PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Genetic and Anthropological Studies in the Human Adaptability Section of the International Biological Programme

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In the U.K. contribution to the H.A. (Human Adaptibility) section of I.B.P., genetic and anthropological studies have focused on three concerns. First, attempts have been made in a number of investigations to gain additional descriptive information about the genetic composition of the world's populations. Concentrating on blood groups, blood enzymes, serum proteins and other polymorphic markers important gaps have been filled in our knowledge of the geographical patterns of human variation and of the affinities of populations with one another. Secondly, genetic information has been gathered for defining and characterizing populations which were being studied for other purposes. For example, it was of critical concern in interpreting results to know in the investigations of climatic physiology and nutrition in Ethiopia and Israel whether the various groups studied in different environments were genetically the same or not. Finally, attention was focused in a number of investigations, especially those in New Guinea, Tristan da Cunha, Tanzania, and the Orkneys, on the factors which determine the genetic structure of populations. In these the effects of such phenomena as inbreeding, genetic drift, founder effects, migration and gene flow and the relation between genetic variety and health were examined and much attention was given to the interaction between demographic forces and genetics.

The U.K. contribution to the I.B.P. in the Human Adaptability section, in contrast with that in other sections, involved many different projects, and ranged over a variety of populations and environments throughout the world. Nevertheless, despite the apparent diversity of concern, the contribution focused on a few central issues in human biology and possesses an essential unity. The most central issue was, as the name of the section suggests, to analyse the ways in which human beings, both as individuals and as groups, adapt or fail to adapt to the environments they occupy. The components of adaptation are many and range from reversible behavioural and physiological responses of individuals, through developmental responses only capable of modification during the growing period, to genetic adaptations which are heterogeneous within the species, and the properties of whole populations which at both the biological and social level facilitate persistence of the group and exploitation of the environmental resources. The full analyses of these components even in just one situation require intensive interdisciplinary investigations of physiology, nutrition, growth, epidemiology, genetics, demography and social anthropology and most of these fields have been embraced in some of the U.K. studies. Insight, however, into some particular aspect of adaptation can be gained by more restricted investigations, and a number of these have also been undertaken within the U.K. H.A. section. It is my brief to review the genetic, demographic and anthropological work and to attempt to show how this has increased our understanding of the ways in which human populations are organized and how the organization relates to particular ecological circumstances and the components of adaptation.

Biological anthropologists have long been concerned with describing the geographical patterns of heritable variation between human populations and attempting to explain in evolutionary terms the marked variation which has been found. For this purpose increasing attention has been given to character variation which is relatively simply inherited and which is not modifiable in development by external environmental factors; variation such as is found in blood groups, histocompatability antigens, serum proteins, isoenzymes and the like which are polymorphic within populations and for which the human species is polytypic. Ever more systems of this kind are being discovered and require geographical mapping. For a long known and easily tested system like the ABO blood groups our knowledge, though still far from complete, is good, but for many systems geographical information is extremely scanty. One objective, therefore, of the H.A. section of the I.B.P. generally and of the U.K. contribution in particular was to help remedy this deficiency. Blood samples were collected from numerous populations throughout the world and many of these, including almost all those obtained by British investigators, were sent for analysis to Dr A. E. Mourant and his colleagues, who acted as a world reference centre for the I.B.P. The British studies provided information on populations in Ireland, the Orkneys, New Guinea, Ethiopia, East Africa (the Hadza and Sandawe), Israel (Kurdish and Yemenite Jews), Jordan, Kurdistan, Bhutan, and the West Indies. They have produced a number of interesting findings. Thus, for example, the Hadza, a small group in Tanzania who are unique in the region for still practising a hunter-gatherer economy, are genetically distinct from their neighbours, and in having a particularly high frequency of the rhesus chromosomal combination *cDe*, show similarities with the Pygmies and with the Khoisan peoples of South Africa. The Sandawe, another group of click speakers of the same region, on the other hand, although linguistically different are genetically very similar to neighbouring Bantu groups. Another case, where geographical proximity appears to be more important than origins concerns the Jewish and Arab groups mentioned (Edholm & Samueloff 1973; Godber *et al.* 1973; Lehmann *et al.* 1973). The Yemenite Jews (sampled in Israel to which many have recently returned) are genetically very close to Arabs of the Yemen and other Arabian groups, and Kurdish Jews show many similarities with Kurds. Both of the Jewish groups, however, are distinctive in comparison with other Jewish populations. Since the date of the original outmigrations of Jewish populations is known with some precision it is possible to estimate the amounts of genetic change which have occurred in a known time interval, but of course many factors can have contributed to this change. Much of the similarity between Kurdish Jews and Kurds has probably arisen by inter-mixture but it is interesting in this case that the frequency of glucose-6-phosphate dehydrogenase deficiency in the Kurdish Jews is higher than in the Kurds themselves, although G6Pd.d. in other Jewish populations is very rare.

Although no new genetic variants have been discovered during the course of the British I.B.P. investigations, more examples of rare variants have been found. Thus, for example, a form of malate dehydrogenase previously known only from a single family of negroes in the U.S.A. and not found among 2000 samples from Africa, appeared three times in a small sample of bloods collected during the I.B.P. investigations in Ethiopia.

The causes of the patterns of genetic variation between populations are matters of on-going debate among population geneticists and anthropologists. Recent common ancestry is clearly an important cause of similarities between populations but convergent evolution may also be involved. Differences may arise either by the stochastic processes of genetic drift or by differential natural selection in different environments. The relative roles of these two forces is a matter

of considerable current controversy and depends upon the extent to which genetic substitutions within a system affect fitness. On the assumption that ancestry and drift have been the principle factors in recent human evolution a number of sophisticated models have been developed, which use multivariate techniques to determine and express the phyletic affinities of human populations. One such analysis of the I.B.P. data from New Guinea has been undertaken by Booth (1974) who shows how closely the patterns of genetic variation in the country follow those of linguistics. Similar work is being done on the Irish data, and when these are combined with other non-I.B.P. studies in Scandinavia, Iceland and northern Scotland it may be possible to trace quantitatively the various migrations which have led to the formation of the populations of this region.

Although the genetic studies in the Ethiopian and Israeli projects have provided further useful information about geographical variation, they were primarily included in the work to define the population units for investigation and to indicate what account might need to be taken of heritable differences in physiological and other quantitatively varying traits. The choice of Ethiopia as a site for study particularly illuminates this (Harrison *et al.* 1969). The aim of the investigators in this project was to analyse the components of individual adaptability and homeostasis to environmental extremes. For this purpose it was desirable to find a situation where there was likely to be little genetic variation between the populations examined. This in itself dictated a region of altitudinal variation since it is only in such regions that one finds dramatic environmental differences in such short geographical distances that the people in the contrasting environments are likely to be genetically similar. In the Simien of Ethiopia, the land rises gradually northwards to an altitude of 3000–3600 m then falls away in an abrupt precipice to 1500 m or less. Both highland and lowland areas are heavily inhabited by Amharas, and in recent years at least there has been considerable movement of peoples between the two regions. It was therefore expected that highlanders and lowlanders would be genetically similar. It was for this reason that the region was chosen and subsequent genetic testing of the populations confirmed the expectation. In a large number of polymorphic systems tested, only one, 6-phosphogluconate dehydrogenase, showed significant variation between highlanders and lowlanders and then only at the 5 % probability level. In testing many systems such events are likely to arise by chance and there is no evidence from elsewhere in the world that this system is related to altitudinal adaptations. It could therefore be reasonably concluded that whatever differences were observable between the highland and lowland groups arose from the direct effects of the altitudinal variation on development. There are, of course, many aspects to this variation besides differences in the partial pressure of oxygen, involving other aspects of climate and the concomitant effects on disease patterns and nutrition. The study of these effects has involved a series of physiological, growth and nutrition investigations which are not within my remit to review, but it seemed of some interest here to indicate how the design of the study arose and how genetic and demographic data were used in this design. In this connection it is also worth pointing out that the examination of migrants of different ages between the two regions also allowed some partitioning of the phenotypic flexibility into reversible physiological responses and irreversible developmental responses. The study of migrants provides a powerful tool for analysing many problems in human biology; one regrets that many more have not been undertaken with modern methods, but they must often be used cautiously, since for many biological attributes it is evident that migrants are not fully representative of the populations from which they come.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

So far I have attempted summarily to review the genetic and anthropological studies which were primarily concerned with the comparison of differences between populations, but the forces of evolution, which produce these differences operate within populations, and it has become increasingly apparent over the last few decades that intensive and detailed examinations of the ways in which populations are structured is necessary if we are ever to understand at all fully the evolution of our species. It may be added that almost any other problem in human biology requires an understanding of population organization, for human groups are never just a collection of individuals and always exist within the framework of a complex structure which has entity over and above the sum of its parts. More particularly, it is invariably necessary to view the present day biology of people within both their present social system and within their history, which often, at least for the immediate past can be reconstructed in some detail. Here the interests of geneticists and anthropologists intimately interdigitate with demography since the factors of concern are determined by or manifest in the demographic ones of population size, and changes in it, mating structure, movement, and variability in fertility and mortality. Four of the British H.A. contributions have focused on analysing population structure: the studies of the people of Tristan-da-Cunha, the Hadza, the Orcadians and New Guinea, especially on Karkar Island.

Special attention was given to the population of Tristan-da-Cunha during the time that the people were evacuated to this country in the 1960s because of a volcanic eruption. Extensive medical research was then undertaken to examine the effects of long isolation and small population size on health, but the opportunity of examining these same factors on demographic and genetic structure was also seized and incorporated in the I.B.P. This work has been largely undertaken by D. F. Roberts and his colleagues and represents one of the most refined and detailed studies of an island population which has ever been undertaken (Roberts 1967*a*, *b*, 1968*a*, *b*, 1969, 1971, 1973). The 270 islanders of the time, disposed in 70 family groups, traced their descent almost entirely from 15 ancestors, the first of which occupied the island in 1817. It was possible to reconstruct the full genealogies of all the islanders and to use these, along with information collected about the present genetic composition, to trace and examine the consequences of the full demographic and genetic history of the population since its foundation. Using the intrinsic rate of natural increase as a measure Roberts calculated the changing genetic fitness of the population. The fitness of the original founders was high, but there has been a general secular diminution due to changed patterns of fertility and reproduction, which involved a decline in the age of cessation of reproduction and an increase in mean interval between births. On two occasions, mainly because of large scale emigrations in 1856–7, and after a boat disaster which caused the death of almost all the able-bodied males in 1885, the 'intrinsic rates of increase' declined to negative levels indicating the precarious state which small populations are in. These critical periods had ramifying demographic consequences, more so because they did not affect the age and sex composition of the island randomly. Roberts also showed what profound effects they had through a dramatic reduction in population size in shaping the genetic constitution of such an isolated population. The other main factor affecting genetic constitution has been differential fertility. Roberts, through the pedigrees reconstructed the contribution of the original ancestors to generations of descendents. He noted that the effects of small annual changes in the gene pool brought about by differential fertility year after year have in the long run brought about practically half of the total changes in genetic constitution that have occurred. Clearly the hereditary composition of the islanders

has been much affected by 'accident' but subsumed in the term are many factors outside what is customarily referred to as genetic drift.

Because of its small size, and closed nature, one would expect the population to become inbred. In fact, partly because of the population's recent foundation and partly because the people have deliberately attempted to avoid marriage with relatives the mean coefficient of inbreeding is still quite low and it is only in those born since 1910 that it exceeds that to be expected under random mating. Roberts notes however that were it not for two ship-wrecked Italians who came to the island in 1892 and two Anglo-Irish women who came in 1908 the coefficients of inbreeding would have been much higher. Further to prevent a continuance of the inbreeding trend an immigration rate of 0.1 per generation is required if the population retains its present size, structure and mating pattern.

Although the mean inbreeding is not great, a number of individuals have quite high coefficients and this has allowed some examination of biological effects of inbreeding. On Tristan, as elsewhere, mortality has tended to be heavier among the inbred and Roberts has also found that mental disabilities increase with increase in the coefficient of inbreeding.

In some ways the study by Professor Barnicot and his colleagues of the Hadza of East Africa, a small group isolated culturally and economically from their neighbours, parallels the Tristan work. So far analysis has concentrated on epidemiological aspects but information was gained not only on the genetic composition of the present population (Barnicot & Woodburn 1975), but also on genealogies and relationships. The technical problems in obtaining these were much greater than in Tristan, with no recorded information and with great linguistic and cultural barriers to overcome. They required the persistent and skilled commitment of a social anthropologist, Dr James Woodburn, over many months but he managed to build up some extensive pedigrees and we may look forward to analyses which will shed light on how a group, still existing with a life-style similar to that which has prevailed throughout most of human evolution, are genetically structured.

While the Tristan and Hadza studies focused on the effects of isolation, the genetic and demographic components of the Orcadian investigations, largely undertaken by A. J. Boyce & D. Tills, concentrated on the effects of movement and the genetic exchange between groups of small populations. Gene flow is the main homogenizing force in evolution and has been a major factor in maintaining the integrity of the human species despite its remarkably wide geographical distribution. The Orkneys are represented by one main island and a number of smaller surrounding ones. Using census and civil register documentation which extends back for 120 years, in essentially complete form, Boyce, Brothwell & Holdsworth (1973) have examined the nature of the movement between the various parishes and made predictions about the form of any genetic heterogeneity from the movement patterns, which they are currently testing by using polymorphic markers. As is to be expected, they find that geographic distance is a major isolating influence, and that the sea separating the islands acts as some barrier to movement. However, many other local factors appear to be operating and in some instances a land separation can be more important than a sea separation of equivalent distance in reducing gene flow Thus the populations on the eastern part of the main island (Mainland) have more exchange with the northern group of small islands than they do with western populations of Mainland. Boyce has gone on to examine the components of the movement: the extent to which it is male or female movement, and the extent to which it can be regarded as movement directly associated with marriage as compared with other causes, e.g. movement of families after marriage. He

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

finds little differentiation between the sexes, which is perhaps surprising in this type of community, and considerable levels of non-marital movement even among the locally born Orcadians. Here it needs to be mentioned that at least in recent times there has been a considerable immigration into the islands, even the small and more isolated ones, and this needs to be taken into account in the genetic modelling. What at first sight might be thought to be a relatively isolated and closed set of communities turns out to be in genetic terms at least an open and dynamic one.

Boyce & Harbison (unpublished) have proceeded to examine other aspects of the marriage patterns which are of biological significance. They have followed the changes in population size in relation to marriage rates and ages and have shown that as populations decline there is an increase in the ages at marriage and in the age differences between spouses. This probably arises from the inevitable shortage of potential mates of similar age when populations become small and is likely to have consequence on the capacity of small units to maintain themselves. When the populations decline there is also a tendency for parish exogamy rates to increase as one would predict from the mate scarcity.

In summary, the Orcadian study well demonstrates the dynamic interplay between genetic and demographic phenomena and highlights the need for more work of this kind if we are ever to understand rigorously the variety of structures which make up human populations.

The New Guinea study, undertaken jointly with Australia and relying heavily on both the administrative and academic support of the Institute of Human Biology (now the Institute of Medical Research), Papua New Guinea, was probably the most comprehensive of the British H.A. projects. It centred on two groups of communities, one on Karkar island just off the north coast near Madang and the other in the Eastern Highlands at Lufa near Goroka. In the course of this work extensive information was collected on demography, genetics, epidemiology, physiology, biochemistry and nutrition, and the results of first analyses formed the basis of a Royal Society Discussion meeting in 1973 (Harrison & Walsh 1974). Dr Durnin and Professor Weiner will be reviewing the specifically nutritional and physiological work, but more can now be said of the genetic and anthropological work as my colleague Dr A. J. Boyce and I were charged, in collaboration with Dr Hornabrook of the Institute of Human Biology, with the task of synthesizing the results of the different disciplinary studies.

This we are currently attempting to do by examining the population structure (especially of Karkar island for which a complete census of the 16 000 inhabitants was obtained), the relationship between the genetic markers and various quantitative traits which have a heritable basis, and the effects of all the biological variation on fertility and mortality – the vehicles for natural selection.

Karkar island is remarkable in that the population is distributed in a circle of villages around the central volcano. In recent times there has been little permanent immigration but there is a considerable gene flow, as evidenced by the census, between the various villages, especially those within one or other of the two tribal groups. Using a migration matrix approach, as Boyce and his colleagues have also been doing in the Orkneys, we were able to predict, from the magnitude of the mate exchanges between villages and from the variations in village size, what the patterns of any genetic variety in polymorphic systems on the island might be expected to be. Additional data on the distribution of the genetic markers have recently been obtained, particularly in villages which play key roles in the movement patterns, e.g. those at the end of the tribal distributions, and it seems from early and very provisional analyses that at least the

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

broad patterns of the predictions are fulfilled. Unfortunately, it is impossible to take any account of temporal changes in movement in this type of society, in contrast with the situation in the Orkneys, but, on the assumption that gene flow is likely to have increased only in recent times, one can conclude that the Karkar populations represent much more closed systems than the Orcadian ones and that it requires a great many generations for any equilibrium level to be reached.

Knowledge of population structure is vital in considering the nature of any associations which may occur between a genetic system and a quantitative trait which has some environmental component in its variance, since it is evident that an environmental determinant may well happen to correlate by chance in its distribution with that of a gene marker. A number of significant associations have been found in the Karkar data. They include ABO with goitre susceptibility in which the O phenotype appears more likely to be affected; haptoglobins with serum globulin levels, where the HpO individuals have higher levels and haptoglobins with splenomegaly and hepatomegaly, with the Hp 1-1 phenotype showing higher frequencies of these conditions; HbJ with vivax malaria in which individuals with this chain variant are more likely to have the parasite present in their red blood cells (HbJ individuals also seem to possess much lower levels of serum phosphorus); and the P blood group with haemoglobin, serum albumin and cholesterol concentrations where the levels of these biochemical constituents of the blood are significantly lower in P-individuals. Evidence has also been obtained that P.T.C. taster capacity is markedly associated with goitre incidence on the island. These associations are not likely to be due to chance statistical significance arising from the larger number of comparisons made, since they occur either at very high levels of significance, or in both sexes considered separately or in different age groups. Nor with the exception of HpO and serum globulin do they appear to arise from coincidental co-variation on the island of the genetic markers with environmental determinants, since they occur in individual villages. Family studies will be required to distinguish between pleiotropy and linkage disequilibrium, though the former seems *a priori* to be the most likely explanation. The findings certainly indicate the profitability of the approach and suggest that it may well be possible to identify the action of natural selection in this type of population, exposed as it still is to the rigours of the natural environment. In the continuing debate about the extent to which human polymorphic variety within and between populations is due to such deterministic factors as selection, rather than to chance, they support the view that gene substitutions usually have effects on fitness as has so long been argued by Fisher & Ford. The fact that these effects, often subtle, are far from easy to detect, and, indeed, in many situations where man has drastically altered the environments which produced his evolution are probably no longer operating, is no basis for asserting that all polymorphic genes are neutral.

The availability of demographic, epidemiological and sociological data on the same individuals on Karkar permits an analysis of the effects of interrelationships between levels of acculturation, health status and fertility and mortality. Socio-economic factors, as expected, influence the pattern of disease distribution, and it can also be shown that the latter, independently of the socio-economic determination, influence not only the mortality of the diseased individual but also, at least in the case of women, fertility and the mortality of their children. Thus for almost every disease state examined the number of children born to affected women over 40 years of age and the proportion of those children surviving are both less than for unaffected individuals. While this is not surprising for severe afflictions it is perhaps remarkable

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

that these demographic consequences can be detected for such conditions as skin and eye diseases. This finding supports the view that in natural environments fertility is extremely sensitive to changes in somatic homeostasis.

Anthropometric studies also indicate the importance of nutritional factors on fertility. In the subsistence economy of Karkar, where food can be limiting, there is clear evidence that women draw upon body-fat reserves during the course of their prolonged lactation (Harrison, Boyce, Platt & Serjeantson 1975). In view of the recent evidence that body composition plays an important role in the time of maturation of girls and in the maintenance of fecundity (Frisch & MacArthur 1974) it seems possible that fat levels fall below critical levels during the course of lactation and that a subsequent period of recovery, no doubt of varying time depending upon economy, is required before the capacity to reproduce is restored. This hypothesis, if confirmed, has not only many practical implications but also would be of profound evolutionary significance particularly in terms of the beginnings of population growth in human history. This is associated with the development of Neolithic cultures, especially in the Middle East where the availability of an abundance of nutritionally rich grasses, which could also easily be kept in store, probably led to an especially rich and constant nutritional environment.

Another anthropological investigation which the New Guinea data allow is the relationship between physiological differences and the evolutionary vehicles of differential fertility and mortality. When allowance is made for the immediate effects of environmental differences on the state of adaptability (e.g. differing levels of acclimatization) inter-population physiological variability generally tends to be small. However, within any one population there would appear to be very considerable variation. There are good reasons for presuming that this intra-population variety both causes and reflects differences in individual fitness, but no attempts have been made to quantify these relationships, especially in simple societies without sophisticated medical attention and living at least periodically at the limits of survival. It is our intention to examine the data obtained by R. H. Fox, J. E. Cotes, J. Durnin and their colleagues on thermal tolerance, work capacity and nutrition in terms of their comparative effects on fertility, and extensive data has been collected recently on the reproductive histories of the subjects and their relatives who were physiologically measured. Unfortunately very little is yet known about the genetics of physiological variety, a state of affairs which is in drastic need of remedy, but it would be of profound anthropological concern were it possible to show a direct relationship between any measure of somatic fitness and demographic characteristics.

In summary, then, we may conclude that the genetic and anthropological studies undertaken in the U.K. I.B.P. have added substantially to our knowledge of human variety, have added sophistication to our understanding of the ways in which human populations are structured, and have pointed the way to some fruitful lines for future research.

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES