41	+ .09	+ .17	+ .02	+ .03	+ .18
head length	190		- .04	+ .08	+ .04	+ .01	+ .13
		213	- .08	+ .00	- .03	- .02	+ .06
head breadth	190		+ .24**	+ .08	+ .28**	- .33**	+ .08
		213	+ .22**	+ .09	+ .26**	- .31**	+ .07
bizygomatic	160		+ .41**	+ .21**	+ .31**	- .21*	+ .26**
		185	+ .34**	+ .19**	+ .27**	- .15*	+ .24**
face height	86		- .05	+ .06	+ .06	- .20	- .12
		112	- .13	- .07	- .05	- .21*	- .18
nose height	105		- .16	- .26**	- .15	- .11	- .21*
		131	- .22**	- .32**	- .20*	- .18*	- .27**
nose breadth	179		+ .49**	+ .05	+ .10	- .33**	.00
		203	+ .42**	+ .02	+ .08	- .35**	- .03

*significant at 5%

**significant at 1%

previously showed no significant correlation of the frequency of this variant with climate, two significant positive correlations now appear: with Hum.- and Temp.-. In the total sample (which includes the zero frequencies), the significant correlations of the Hb^s increase in value and that with Hum.+ becomes significant. On the contrary, all the previously significant correlations of the Hb^c fall below the significance level in the enlarged samples, the total ones as well as the ones of non-zero frequencies.

G6PD deficiency shows significant correlations with all the climatic variables but one, despite the low number of populations in the total sample ($N=26$). When the sample is restricted to non-zero frequencies, only the correlation with the Hum.+ remains significant. For a sample size identical to that for G6PD, Tf^D shows no significant correlation.

As previously, fingerprint patterns are totally independent from climate.

The correlations of the longitudinal measurements (stature, sitting height and upper limb length) and of the trunk widths (biacromial and biiliac) remain unchanged in their significance level, and only little changed in their value. Only minor changes occur in the correlations of weight (its positive correlation with Temp.+ becomes significant), of the thoracic diameters (only the negative correlation of the transverse diameter with rainfall remains significant), and of calf circumference (which loses all significance).

Head length remains independent of climate, whereas head breadth keeps the same pattern of correlations, with nearly identical values. Bizygomatic diameter keeps its pattern of significant correlations with all climatic variables. Face height, previously totally uncorrelated, gains one negative significant correlation (with Temp.+), with a nearly unchanged coefficient. Nose height is now significantly correlated with all five climatic variables, instead of two previously, whereas nose width keeps its set of coefficients practically unchanged.

DISCUSSION

The interpretation of the significant correlations between anthropobiological attributes and climatic variables is fraught with difficulties. How much of the climate-linked variation of the anthropometric means concerns the gene pool and how much of it concerns phenotypic expression, the correlation coefficients do not tell. Unlike those of metric means, the correlations of allele frequencies can only concern the gene pool, but no more than those of anthropometry do they necessarily imply that climate directly acts as a causative factor: the causal agent may be an

environmental factor which is itself associated with climate. Moreover, if the sample of populations departs from randomness in such a way that genetically close populations inhabiting a climatically homogeneous environment are over-represented, a significant correlation may appear without necessarily implying a causal link, even an indirect one.

Now the samples of populations considered here are not randomly taken: availability of suitable data is the only criterion for inclusion. To the extent to which it reduces the departure from randomness, the addition of new populations will tend to weaken the fortuitous correlations of the last kind.

This is particularly clearly illustrated by the case of the M allele of the MN blood groups. In the previous sample of 42 populations, it showed two significant negative correlation coefficients, both over 0.5: with Hum.+ and Temp.-. Ethiopian highlands, whose populations all have a high M frequency, were strongly overrepresented in the sample, which made us question the possibility that the correlation of M with cold and dryness might result merely from this bias. In the new sample of 67 populations, who are more evenly distributed, all correlations are weakened; only one (-0.34 with Hum.+) remains significant. This strong reduction of the correlations favors the hypothesis that no significant correlation would appear in a truly random sample.

Overrepresentation of central Ethiopia was still more pronounced in the still smaller sample previously available for the Rh system ($n_1 = 37-39$). However, neither R_0 nor r showed any significant correlation with climate despite the relatively low frequency of R_0 in all the area, whereas R_1 showed highly significant correlations with all climatic variables but Temp.+ , the only one with which R_2 was correlated. This pattern of correlations seemed hardly explainable in terms of sample bias only. In the new sample ($N = 49-59$), R_0 and r remain uncorrelated with climate; R_2 remains negatively correlated with Temp.+ , though by a lower value; R_1 loses its significant correlation with Temp.- but still gains in correlation with rainfall (-0.46). Apparently, the reduction of overrepresentation of Ethiopia does not tend towards the Rh alleles being independent of climate in a random sample of populations. In particular, the association of a low R_1 with a wet climate all year long would probably persist in a representative sample.

So would almost certainly do the only significant correlation present in the new set of ABO frequencies: a positive correlation of B with Temp.+ , which remains unchanged (0.24) from the former set of 184 populations to the present one of 214.

It seems that the case of the Hb^s frequency may serve as a model for

interpreting the correlations of blood polymorphisms with climate: by its large sample size with an approximately even distribution over the subcontinent, and by our firm knowledge of an environmental agent that strongly influences its variation: falciparum malaria. It is hard indeed to imagine how climate could exert a direct selective influence on blood polymorphisms. On the contrary, climate is known to influence, directly or through intermediary hosts, the spread and reproduction of a number of parasites of man which are responsible for a part of human mortality before the end of reproductive life, and are therefore capable of exerting selective pressure. Most probably, significant correlations of blood polymorphism allele frequencies with climatic variables express the underlying associations of the real selective agents with climate.

This seems clear for Hb^s . A wet climate favors the formation of the egg-laying places of the *Anopheles* mosquito, the intermediary host of *Plasmodium falciparum*; the less pronounced the dry season, the more endemic malaria will be. *P. falciparum* requires a high temperature for the development of its sexual cycle in the mosquito (the optimum being at 30°C); temperature also governs the time required for the mosquito to become infective after absorbing his plasmodial meal (Van Riel, 1966). Falciparum malaria will therefore tend to be more severe where the dry season is less marked and the minimum temperature is higher. Hb^s frequency just shows these two correlations: it tends to be greater where the humidity of the driest month is higher and where the mean daily minimum temperature of the coldest month is higher. There is little doubt that these correlations are the product of the selective power of falciparum malaria (a great killer of infants) in favor of Hb^s .

The low value of the two correlation coefficients in the sample of populations in whom the variant is present (0.17 and 0.19) is not surprising: air moisture and temperature are only two among the many known determinants of malarial mortality, with which in turn Hb^s frequency is certainly not perfectly correlated. Including the populations with zero Hb^s frequencies in the sample increases all correlations. Although the strong departure from normality so created lowers the validity of the correlation coefficients, this seems to indicate that the absence of Hb^s is associated with particularly low values of temperature and humidity, so that *P. falciparum* cannot live.

That G6PD deficiency also is positively correlated with air moisture and with temperature of the coldest month whereas Hb^c frequency appears to be independent of climate is consistent with the epidemiological evidence: this strongly suggests that G6PD deficiency also protects against malaria, whereas no direct evidence for malaria selection in favor of Hb^c has been collected (Livingstone, 1973).

By analogy with the Hb^s case, it may be supposed that the selective agents possibly acting on the A , O , R_0 , r , and probably M frequencies are not associated with climate in sub-Saharan Africa, whereas such an association may be suspected for B , R_1 and R_2 frequencies.

That fingerprint patterns are independent of climate is confirmed in the enlarged set of data. This implies that climate does not influence the phenotypic expression of fingerprints and that, whatever the selective forces, if any, that may act on these features, they are not of a climatic nature, nor are they associated with climate.

In the field of anthropometry, all the conclusions are strengthened by being based on larger samples.

The two main indicators of body size (stature and weight) vary in contradiction with Bergmann's rule, according to which body size tends to vary in inverse ratio to air temperature: in sub-Saharan Africa, stature tends to be taller where heat is more extreme. It does so also where rainfall is lower and where the seasonal contrast in air moisture is stronger. The only significant correlation of body weight is a positive one with heat. Relative weight tends to be higher in the moister zone, which invalidates any explanation of the size reduction in the rain forest in terms of undernutrition. The relation between stature and weight in West Central Africa has been discussed elsewhere (Hiernaux, Rudan and Brambati, 1975): by increasing the body surface/volume ratio, size reduction in the rain forest apparently represents a genetic adaptation to the test that constantly hot, wet and still air puts on thermolysis. On the contrary, morphological adaptation to the tropical savanna or steppe leads to an elongated physique. Both biomes, the forested and the open, are hot but they nevertheless exert largely different constraints on human physiology: the drier and more windy air of the open tropical biomes makes sweating a much more efficient means of heat loss than in the forest. As a matter of fact, mean annual temperature differs little between the equatorial forest, where the shortest statured population of the world lives, and the savanna around 8°N, where very tall populations live. Bergmann's rule fails to apply to sub-Saharan Africa because there body size responds mainly to climatic factors which are not included in its formulation.

The two trunk widths show inverse correlation with rainfall: with an increase in rainfall, shoulder width tends to increase and hip width to decrease. Thorax width varies like hip width, whereas thorax depth is independent of climate. The correlation coefficients of the first three variables with rainfall are relatively high: between 0.43 and 0.45. We have no explanation to suggest for these correlations.

With increasing rainfall, nose breadth tends to increase and nose height

to decrease. The nose tends to be higher where the cold is more severe and, but less strongly so, where heat is more extreme, where it also tends to be narrower. All these correlations agree with an hypothesis of selection based on the functional aspects that Weiner (1952) assigns to nose shape: the main physiological role of the nose is to bring the inspired air to saturation in water vapor and to body temperature. These modifications take place at the surface of the nasal mucosa, with which the inspired air will be in closer contact if the nose is high and narrow. Hence a maximum selective advantage of these features where atmospheric air departs the most from its initial state: in being too dry, or too cold, or too hot.

Face height has the same pattern of correlations as its nasal segment, but with much weaker coefficients. Apparently, only nose height, in face height, is sensitive to climate.

Head breadth and face width, which are intercorrelated, show a similar pattern of correlations: they tend to increase with rainfall, humidity, and the coldest temperature, and to decrease with the hottest temperature. In other words, the head and face will tend to be narrower in a hot and dry climate. The only indication of an underlying advantage that we could find in the literature is the observation made by Volkov-Doubrovine (1960, cited by Schreider, 1964): when a heating lamp is lit at the vertex of a skull, temperature within the latter rises the more slowly as the skull is higher and narrower.

There are good reasons to believe that the influence of climate on anthropometric variables is a direct one (Roberts 1952, 1973; Weiner 1971). As this discussion clearly shows, this is contrary to the situation in blood polymorphisms. Since many observations show that, in sub-Saharan Africa, migration to a different climatic environment does not induce important anthropometric changes during the first generations, it may be inferred that the many significant correlations of anthropometry with climate result largely from processes of genetic adaptation.

This study has shown the importance of the size and degree of randomness of the samples of populations for attaining a correct interpretation of the correlations between anthropobiological and climatic variables. It has also repeatedly shown that, in sub-Saharan Africa at least, human morphology responds adaptively to the combined effects of air temperature and humidity, and that it responds also to the extent of seasonal variation of climate. It is to be expected that a population may adapt not to its average conditions, but rather to its most extreme conditions (Templeton and Rothman, 1974) of which four out of five climatic variables considered in this study are estimates. But mean annual figures for climatic variables

themselves reflect the pattern of monthly extremes, and this presumably accounts for the associations between human morphology and mean annual temperature, as for example shown by Roberts (1973) who finds body weight, surface and chest girth negatively correlated with temperature. The differences in sample sizes and in the nature of the climatic variables considered are certainly major factors of the difference between the results of the two studies.

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