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THE EFFECTS OF ALTITUDINAL VARIATION IN ETHIOPIAN POPULATIONS

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CONTENTS

A study has been made of three neighbouring populations living at 1500, 3000 and 3700 m in the northern Simien of Ethiopia. The environments of these populations not only differ in many climatic elements, but also probably in nutritional factors and exposure to infections. The growth and physique of the people vary with altitude and the lowlanders (at 1500 m) tend to have a more linear body build. Differences in chest dimensions can be related to functional differences in respiratory physiology, since the highland groups, both male and female, have larger forced expiratory volumes and forced vital capacities as compared with the lowlanders. The relationships between these measures of respiratory function and age, stature and weight also tend to be dependent on altitude, but in all the Ethiopian groups there is a closer relationship between body weight and respiratory capacity than in other populations. This distinctiveness is probably due to the characteristics of Ethiopian physique. A slight polycythaemia and elevated packed cell volume are evident in the highland groups but, unexpectedly, there is some evidence that at least at the time of the expedition the haemoglobin concentrations were lower. The highlanders also show a raised systolic blood pressure. Blood-group and demographic data suggest that the various populations are probably genetically very similar, and the findings are discussed in terms of physiological and developmental adaptability.

INTRODUCTION

Many studies have now been made of the physiological effects of decreased barometric pressure and the concomitant reduction in partial oxygen pressure on healthy young adult European males (reviewed in Weihe 1964; Hurtado 1964; Pugh 1965), particularly the effects of ascending high mountains. Until recently, however, very little attention has been given to the indigenous peoples who normally inhabit these exceptional environments, and then largely in the Andes (Mongé 1948; Hurtado 1964; Baker 1966). It has, nevertheless, been appreciated that regions of great altitude variation afford ideal circumstances for studying many general aspects of human adaptation (Harrison 1966) and studies in these regions figure prominently in the programme of British contributions to the International Biological Programme. This paper deals with one such study which was carried out in northern Ethiopia in late 1965 and early 1966.

LOCATION AND PEOPLES

Whilst Ethiopia does not contain mountains of exceptional height (the highest point is Ras Dashan with an altitude of 4620 m) a large part of the country is above 2500 m, and extensive areas at 3000 m or more. Not all the country, however, is highland and one of the advantages of it for studies of adaptation is the dramatic changes of altitude which take place over very short horizontal distances. One of the regions where one finds this contrast particularly marked is in the northern Simien, where the high plateau at around 3000 m falls away abruptly as a wide precipice to lands at 1500 m or less.

The places chosen for study are in this region and are represented by the towns of Debarech and Adi-Arkai, and the small village of Geech. Debarech is situated near the edge of the Simien plateau at a height of around 3000 m. It is on one of the few permanent roadways in the area, running from Gondar, 120 km to the south and capital of Begemdir Province, to Asmara, capital of Eritrea. It is a market town of some 5000 people and serves an extensive area of undulating highland on either side of the road. Adi-Arkai is farther north along the same road, 74 km from Debarech. Although the two towns are separated by this considerable distance, Adi-Arkai is at the base of the same cliff, at the top of which Debarech stands, since the road, having passed through the Wolkavit Pass, runs parallel to the escarpment. Adi-Arkai is of approximately the same size as Debarech but it is at an altitude of around 1500 m. The road was constructed during the Italian occupation of the country and has led to considerable inter-communication between the two towns, and, indeed, with the rest of the country. The village of Geech is situated almost immediately above Adi-Arkai at a height of around 3700 m. It has to be approached, however, from Debarech, a journey which involves a 2-day mule ride. The approximate population of the village is between 100 and 200.

The northern Simien is quite densely inhabitated both in the lowland and highland areas. No reliable census figures are available, but in travelling through the country, along the road, one is constantly passing through small villages. The people are mainly Amharas, particularly in the mountains, but there are also a number of Tigrinyans and some recent immigrants from the Yemen and Aden. The region also contains small isolated communities of Falasha (Ethiopian Jews), but in the present study only two individuals of this group were encountered, and they, like the recent migrants from southern Arabia, have been excluded from the analysis.

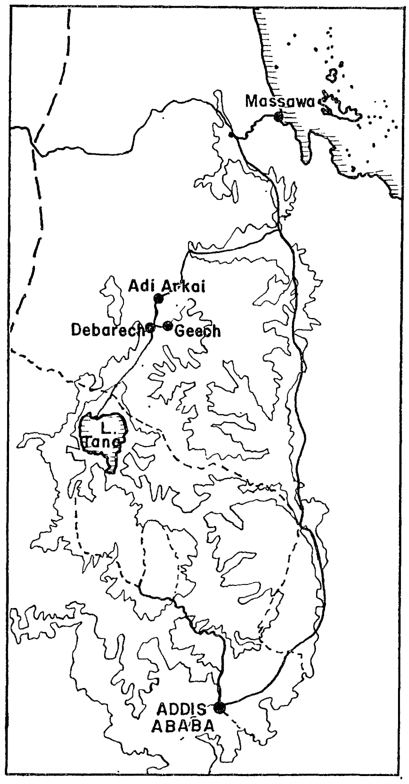

FIGURE 1. Sketch map of Ethiopia.

The origin of the Amharas is far from certain, though the history of Ethiopia is fairly well known for the last 2500 years (Luther 1958). The great Aksumite Empire was founded in Northern Ethiopia in the first millennium B.C. by immigrants from Southern Arabia, but the area has been subjected to many subsequent invasions. The languages, Amharic and Tigrinyan, are essentially semitic, though there are many hamitic influences which are at least partly due to contact with peoples like the Galla, who now occupy the south-eastern part of Ethiopia. The blood group evidence (Ikin & Mourant 1962) suggests that Amharas, like several other Ethiopian tribes, have about equal numbers of genes derived from Mediterranean (Caucasian) and Negro stocks. They are, however, usually classified by physical anthropologists as belonging to the Mediterranean stock of Caucasians.

The majority of the people are Coptic Christians, but in this northern region there are also many Mohammedans, and the village of Geech is entirely Mohammedan. The Mohammedan influence is largely attributable to a series of invasions from the north, especially that led by Muhammed Gran in the sixteenth century.

The altitudinal variation in the region is not only responsible for differences in barometric pressure, but also for considerable temperature variation. During the period of the expedition,

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which was in 'winter', the maximum day temperature at Adi-Arkai ranged between 35 and 40 °C and there was little diurnal variation. At Debarech, however, although afternoon temperatures reached 35 °C, there was an enormous diurnal variation and temperatures below 0 °C were frequently recorded at night. And at Geech even the day temperatures were markedly affected by the altitude and tended to be only around 20 °C at the hottest time of the day. No measurements were made of the solar radiation load, but it appeared, by subjective assessment, intense in all three environments.

MATERIALS AND METHODS

In all population studies there are difficult problems of sampling and this is particularly so in short-term expeditionary work when it is often impossible to obtain detailed information on the structure of the community. Under these circumstances it is all too easy to introduce various biases in sampling. In the present study, where interest is focused on the comparative differences between populations at different altitudes, what was required was a random sample of healthy adults from the three localities. To gain the cooperation of the subjects, however, it was necessary to dispense medical treatment and this, of course, could well in principle introduce some bias. As it happened, however, the majority of patients were young children, and, since in the main study interest was focused only on adults, the parents were subjected to the routine investigation, whilst their offspring were being treated. No adults who were acutely ill at the time of the study were included in the sample. The provision of medical aid was not the only incentive to prospective subjects. In addition, the local authorities urged people to participate in the study, and the provision of polaroid photographs acted as a considerable inducement. The latter were useful, not only for this reason, but also for identification of subjects when they subsequently returned for the collection of blood samples.

The same approach was adopted at all three localities and produced 216 adult subjects at Debarech, 208 at Adi-Arkai and 32 at Geech. These samples are composed of males and females between the ages of about 18 and 50. Individuals whose third molars had not erupted and those who were aged were excluded from the study. In addition, however, a sample of 135 school boys at the local school at Debarech and 93 boys at the school at Adi-Arkai were measured for certain parameters. The ages of these schoolchildren ranged from 6 to 23 years and are probably as close as one can get to a random sample, though the socio-economic background of children who attend school in this part of Ethiopia is probably not completely representative of that of the children generally.

In the course of the study of individual subjects, information was collected, by interview, of their family histories, and, so far as females were concerned, of their reproductive histories also. A detailed medical examination was undertaken on the majority of subjects, and a retrospective study made of the diseases and ailments from which they had suffered, using the classification devised by the College of General Practitioners. Blood pressure and pulse rate recordings were made at this time, along with a routine haematological study of some of the subjects chosen at random. Subsequently, measures of respiratory function were made using a spirometer for measuring forced vital capacity and forced expiratory volume, and the examination was completed by undertaking anthropometric measurements, which always included height and weight as well as measurements of skin colour taken with an EEL reflectance spectrophotometer. The particular procedures are described in detail in the individual sections.

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RESULTS

Demography

Whilst it was not possible within the short time that the expedition was in the field to make a detailed study of the demographic structure of the populations, some parameters of particular relevance to the biological and medical investigations were established.

One of the most important of these was the mobility of the populations, and subjects were asked where they were born, at what age they had moved to their present home if they were migratory, and how frequently they travelled to the highlands or the lowlands, as the case might be.

The 216 adult subjects at Debarech were composed of 125 males and 91 females. Of the males, 82 were born in the town or its immediate environs (i.e. within a 2-day mule ride), whilst the remainder were born outside this region. Of the latter, 24 came from other high altitude regions and 19 from lowland areas. Thirty-three of the 91 females were born outside the Debarech region, and of these 16 came from highland regions and the remainder from the lowlands.

The situation is somewhat similar at Adi-Arkai where 52 of the 123 males were born outside the immediate region round the town, and of these 11 came from other lowland regions and 41 from the highland zone. Amongst the 85 females, 49 were migrants, of whom 23 came from the lowlands and 26 from the highlands. By contrast, the village of Geech contained no migrants and all the 32 male subjects studied there were born in the village. This isolation was no doubt partly due to Mohammedanism, but is probably characteristic of all villages which are some distance from the road. The building of the road must certainly have increased considerably both emigration and immigration and in particular has facilitated intercommunication between the highlands and the lowlands. For the purpose of the present study the existence of migrants, especially those from one altitude zone to another, was of considerable value in analysing the development of phenotypic changes. In the majority of instances migration took place at ages after the individuals would normally have completed their growth.

Although the composition of samples suggests that the females are as mobile as the males, it would appear that most of the female mobility is attributable to exogamy. When among the local groups the frequency of journeys from the highlands to the lowlands and vice versa are compared in the two sexes, there are clear differences. These are difficult to quantify on the present data, but the majority of the men stated that they moved quite frequently for short periods of time over the escarpment. By contrast many of the locally born women had never been outside their home area.

Determination of an individual's age presents a difficult problem in preliterate societies. In the samples of children some objective estimates could be made from the stages of dental eruption but in the adults it was impossible to do more than make an informed guess. The subjects of course were asked their age and in most cases there was a fairly close agreement between the reported age and the previously made subjective assessment. In these instances the reported age was used in the analyses. Sometimes, however, there was a considerable discordance, particularly among the older subjects, and in these cases the assessed age was used. The mean ages of the various adult samples thus determined are presented in table 1. Not only are these means very similar but the age structures of the different groups are also comparable.

The reported information which was obtained on the reproductive histories of the females is presented in table 2. Again, those parameters which depend upon the establishment of subjects' age will have a high component of error in them, but it seems likely that information on the sequence of events will be reliable. Thus, for instance, it can be said with reasonable confidence that Ethiopian women tend to be married before their menarche. The distribution of marriage age of course has a high variance with a marked tendency to positive skewing, but despite this the mean age of marriage is less than the menarchical age in all the various samples and quite a large proportion of girls are married before they are ten. The youngest age recorded was seven. The social significance of this is not known, and it was not established whether the marriage is consummated during these early years. Although monogamy is the rule even among the Mohammedan sect, divorce is very common in the Simien and both men and women are frequently married a number of times. The first marriage is often a barren one. However, so far as can be judged on the present very limited data, there is no relationship between the likelihood of divorce and the barrenness of the marriage, and couples who have had children are as likely to separate as those who have not. The high frequency of divorce and re-marriage, clearly indicated in table 2 from the mean number of husbands women in the samples had had, and from the comparatively low mean age of these women, will inevitably have implications on the genetic structure of the population. Whilst the re-marriage does not appear to be related to fertility, and it will have no effect on over-all population variability, it will obviously tend to increase within-family variance at the expense of between-family variance.

TABLE 1. MEAN AGES OF SAMPLE

	males		females	
	n	*m*	*n*	*m*
Adi-Arkai				
lowland migrants	11	36.4	23	28.7
locals	71	29.7	36	27.1
highland migrants	41	35.6	26	30.7
Debarech				
lowland migrants	19	35.7	17	28.1
locals	82	34.5	58	29.9
highland migrants	24	36.5	16	31.6
Geech	32	31.9	—	—

As a rough estimate of the fertility of the populations, the number of pregnancies of each woman was divided into the number of years over which she was married from her menarche to the time of study or to her menopause as the case might be. The mean values for these estimated intervals between pregnancies are also shown in table 2. They must be treated with considerable caution, since they assume that a woman is equally fecund over the whole of her reproductive life, and no weighting has been given to those cases where a woman had a single child early in her married life, and no subsequent children. Although few, these cases dramatically increase the estimated pregnancy interval when the woman happens to be approaching her menopause. It does appear, nevertheless, even when no account is taken of completely barren women, that fertility is below the theoretical total fertility, usually estimated at about a child in every $2\frac{1}{2}$ years (Weiner 1964) and it seems to be particularly low in the various migrant groups. As in many African countries, Ethiopian women tend to wean their babies late, but, in contrast with other areas, there does not appear in Ethiopia to be any restriction on sexual relations during the period of lactation. The general estimate of the frequency of sexual intercourse (table 2) cannot be considered as very reliable, but it is remarkably consistent in the different groups.

The majority of the women (76 out of 80 at Debarech and 64 out of 70 at Adi-Arkai) stated that their menstrual cycles were regular, but characteristically, though not invariably, they do not menstruate during lactation even though this is often prolonged.

Table 2. Reproductive histories of females

	age of sample (mean)	age of menarche (mean)	age of marriage (mean)	regularity of menstruation: regular	regularity of menstruation: irregular	no. of pregnancies	estimated pregnancy interval mean years	no. of: miscarriages	no. of: stillbirths	no. of: neonatal deaths	no. of: preweaning deaths	no. of: postweaning deaths	no. of: total	no. of husbands (mean)	intercourse frequency/week (mean)
Adi-Arkai															
lowland migrants	32.1	15.5	14.4	14	0	41	4.9	0	0	2	9	2	13	1.53	1.60
n	15	16	14	—	—	11	11	—	—	—	—	—	—	15	12
locals	27.7	14.7	13.1	31	4	94	4.4	0	0	2	5	1	8	1.56	1.66
n	36	36	35	—	—	26	25	—	—	—	—	—	—	36	36
highland migrants	29.5	14.5	13.1	19	2	38	6.8	1	0	1	1	2	5	1.87	1.65
n	24	22	14	—	—	14	13	—	—	—	—	—	—	24	22
Debarech															
lowland migrants	29.3	13.93	12.6	14	1	43	6.7	5	0	2	3	1	11	1.94	1.63
n	16	15	16	—	—	13	13	—	—	—	—	—	—	16	15
locals	28.9	14.5	12.4	51	2	147	4.2	7	1	5	8	11	32	1.63	1.71
n	54	53	53	—	—	54	41	—	—	—	—	—	—	54	49
highland migrants	31.7	13.6	12.3	11	1	42	6.8	9	1	4	1	3	18	2.14	1.54
n	15	14	16	—	—	10	9	—	—	—	—	—	—	14	12

The pregnancy histories and postnatal mortality rates are also recorded in table 2. Although the numbers are small it is evident that there is a high mortality in both the highland and lowland populations during the first few years of life. What perhaps is more interesting is the clear suggestion that the miscarriage rate is higher in the highland area. Among the 232 pregnancies recorded at Debarech in both local and migrant groups there were 21 reported miscarriages, whilst at Adi-Arkai there was only one reported case in 173, and that from a woman who was a migrant from the highlands. The χ^2 value for this difference is 11.9 and the probability, therefore, that it is attributable to chance, less than 1 in 1000. Pregnancy difficulties have frequently been reported in European women living at high altitudes but so far as is known it has not been recorded in indigenous peoples.

The women in the study were also asked whether they experienced difficulties in labour during childbirth. At Debarech 39 out of 65 said they had difficulties with at least some pregnancies, whilst at Adi-Arkai the numbers were 33 out of 50. It is of course appreciated that the subjectivity of the assessment must introduce a large component of error but it would appear that the over-all environmental differences do not affect this parameter of reproduction. If, however, attention is restricted to non-migrant groups, the comparative numbers at Debarech are 20 out of 42 who said they had difficulties and at Adi-Arkai 19 out of 26, and this difference is statistically significant.

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Medical examination

(*a*) *Blood pressure*

Blood-pressure readings were taken by means of a 'cuff' sphygmomanometer with the subject lying down. Prior to the readings the subjects had been at rest for at least 10 min as their medical histories were collected. The results on the various local groups are presented in table 3. There is some evidence that systolic blood pressure is somewhat raised in the highland groups. The difference between the Debarech and Adi-Arkai males is significant at the 5% probability level ($P < 0.05 > 0.02$) and, although the difference between the females is not significant, the difference in magnitude of the means is in the same direction and of the same order. Further, whilst the male difference between Adi-Arkai and Geech is also not significant, again the highland population has the greater mean. In contrast, none of the diastolic blood pressures is significantly different from another, nor do they show any systematic trend with altitude.

(*b*) *Pulse rate*

The number of pulses in the radial artery per minute, determined over a half-minute period, are also presented in table 3. Again, measurements were taken only after the subject had been at rest and it may be recalled that measurements were only taken on subjects who were not suffering from any acute illness. Despite the marked differences in atmospheric oxygen tension between Debarech and Adi-Arkai, neither the males nor females from these areas show significant differences in pulse rate. By contrast, the males at Geech have very significantly lower rates than the Debarech males ($P < 0.001$) and Adi-Arkai males ($P < 0.01$). This somewhat surprising finding is possibly related to atmospheric temperature. Although it was cold at night in Debarech, during the day when subjects were examined they were probably exposed to as great a heat load as at Adi-Arkai from the intense solar radiation. At Geech, however, it was more or less constantly cool or cold.

TABLE 3. BLOOD PRESSURE AND PULSE RATE

	Adi-Arkai			Debarech			Geech		
	m	*n*	S.E.	*m*	*n*	S.E.	*m*	*n*	S.E.
				local males					
blood pressure (mmHg)									
systolic	119.0	71	1.20	123.2	76	1.52	121.0	22	2.62
diastolic	76.3	71	1.32	76.5	76	1.29	79.9	22	2.15
pulse rate	73.7	71	1.52	76.0	76	1.67	64.6	22	2.62
				local females					
blood pressure (mmHg)									
systolic	115.0	35	2.41	119.2	34	2.28	—	—	—
diastolic	75.9	35	1.70	74.4	34	1.85	—	—	—
pulse rate	84.6	35	1.88	83.4	34	2.28	—	—	—

TABLE 4. FREQUENCY OF COMMUNICABLE DISEASE (MALES AND FEMALES)

	Adi-Arkai		Debarech	
	no. affected	no. non-affected	no. affected	no. non-affected
measles	90	98	33	112
malaria	85	103	21	124
dysentery	13	175	1	144
scabies	9	179	17	128
syphilis	47	141	31	114

(*c*) *Medical history*

A general medical examination of each subject was made, mainly to exclude the acutely sick from the samples and to ascertain the severity of any respiratory disease. In addition, a retrospective study by questioning was made of diseases which the subject had contracted at some time in his life, and for this purpose the morbidity classification devised by the College of General Practitioners was used. Although this classification was not drawn up with tropical diseases in mind, in the hands of an Ethiopian doctor and with no language difficulties it proved completely adequate for determining the frequency of the main diseases from which the population suffered.

The major communicable diseases of the area are measles, malaria, dysentery, scabies, and syphilis but, with the exception of syphilis, there are striking altitude variations in the frequency of infection. This is shown in table 4 where the numbers of subjects at Adi-Arkai and Debarech who had contracted those diseases at some time or other are compared with the numbers who reported a history free of them. The incidence of measles, malaria and dysentery are all greater in the low altitude population, but scabies appears to be commoner in the highlanders. However, the total incidence of communicable disease is much greater in the lowland environment, since if a comparison is made of the numbers of people who have had one or more communicable diseases during their life with the numbers who have been completely disease free, the χ^2 value is 32.1 which, with one degree of freedom, gives a probability value of less than 0.001. Other communicable diseases found in the area include respiratory and other forms of tuberculosis, infective hepatitis, schistosomiasis, and gonococcal infections, but they are rare by comparison with the aforementioned diseases, and on the present data it is impossible to distinguish any altitude effects.

Among non-communicable diseases, disorders of the alimentary system appear to be most common, but the samples are too small to establish reliable frequencies. Some cases of cardiovascular disease were encountered in the clinical work, and treatment for minor ailments of the skin and eyes was extensive, especially in young children.

(*d*) *Haematology*

Routine haematological studies were carried out on a number of the non-migrant subjects. Red and white cell counts were taken with a haemocytometer, and smears were made for subsequent examination in the laboratory of differential white cell counts. Packed cell volumes were determined from a 10 min spin with a hand centrifuge and haemoglobin estimates made with a Sahli haemoglobinometer.

It is appreciated that, even under good laboratory conditions, haemocytometer values are notably inaccurate and under field conditions, where it is not always easy to maintain the cleanness and dryness of glassware, etc., there must be a yet larger component of error. Further, cross-comparison tests showed that the estimates of packed cell volumes made with the hand centrifuge were on average greater by 7.87 than those routinely established in the laboratory. However, despite this sort of difficulty, it seemed reasonable to suppose that different biases would not be introduced at the different localities, and although some locality differences might be concealed by the error those that were found would be real.

In table 5 the mean values of the results are presented along with their standard errors. For comparisons between the populations here studied it seems preferable to use the data as measured, rather than calculate individual M.C.VS and M.C.HS, partly because of the technical errors already mentioned, and partly because not all the individuals tested were tested for all the parameters.

The comparison reveals that whilst there are no differences in the total white cell counts at the different altitudes, the red cell count is significantly greater in the sample of Debarech males than in the Adi-Arkai males ($P = 0.02$). The estimated packed cell volumes, in both males and females, are also significantly greater at Debarech than at Adi-Arkai ($P < 0.001$ and $P < 0.02$ respectively).

TABLE 5. HAEMATOLOGY OF LOCAL GROUPS

	Adi-Arkai			Debarech			Geech		
	m	*n*	S.E.	*m*	*n*	S.E.	*m*	*n*	S.E.
				Males					
R.B.C.	3982127	47	59090	4274324	37	92340	4078667	15	88770
W.C.C.	6007	46	265	6073	37	291	6845	15	495
P.C.V.	54.6	46	0.73	58.9	45	1.09	55.0	15	0.82
haem. conc.	107.8	47	0.70	101.2	56	1.94	102.9	17	1.21
				Females					
R.B.C.	3597368	19	85320	3622500	12	102600	—	—	—
W.C.C.	5497	19	331	6097	12	268	—	—	—
P.C.V.	50.2	17	0.93	53.3	20	1.07	—	—	—
haem. conc.	97.3	19	1.17	91.5	17	1.40	—	—	—

In contrast, the data obtained in this study indicate lower haemoglobin concentrations in the highland populations. The means for the Debarech population are significantly smaller than those for Adi-Arkai, at a probability level between 0.01 and 0.001 in the males and at less than the 0.001 level in the females. Further, although the sample of Geech males is small, the recorded haemoglobin concentrations are again significantly smaller than those obtained on the Adi-Arkai males, at a probability level between 0.01 and 0.001. These remarkable, and statistically very significant, findings are hard to explain. They are certainly not due to errors arising from changes in reagents during the course of the expedition. These reagents were checked on return to the laboratory, and anyway the Adi-Arkai population was measured between the Debarech and Geech ones. They are also not due to the presence in the samples of a few highly anomalous individuals; most of the highland individuals recorded lower measurements of haemoglobin concentration than most of the lowlanders. On the other hand, during a subsequent expedition led two years later to the same area, the reverse situation was found with the haemoglobin concentrations at Debarech being higher than those at Adi-Arkai (E. J. Clegg, personal communication). It is, therefore, worth noting that whilst the measurements recorded here were obtained with a Sahli-haemoglobinometer, the more recent results were made with a photoelectric colorimeter. This might suggest that the visual colour matching involved in the Sahli-method is affected by altitude-determined variations in light. There appears to be no evidence for or against this possibility and the differences obtained in the two studies may be due to the fact that the measurements were taken at different times and on samples of different composition. On balance, it seems most likely that the aforementioned results on the haemoglobin concentrations are due to some unrecognized technical error factor, but it is possible that they present a true picture of the situation at least at the time of the study.

For comparative purposes the mean corpuscular haemoglobin concentrations as well as the mean corpuscular volumes have, therefore, been calculated and are presented in table 6. In calculating these values, the means of the erythrocyte count, packed cell volumes and haemoglobin concentrations have been used and the estimated mean packed cell volume has been reduced by 7.87 (the correction factor between the laboratory and field technique). The evidence might be taken as suggesting that in all three populations the mean corpuscular volume is large by comparison with other populations, but this is probably due to error in the estimation of red cell count. A low red cell count is not typical of Ethiopians and it is reported from the hospital laboratory at Addis Ababa that general patients have 'as their expected normal a count between 4 and 6 million r.b.c./mm^3'.

TABLE 6. CORPUSCULAR VOLUME AND HAEMOGLOBIN CONCENTRATION

	Adi-Arkai		Debarech		Geech
	m	*f*	*m*	*f*	*m*
mean corpuscular volume (μm^3)	117.4	117.5	119.5	125.5	115.5
mean corpuscular haemoglobin concentration (%)	33.4	33.3	28.7	29.2	31.6

On the other hand, the low mean corpuscular haemoglobin concentration of the highland groups, especially the Debarech population, which does not arise solely from variation in the estimated haemoglobin concentration, could well be real. The over-all impression among the highlanders is one of a comparative macrocytic anaemia, and if this were of nutritional origin, then, no doubt, the situation might well change from time to time.

The differential white cell counts reveal some interesting phenomena. As already observed, the total white cell counts show no general leukocytosis, indeed on average they tend to be lower than would be expected in European populations, though this again may be due to difficulties in obtaining reliable counts. However, within this more or less normal range, there are atypical compositions, and if one considers, for instance, the comparative numbers of neutrophil polymorphs and lymphocytes, one finds in the Adi-Arkai sample that 33 out of 70 individuals, and in the Debarech sample 72 out of 116, have a greater proportion of lymphocytes in the peripheral circulation than polymorphs. The difference between the two populations is approaching significance at the 5% probability level, but the main feature of interest is that very few individuals in either population show the proportion of polymorphs to lymphocytes usually found in healthy European populations (i.e. about 7 : 3). The peculiarities in the differential count are no doubt related mainly to the patterns of infectious disease, but it would be dangerous on the present evidence to ascribe them to particular agents. There is little or no correlation between the reported medical histories of individuals and their differential counts.

Another, and not unrelated, feature of the differential counts is the striking evidence for a widespread eosinophilia, particularly in the Adi-Arkai population. The distribution of the percentage of eosinophils among the Debarech group tends to show a clustering below the 5% level. If this, though high, is taken as the limit of normal variation, 26 out of 58 males at Debarech can be said to be eosinophilic, whilst the proportion at Adi-Arkai is 43 out of 50. χ^2 for the difference between the two localities is 17.9 and is highly significant. The high level of eosinophilia in both populations, which occasionally reaches levels of nearly 40% eosinophils in the differential count, is almost certainly due to a high infestation rate with parasitic worms, especially nematodes, for which there is a history in the region. Unfortunately it is impossible to say whether the difference between the two localities is due to variation in this infestation, or whether the level at Debarech is lower because the population is showing the known effects of altitude on eosinophil count.

TABLE 7. ANTHROPOMETRY OF LOCAL MALES

	Adi-Arkai			Debarech			Geech		
character	*m*	*n*	S.E.	*m*	*n*	S.E.	*m*	*n*	S.E.
weight (kg)	53.65	68	0.7652	56.83	81	0.8202	56.93	20	1.565
body measurements (cm)									
height	168.77	71	0.8522	167.27	81	0.5704	169.98	20	1.601
sitting height	85.61	42	0.5353	84.46	17	0.7325	—	—	—
suprasternal height	137.31	43	0.8789	135.65	53	0.6374	141.57	17	1.461
anterior iliac spine height	97.49	44	0.8143	96.79	52	0.6590	100.80	17	1.091
transverse chest	26.26	44	0.2124	26.87	55	0.1715	—	—	—
antero-posterior chest	18.43	44	0.2047	19.19	55	0.1954	—	—	—
biacromial	38.12	44	0.2110	37.92	53	0.4088	—	—	—
biiliac	25.21	44	0.2441	26.92	54	0.2656	—	—	—
total arm length	75.39	44	0.5115	75.46	52	0.4098	76.71	14	1.0530
wrist breadth	5.29	44	0.0407	5.38	54	0.0405	5.44	17	0.0824
hand breadth	8.96	44	0.1063	9.00	54	0.0974	8.86	17	0.1081
ankle breadth	6.95	44	0.0657	6.82	54	0.0522	7.00	17	0.2951
bicondylar humerus	6.22	44	0.1539	6.52	54	0.2331	6.57	17	0.0939
bicondylar femur	8.81	43	0.0577	9.00	54	0.0725	9.03	16	0.1258
neck circumference	31.60	44	0.1640	32.47	54	0.3214	31.51	17	0.3571
upper arm circumference	21.91	44	0.2635	22.86	54	0.2292	23.24	17	0.9898
calf circumference	30.30	44	0.3098	30.82	54	0.2604	29.86	16	0.5273
chest circumference expired	82.08	70	0.5495	85.44	80	0.5473	84.03	19	1.117
chest circumference inspired	86.66	70	0.5300	89.98	80	0.5283	88.75	19	1.151
Skin folds (cm)									
triceps	5.11			4.91			4.85		
log	0.696	43	0.0152	0.674	55	0.0165	0.672	17	0.0274
subscapular	6.88			7.11			6.92		
log	0.824	44	0.0154	0.839	43	0.0160	0.817	17	0.0324
supra-iliac	9.51			8.32			8.18		
log	0.957	44	0.0641	0.887	34	0.0294	0.886	17	0.0377
medial calf	5.02			4.59			3.69		
log	0.688	42	0.0204	0.625	50	0.0233	0.560	16	0.0193
Head measurements (cm)									
head length	19.11	44	0.0900	19.37	54	0.1856	19.15	17	0.1368
head breadth	14.66	44	0.0777	14.96	55	0.0778	14.75	17	0.0960
nose height	5.13	44	0.0581	4.98	55	0.0593	5.38	18	0.0925
nose breadth	3.60	44	0.0360	3.60	54	0.0387	3.51	18	0.0693
bizygomatic diameter	13.32	44	0.0615	13.37	55	0.0597	13.34	17	0.1161
bigonial diameter	9.83	44	0.0723	10.17	55	0.1040	9.87	17	0.1290
face length	11.70	43	0.1166	11.57	55	0.0873	12.40	17	0.1600
mouth width	5.18	44	0.0511	4.97	55	0.0650	5.44	17	0.1035
lip thickness	2.08	45	0.0452	1.96	55	0.0462	2.10	17	0.0700

Anthropometry

Anthropometric measurements were carried out on samples of subjects at the three localities. The list of measurements made is itemized in table 7. These measurements include those which have been recommended for use in International Biological Programme surveys, and were made according to the instructions given in the IBP handbook of agreed methods, with the exception that total arm length was taken with a tape, because a suitable anthropometer was not available. In addition to the recommended measurements, expired and inspired chest circumferences were recorded with a tape, measured at the level of the nipples.

In taking the measurements subjects were unclothed as far as possible, though in the case of females only the removing of 'top clothing' was permitted. In all cases, weight and the various height measurements were taken with the subjects in their bare feet.

The majority of the locally born males at the different localities were subjected to the full array of measurements, though at Geech certain of them could not be taken. Only weight, height and chest circumference were recorded for the non-local males and only weight and height for the whole of the female samples. Weight, height and chest circumference were also taken on the samples of boys from the schools at Debarech and Adi-Arkai.

TABLE 8. ANTHROPOMETRY OF MIGRANT MALES

	lowland migrants			highland migrants		
	m	*n*	S.E.	*m*	*n*	S.E.
Adi-Arkai						
weight (kg)	53.36	11	1.579	55.91	30	1.156
height (cm)	165.55	11	1.640	168.28	40	1.003
chest circumference expired (cm)	82.70	11	1.318	84.87	41	0.964
chest circumference inspired (cm)	87.15	11	1.466	89.33	41	0.972
Debarech						
weight (kg)	55.74	19	1.609	59.80	24	2.028
height (cm)	165.97	19	1.849	166.53	24	1.455
chest circumference expired (cm)	85.08	21	1.204	87.04	22	1.276
chest circumference inspired (cm)	88.50	21	1.133	90.96	22	1.176

The mean values of the measurements for the different groups of local adult males are presented in table 7. Comparisons of these means, with *t*-tests, reveal that the Debarech males are significantly larger (at the 5% probability level or less) than the Adi-Arkai males in weight, inspired and expired chest circumference, transverse, and antero-posterior chest widths, bi-iliac breadth, bi-condylar femur breadth, upper arm and neck circumferences, head length, head breadth and bigonial width. On the other hand, mouth width and medial calf skin thickness are significantly larger at Adi-Arkai. Between these two populations there are no significant differences in any of the height measurements, though the means for the Adi-Arkai sample are consistently greater. Comparisons of the Geech sample with both the others show that they have significantly larger suprasternal and iliac heights, face lengths, nose heights, mouth widths, and medial calf skin fold thicknesses, than either the peoples of Debarech or Adi-Arkai. The other measurements are not significantly different.

The mean values for the migrant male groups are presented in table 8 and in figure 2 the comparative magnitude of the means of body weight of these migrants and of the local groups are also shown. The only significant differences in weight, except for the already mentioned one between Debarech and Adi Arkai locals, concern the migrants to Debarech from other high altitude regions, who differ from the Adi-Arkai locals and the lowland migrants to Adi-Arkai. However, some of the means are based on rather small numbers and have large standard errors, and figure 2 is a more revealing comparison. It shows that both the migrant as well as the local high-altitude populations tend to be heavier than the lowland groups, and it is interesting that the lightest of the highland groups is the migrant one from low altitude, whilst among the lowlanders the heaviest are the migrants from high altitude.

None of the differences in height between the local and migrant groups are significant or show any very noticeable trend. The magnitudes of the chest circumferences, both mean inspired and mean expired, however, show almost identical trends to those in body weight in the different groups of males. The differences which reach significance at the 5 % probability level or less, in addition to the local Adi-Arkai–Debarech comparison already mentioned, are those

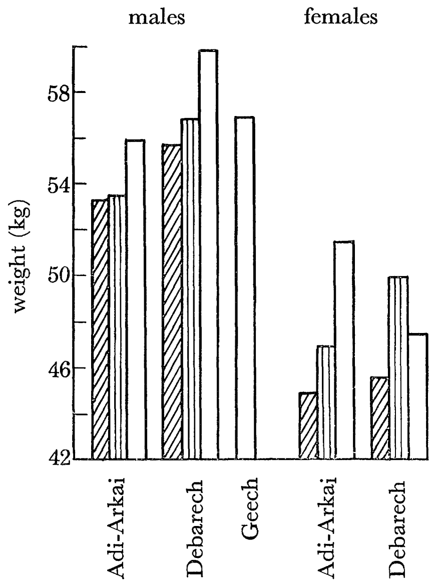

FIGURE 2. Comparative body weights.
▧ lowland migrants: ▥ locals: □ highland migrants

between Adi-Arkai locals and Adi-Arkai migrants from the highlands, between Adi-Arkai locals and highland migrants at Debarech and between Adi-Arkai locals and lowland migrants at Debarech (significant only on expired chest circumference). In general it would appear that the highland groups, including the migrants from low altitude, have greater chest circumferences than the local and migrant lowlanders at low altitude, whilst the migrants from the highlands to the lowlands retain at least to some extent the larger thorax dimensions of the highland populations.

The data on the anthropometry of the females are limited to height and weight, and are presented in table 9 and for weight shown schematically in figure 2.

The general pattern of weight variation is similar to that found in the males, with clear evidence that the indigenous highlanders, and the highlanders who migrated to the lowlands, are heavier than the indigenous lowlanders. [The local Debarech population are significantly heavier than the Adi-Arkai locals, the lowland migrants at Adi-Arkai and the lowland migrants at Debarech, and the highland migrants at Adi-Arkai are likewise significantly heavier than the same three lowland born groups.]

In the female sample there is also some statistical evidence that highlanders are taller than the lowland people, and the local Debarech females and the highland migrants at Adi-Arkai are both significantly taller than the locals at Adi-Arkai. It is to be noted, however, that there

Table 9. Anthropometry of females

	weight (kg)			height (cm)		
	m	n	s.e.	m	n	s.e.
Adi-Arkai						
lowland migrants	44.97	17	1.341	155.03	16	1.165
locals	46.96	35	0.287	152.64	34	0.831
highland migrants	51.47	23	1.860	155.86	23	1.179
Debarech						
lowland migrants	45.62	12	1.853	153.97	12	2.220
locals	49.98	37	0.878	156.64	37	0.860
highland migrants	47.48	12	1.572	153.31	12	1.346

Table 10. Ponderal index of local males and females

	males			females		
	m	n	s.e.	m	n	s.e.
Adi-Arkai	44.83	68	0.2380	42.51	34	0.2704
Debarech	43.64	79	0.1728	42.57	37	0.2548
Geech	44.28	20	0.2391	—	—	—

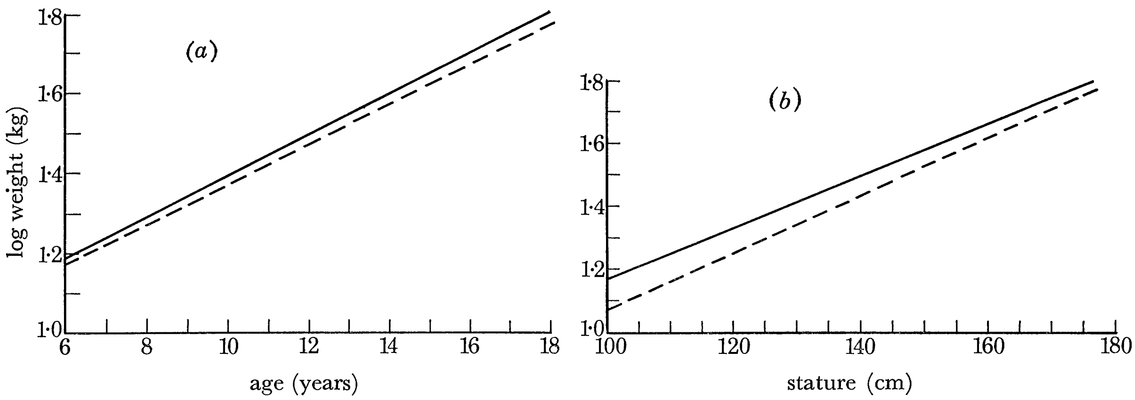

Figure 3. Relationship between body weight variation and (*a*) age, (*b*) stature.

(*a*) ---, Adi Arkai, log wt. = 0.8461 + 0.04966 age; —, Debarech, log. wt. = 0.8805 + 0.05161 age. (*b*) ---, Adi Arkai, log. wt. = 0.2996 + 0.00832 stature; —, Debarech, log wt. = 0.3508 + 0.00820 stature.

are fewer significant differences in height than in weight which suggests that height for weight the Adi-Arkai females are more linear in their physique.

A direct measure of this component is the ponderal index (height/$\sqrt[3]{\text{weight}}$), and the means of this index for the local groups of males and females are presented in table 10. The differences between the females are not significant, but the Debarech males have a very significantly lower

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index than Adi-Arkai males, and as one would expect from the previously mentioned differences in weight and height, they are less linear in their physique. The index for the Geech males, however, is intermediate, and is actually significantly different from that for the Debarech males, which suggests that altitude is not the only determinant of the differences.

The data obtained of the heights and weights of the school boys are compared by linear regression analysis in figures 3*a* and *b*, which show the relationship between log weight and age, and log weight and stature respectively. In neither case are the differences between the regression coefficients significant, but it would appear that the Debarech boys tend to be heavier, both for their height and for their age, than the Adi-Arkai ones. The regression of expired chest circumference on body weight indicates that the relationship between these two parameters is more or less identical in the two populations (figure 4).

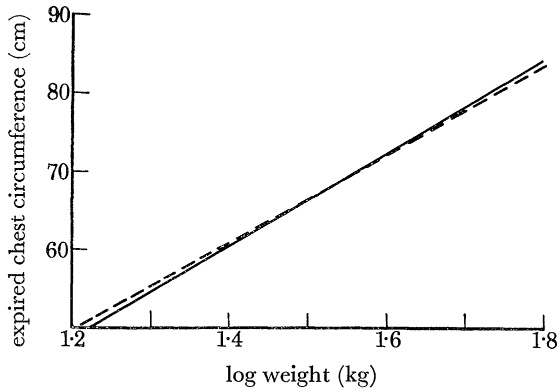

FIGURE 4. Relationship between chest circumference variation and body weight.
---, Adi Arkai, exp. chest circ. = 15.45 + 54.46 log wt.; —, Debarech, exp. chest circ. = 20.67 + 57.85 log wt.

Hand grip

A crude measure of muscular strength was made on the local male populations at Debarech and Adi-Arkai using a Salter's hand-grip dynamometer. Posture was standardized as far as possible and each subject undertook four consecutive tests. The means of the best performance of each individual are for Adi-Arkai 93.29 kg ($n = 41$; S.E. 2.748) and for Debarech 85.78 ($n = 52$; S.E. 2.694). The difference between the means for the two populations is approaching significance at the 5% probability level.

Skin colour

Measurements of skin colour were taken with an EEL spectrophotometer at 425, 545 and 685 nm on the medial aspect of the upper arm after gentle washing. It has been shown that to make comparisons of population differences it is necessary to undertake log transformations of reflectance at 425 nm and antilog transformations of reflectance at 685 nm (Harrison & Owen 1964). The means of the local adult males and females, along with their standard errors, at Debarech and Adi Arkai are presented in table 11. As in other populations, there is clear evidence that females are lighter than males in both these groups and it would appear, particularly from the measurements taken with the blue and green filters, that the Adi-Arkai population has a more heavily pigmented skin than the Debarech population.

Table 11. Percentage skin colour reflectance

		Adi-Arkai			Debarech		
		m	*n*	S.E.	*m*	*n*	S.E.
Males							
	425 nm	8.27	—	—	9.54	—	—
$\log_{10}$	425 nm	0.910	59	0.0088	0.957	43	0.0075
	545 nm	10.98	61	0.3194	12.73	44	0.6745
	685 nm	30.24	—	—	31.41	—	—
antilog	685 nm	0.201	61	0.00315	0.210	43	0.00639
Females							
	425 nm	9.84	—	—	10.30	—	—
$\log_{10}$	425 nm	0.950	29	0.0336	1.008	13	0.0208
	545 nm	13.13	34	0.5914	14.25	13	0.6657
	685 nm	33.19	—	—	35.73	—	—
antilog	685 nm	0.217	33	0.00632	0.229	13	0.00771

Respiratory function

Measures of forced vital capacity (F.V.C.) and forced expiratory volume (F.E.V. 1.0 s.) were taken on the majority of subjects, both adult and child, using a dry 'spirometer' and a standardized technique (Collins, McDermot & McDermot 1964). The results were converted to B.T.P.S.* Five consecutive readings were taken on each subject and the largest readings of both F.V.C. and F.E.V. used for analysis, whether or not they occurred in the same test. In work with European subjects (Cotes 1965) it has been customary to use the mean of a number of performances as the measure of respiratory capacity, but from a judgement of the attitudes of Ethiopians towards the test situation it seemed that an analysis of maximum values would be most meaningful. Certainly the within-individual results are highly variable and it has been shown even among Europeans that there is merit in using best performance figures when subject motivation is poor (Denolin, Sadoul & Orie 1964).

Only those individuals who, on a subjective assessment, were judged to have made at least one 'good' performance are included in the analysis. This has meant that a considerable number of female subjects have been excluded, since they appeared unable to execute the procedure satisfactorily.

Adult sample

The mean values of F.E.V. and F.V.C. for the different population groups are presented in table 12 and the comparative magnitudes are shown diagrammatically in figure 4. In both F.E.V. and F.V.C. the Adi-Arkai males differ significantly from the Debarech and Geech males, and the difference between the latter two is approaching significance. Both measures clearly indicate increasing respiratory capacity with increasing altitude, and the female samples suggest a similar relationship.

The samples of migrants are small, and only a few of the differences between them are statistically significant. In F.E.V. the difference between the lowland and highland migrants at Adi-Arkai is significant at the 5% probability level, and in both F.E.V. and F.V.C. the lowland migrants at Adi-Arkai differ significantly at the same level from the highland migrants at Debarech. The general relationships, however, are suggested by the comparative magnitudes of the means (figure 4) which indicate little or no difference between the various highland

* B.T.P.S., abbreviation for: Body temperature and pressure, saturated with water vapour (Cotes 1965).

groups, whether they are migrant or local, and little difference between the local and lowland migrants at Adi-Arkai. However, the highland migrants at Adi-Arkai are clearly intermediate between the local Debarech and Adi-Arkai groups, and as already mentioned differ significantly from the lowland migrants in F.E.V.

Table 12. Respiratory function of adults

	F.E.V. (litres)			F.V.C. (litres)		100 F.E.V./F.V.C.		
	n	*m*	S.E.	*m*	S.E.	*m*	S.E.	age, *m*
				males				
Adi-Arkai								
lowland migrants	10	2.57	0.156	3.19	0.209	80.92	1.803	38.30
locals	61	2.87	0.044	3.47	0.052	82.92	0.725	30.72
highland migrants	30	2.91	0.077	3.59	0.108	80.92	1.044	34.87
Debarech								
lowland migrants	10	3.09	0.176	3.79	0.254	82.21	1.989	36.85
locals	71	3.05	0.059	3.74	0.076	81.82	0.761	33.83
highland migrants	20	3.19	0.132	3.81	0.119	80.92	1.278	35.75
Geech								
locals	15	3.23	0.108	4.01	0.129	80.73	1.751	32.73
				females				
Adi-Arkai								
lowland migrants	16	1.99	0.091	2.37	0.121	84.25	1.368	31.00
locals	32	2.11	0.056	2.53	0.074	83.78	1.101	27.44
highland migrants	21	2.29	0.106	2.81	0.160	82.12	1.695	28.43
Debarech								
lowland migrants	11	2.13	0.087	2.54	0.121	84.30	1.586	30.18
locals	30	2.15	0.067	2.70	0.068	79.58	1.504	30.30
highland migrants	11	2.03	0.073	2.50	0.068	80.89	1.592	31.45

The samples of migrant females are very small, and none of the differences between them, or between them and the local groups, are significant. Nevertheless, the comparative magnitudes of the means show similar relationships to those of the males, and again there is evidence that migrants from the highlands to the lowlands retain some highland characteristics.

In European populations there is clear evidence that there is a relationship of F.E.V. and of F.V.C. with age and height (Cotes 1965). The partial linear regressions between these parameters have, therefore, been calculated and are presented in table 13. In contrast, however, with European populations, there is a residuum of variation in F.E.V. and F.V.C. in some of these Ethiopian populations, which, after account has been taken of age, and height, appears to be related to variation in body weight. Further linear regressions have therefore been calculated and are presented in table 14 in which the role of body weight has been included.

Effects of age

Within the age distribution of the Adi-Arkai local and lowland migrant samples there appear to be no significant regressions of either F.E.V. or F.V.C. on age in adult males or females. This situation contrasts strikingly with the local and migrant male groups at Debarech where there is clear evidence that both F.E.V. and F.V.C. diminish with increasing age, and many of the regression coefficients for these groups differ significantly from zero. The regression for F.V.C. on age is also significant among the Geech males. This clear difference between the highlanders and the lowlanders is independent of weight as well as height.

Among the males, for whom there are three groups to compare, there is a linear inverse relationship between the magnitude of the regression coefficient for the age effect and altitude. Unfortunately the information on the incidence and severity of bronchitis is meagre and not

TABLE 13. PARTIAL LINEAR REGRESSIONS OF RESPIRATORY FUNCTION ON AGE AND HEIGHT

	forced expiratory volume age			height	
	a	*b*	S.E.	*b*	S.E.
		males			
Adi-Arkai					
lowland migrants	−4.92	−0.006	0.0116	0.047	0.0270
locals	−0.88	−0.003	0.0050	0.023***	0.0060
highland migrants	−3.58	−0.17*	0.0086	0.042**	0.0131
Debarech					
lowland migrants	−5.02	−0.025*	0.0108	0.054**	0.0137
locals	−2.68	−0.022***	0.0051	0.039***	0.0099
highland migrants	−3.82	−0.024**	0.0091	0.047***	0.0123
Geech					
locals	−3.63	−0.021	0.0126	0.044**	0.0148
		females			
Adi-Arkai					
lowland migrants	−4.61	−0.015	0.0075	0.045*	0.0225
locals	−1.24	−0.006	0.0073	0.023*	0.0098
highland migrants	−4.88	−0.001	0.0137	0.046***	0.0134
Debarech					
lowland migrants	0.53	−0.015	0.0085	0.013	0.0100
locals	−2.08	−0.016*	0.0063	0.030*	0.0121
highland migrants	2.82	0.006	0.0120	−0.006	0.0176
		males			
Adi-Arkai					
lowland migrants	−7.14	0.001	0.0159	0.062	0.0371
locals	−1.31	−0.001	0.0058	0.029***	0.0069
highland migrants	−4.93	−0.007	0.0130	0.052*	0.0197
Debarech					
lowland migrants	−7.62	−0.021	0.0174	0.073**	0.0221
locals	−5.15	−0.020***	0.0067	0.057***	0.0129
highland migrants	−3.68	−0.016	0.0114	0.048**	0.0154
Geech					
locals	−6.95	−0.025*	0.0095	0.069***	0.0111
		females			
Adi-Arkai					
lowland migrants	−7.94	−0.016	0.0101	0.070*	0.0303
locals	−3.08	0.001	0.0093	0.037**	0.0125
highland migrants	−7.25	0.008	0.0168	0.063***	0.0165
Debarech					
lowland migrants	−2.16	−0.006	0.0118	0.032*	0.0138
locals	−3.15	−0.015*	0.0060	0.040***	0.0011
highland migrants	1.62	0.017	0.0099	0.002	0.0146

* Represents a significant regression at the 5 % level.
** Represents a significant regression at the 1 % level.
*** Represents a significant regression at the 0.1 % level.

TABLE 14. PARTIAL LINEAR REGRESSIONS OF RESPIRATORY FUNCTION ON AGE, HEIGHT AND WEIGHT

forced expiratory volume

	Age			height		weight	
	a	*b*	S.E.	*b*	S.E.	*b*	S.E.
males							
Adi-Arkai							
lowland migrants	−1.95	−0.002	0.0091	0.006	0.0270	0.068*	0.0284
locals	−0.34	−0.005	0.0050	0.015*	0.0070	0.016*	0.0077
highland migrants	−1.56	−0.023*	0.0086	0.023	0.0156	0.023	0.0117
Debarech							
lowland migrants	−4.70	−0.027*	0.0116	0.049*	0.0185	0.011	0.0225
locals	−1.85	−0.023***	0.0052	0.031*	0.0127	0.010	0.0098
highland migrants	−8.82	−0.024**	0.0076	0.092***	0.0188	−0.044*	0.0153
Geech							
locals	−6.46	−0.18	0.0103	0.075***	0.0166	−0.43*	0.0161
females							
Adi-Arkai							
lowland migrants	−4.74	−0.015	0.0078	0.048	0.0246	−0.005	0.0177
locals	−1.10	−0.004	0.0077	0.019	0.0111	0.008	0.0111
highland migrants	−4.15	0.0001	0.0141	0.038*	0.0170	0.010	0.0119
Debarech							
lowland migrants	0.68	−0.015	0.0091	0.014	0.0107	−0.004	0.0131
locals	−2.10	−0.016*	0.0065	0.030*	0.0145	−0.001	0.0133
highland migrants	2.78	−0.006	0.0137	−0.007	0.0197	0.002	0.0206
males							
Adi-Arkai							
lowland migrants	−3.19	0.006	0.0129	0.008	0.0382	0.090*	0.0402
locals	−0.44	−0.005	0.0056	0.016*	0.0077	0.026**	0.0085
highland migrants	−1.69	−0.016	0.0129	0.022	0.0234	0.037*	0.0174
Debarech							
lowland migrants	−6.25	−0.026	0.0177	0.052	0.0283	0.040	0.0342
locals	−3.78	−0.022***	0.0068	0.044**	0.0165	0.016	0.0127
highland migrants	−10.48	−0.016	0.0091	0.110***	0.0226	−0.060**	0.0184
Geech							
locals	−6.45	−0.026*	0.0099	0.064***	0.0159	0.008	0.0154
females							
Adi-Arkai							
lowland migrants	−8.09	−0.015	0.0105	0.072*	0.0332	−0.006	0.0238
locals	−2.70	0.006	0.0095	0.026	0.0136	0.023	0.0137
highland migrants	−7.05	0.008	0.0177	0.060**	0.0213	0.003	0.0149
Debarech							
lowland migrants	−1.99	−0.007	0.0126	0.032*	0.0148	−0.005	0.0181
locals	−2.58	−0.016*	0.0060	0.031*	0.0135	0.014	0.0123
highland migrants	1.73	0.015	0.0112	0.005	0.0160	−0.008	0.0168

* Represents a significant regression at the 5 % level.
** Represents a significant regression at the 1 % level.
*** Represents a significant regression at the 0.1 % level.

open to detailed analysis. No subjects classified as suffering from acute bronchitis were included in the respiratory study, and on the data available the individuals classified as chronic bronchitics performed as well in the tests of respiratory function as those who were identified as being free from respiratory disease. It seems likely that the type of reduction in respiratory capacity that one finds in chronic bronchitics in European populations would probably be incompatible with survival in the high altitude environment of Ethiopia. This leaves the interesting possibility that, because homeostatic control has to be set at a higher level in the highland populations

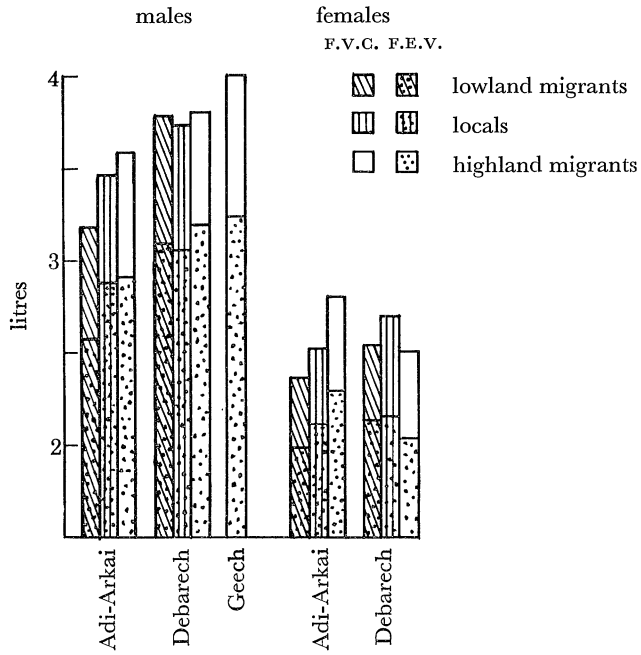

FIGURE 5. Comparative respiratory function.

than in the lowland one, the respiratory system is ageing more rapidly. It needs to be remembered here that, although the age distributions in the different samples are very similar, only subjects estimated as being under 50 years old were included in the study.

Effects of stature

With the single exception of F.E.V. in the female highland migrants to Debarech, the partial regression coefficients for both F.E.V. and F.V.C. on stature are positive, and in both males and females these coefficients in most cases are significantly greater than zero (table 13). There is no significant heterogeneity in the regression coefficients for the local groups of males and females with the exception that for F.V.C. the coefficient for Geech males is significantly greater than that for the Adi-Arkai males However, the comparative magnitude of the coefficients in both males and females strongly suggests that with increasing stature there is a greater increase in F.E.V. and F.V.C. in highlanders than in the lowlanders. Indeed, there appears to be a direct proportional relationship between the magnitude of the regression coefficients and the altitude at which the populations live.

Effects of weight

Although there are no significant regressions of body weight and respiratory function in the females, clear correlations are evident in some of the male groups. Thus the regression coefficient between F.E.V. and weight differs significantly from zero in the local and lowland migrants at Adi-Arkai, the highland migrants at Debarech and the Geech males. Similar significant regressions between F.V.C. and weight are found in the first three of these populations and in addition in the highland migrants to the lowlands. Surprisingly, however, in the highland migrants to Debarech, both F.E.V. and F.V.C., and in the Geech locals, F.V.C. show significant negative relationships with weight, though it must be noted here, that these samples are small and the levels of significance low.

The general effect of including weight in the regression analysis is to reduce the significance of the relationship between stature and respiratory function, and this is evident as much in the females as in the males. The weight factor, however, has no effect on the relationship between age and respiratory function.

Juvenile sample

The importance of body weight in considering respiratory function among Ethiopians is also evident from analysis of the samples of schoolboys at Adi-Arkai and Debarech. In table 15 the linear regression of F.E.V. and F.V.C. on age, height and weight are shown, in which these three parameters are first considered separately, then in pairs, and finally all together. In the samples at both localities, one finds the expected very significant regressions of respiratory function on each of these variables, but in the paired comparisons the age effect tends to disappear when either height or weight is taken into account. The only exception to this generalization is for F.V.C. in the Adi-Arkai boys where a significant residual regression on age remains. This could be due to inaccuracies in the age determination. The effect of height variation also disappears whenever weight is also considered, and in all cases when the regressions on age, height and weight are considered together the only partial regression coefficient to differ significantly from zero is that for weight.

It is perhaps worth mentioning here, that this effect of weight is not significantly altered by taking the cube of height rather than height itself, although this transformation improves the correlation between stature and respiratory function. Even so, the correlations of F.E.V. and F.V.C. with body weight are still always greater than with height cubed.

The pattern of the relationships, with the exception of the aforementioned age effect at Adi-Arkai, is exactly the same at the two localities, but in every case where a significant regression is found, the regression coefficient for the Debarech boys is larger than that for the Adi-Arkai boys, and in some of these cases, especially in the single regressions, the differences between them are statistically significant. This clearly indicates that for any particular increment in age, or height, or, and most important, weight, there is a greater increment in respiratory capacity, both F.E.V. and F.V.C. in the highland boys than in the lowland ones.

Gene marker studies

The aims of testing blood specimens for blood groups and other inherited factors were to define the populations under investigation in relation to the surrounding peoples, and to find out whether the two main populations, at Adi-Arkai and Debarech, differed genetically from one another, the latter aim being particularly important in the context of physiological studies.

The numbers of specimens collected at the time of the 1965–66 expedition were barely sufficient in number for the second purpose, and it was therefore decided to test further speci-

Table 15. Effects of age, height and weight on respiratory function of children

		age		height		weight	
	a	*b*	S.E.	*b*	S.E.	*b*	S.E.
Adi-Arkai							
forced expiratory volume	−0.64	0.198	0.0137***	—	—	—	—
	−3.76	—	—	0.036	0.0017*	—	—
	0.10	—	—	—	—	0 053	0.0019***
	−2.97	0.036	0.0216	0.030	0.0036***	—	—
	−0.04	0.024	0.0159	—	—	0.048	0.0038***
	−0.36	—	—	0.005	0.0045	0.046	0.0064***
	−0.26	0.020	0.0175	0.002	0.0049	0.045	0.0065***
forced vital capacity	−0.80	0.236	0.0155***	—	—	—	—
	−3.83	—	—	0.042	0.0020***	—	—
	0.14	—	—	—	—	0.062	0.0023***
	−3.36	0.056	0.0247*	0.034	0.0041***	—	—
	−0.13	0.045	0.019*	—	—	0.052	0.0044***
	−0.67	—	—	0.008	0.0054	0.050	0.0077***
	−0.47	0.040	0.0207	0.004	0.0058	0.048	0.0076***
Debarech							
forced expiratory volume	−0.90	0.237***	0.0137	—	—	—	—
	−3.41	—	—	0.038***	0.0017	—	—
	−0.01	—	—	—	—	0.058***	0.0022
	−3.16	0.034	0.0280	0.033***	0.0042	—	—
	−0.14	0.025	0.0221	—	—	0.0052***	0.0049
	−0.55	—	—	0.006	0.0056	0.049***	0.0083
	−0.45	0.019	0.0248	0.004	0.0063	0.49***	0.0084
forced vital capacity	−0.97	0.269	0.0160***	—	—	—	—
	−3.78	—	—	0.042	0.0020***	—	—
	0.05	—	—	—	—	0.065	0.0027***
	−3.42	0.048	0.0339	0.036	0.0051***	—	—
	−0.15	0.038	0.0274	—	—	0.057	0.0061***
	−0.61	—	—	0.007	0.0070	0.055	0.0104***
	−0.43	0.032	0.0309	0.003	0.0078	0.053	0.0104***

* Represents a significant regression at the 5 % level.
** Represents a significant regression at the 0.1 % level.

mens from the same populations, and these were collected by Dr E. J. Clegg during a later expedition (1967–68). There were facilities by this time for a much wider range of tests, including some which had hitherto been little used in any population survey.

Collection and testing

Blood specimens were taken by venepuncture into Vacutainers containing Sequestrene (EDTA). These were sent in thermos flasks, with ice where available, by the most rapid means available of land and air transport, to the Serological Population Genetics Laboratory, London.

From the first expedition there were received specimens from 81 unrelated subjects at Adi-Arkai and 56 at Debarech. From the second expedition 75 specimens came from Adi-Arkai and 102 from Debarech.

The specimens from the first expedition were tested for the blood group antigens A, A_1, B, M, N, S, He, C, C^w, c, D, D^u, E, e, V, Lu^a, K, k, Js^a, Le^a, Fy^a, Fy^b, Di^a, Jk^a, and Wr^a. Tests were also carried out for the Gm groups, haemoglobin variants (including an examination for possible raised contents of HbA_2) and for haptoglobins, transferrins, glucose-6-phosphate dehydrogenase deficiency and adenylate kinase variants.

The specimens from the second expedition were tested for all the above factors except Le^a, and in addition for variants of the enzymes: acid phosphatase, phosphoglucomutase, 6-phosphogluconate dehydrogenase and lactate dehydrogenase, as well as for the esterase C5 variant. Screening tests for glucose-6-phosphate dehydrogenase deficiency were not performed, but the specimens were examined for electrophoretic variants of the enzyme.

Results of the tests

In none of the specimens from either place were any examples found of C^w-, Di^a- or Wr^a-positives; there were no abnormal haemoglobins and no raised levels of HbA_2 which might have indicated β-thalassaemia.

In the first series no example of glucose-6-phosphate deficiency was found. In the second series, one specimen, of a male from Adi-Arkai, failed to show a band on electrophoresis. In view of the age of the specimen when tested this must be regarded as a doubtful case of deficiency. Only eight examples of esterase C5+ were found, three at Adi-Arkai and five at Debarech. The results of the remaining tests are shown in tables 16 to 31 and are discussed below.

Before any gene frequency calculations were performed, the two populations were compared, taking each genetic system separately and examining the frequencies of the corresponding phenotypes in each population. In only one case, that of the 6-phosphogluconate dehydrogenase variants, was any significant difference found (at 1 in 20 probability level) between the populations. In all other cases differences were considerably below the level of significance. Therefore, while in each table the numbers of each phenotype are set out separately for the two populations, all calculations, except for 6-phosphogluconate dehydrogenase, are based on the total for the two populations. For the 6-phosphogluconate dehydrogenase variants the results for the two populations are shown separately. A much higher frequency of the PGD^C variant was found at Debarech than at Adi-Arkai; the possible meaning of this is discussed later (pages 172, 173 and 175).

Discussion of results of marker studies

While the primary object of the tests was a comparison of the two populations under study, the results have yielded much new information on the relationship of these two populations, and of the Amhara generally, to other populations in and beyond north-east Africa.

It seems desirable to discuss the implications of this information fairly fully both because of its relevance to the present investigations and because it appears likely that much further work will be done on the biology of these and neighbouring populations.

A large amount of data is available on the frequencies of the blood groups, in the strict sense, in the neighbouring peoples; rather less is known about the distribution of the serum factors, while for the red-cell isoenzymes published data are very few, even if we take into consideration the whole world.

Blood group frequency data are available for the following relevant populations: the Amhara, Tigré and Billen (Ikin & Mourant 1962), Falasha, Galla and Guraghe (Bat Miriam 1962), the Northern Nilotes of the Sudan (Roberts, Ikin & Mourant 1953), Northern Sudanese (Brooks, Garner, Ikin, Mourant & Drysdale 1952) and the Beja of the Sudan (El Hassan, Godber, Kopeć, Lehmann, Mourant & Tills 1968).

Blood groups (tables 16 to 22)

The results obtained in the present survey resemble closely those previously obtained for the Amhara, as well as for other Ethiopian tribes: the Billen, Tigré, Galla, Guraghe and Falasha, and also those for the Northern Sudanese, but all these were tested for a much narrower range of factors than the present Amhara populations. The resemblance to the Beja of the Sudan is slightly less close; the latter have higher frequencies of *O*, *N*, R_1 (*CDe*) and *Fy*, and lower ones of *V* and Js^a; it is difficult to say which possesses the larger Negroid component.

Table 16. The ABO blood groups

group	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
0	62	62	124	0.3949	0.4042	126.92
A_1	27	32	59	0.1879	0.1728	54.26
A_{int}*	2	6	8	0.0255	0.0206	6.47
A_2	12	13	25	0.0796	0.0890	27.95
B	45	36	81	0.2580	0.2473	77.65
A_1B	3	4	7	0.0223	0.0383	12.03
$A_{int}B$	0	0	0	0.000	0.0050	1.57
A_2B	5	5	10	0.0318	0.0228	7.16
totals	156	158	314	1.0000	1.0000	314.01

* A_{int} is intermediate in type between A_1 and A_2.

gene frequencies

p_1	0.1118
p_{int}	0.0145
p_2	0.0665
q	0.1714
r	0.6358
total	1.0000

The frequencies in Africans of the blood groups of the Duffy (Fy) and Kidd (Jk) systems are known to differ greatly from those of Europeans, but shortages of sera have hindered detailed comparison. It was fortunately possible to test the present samples with anti-Fy^b (as well as the common anti-Fy^a) and with anti-Jk^a. In Europe the frequency of the Fy^a gene is about 80 % and that of the amorph *Fy* is extremely low, whereas in Africans *Fy* is by far the commonest gene. In the present series the *Fy* frequencies (table 21) are intermediate between European and African values. Europeans have a Jk^a gene frequency of about 50 %, whereas the few African series show about 80 %. Again, with a Jk^a frequency of 70 %, the present population is intermediate between the two.

The Kell and Js blood groups are now known to form a single genetic system but the *K* gene is almost confined to Europe and the Js^a gene to Africa. Here again the presence of the two genes implies an intermediate or mixed population, but unfortunately no examples were found of individuals carrying both genes, whose genetic investigation might have been of great interest.

Serum groups (tables 23 to 25)

Tests were done on 171 specimens of serum, for Gm antigens numbered 1, 2, 4, 5, 10 and 11, and show the presence of the alleles Gm^{1}, $Gm^{1,2}$, $Gm^{4,5,10,11}$ and $Gm^{1,5,10,11}$. The first three, with a total frequency of 37 %, are regarded as mainly of Caucasoid origin, whilst $Gm^{1,5,10,11}$ with a frequency of 62 % is associated with Negroid populations. In this respect the present population appears more African than the Beja with 51 % of Negroid and 49 % of Caucasoid alleles.

As is usual in African populations, there was a fairly high frequency (6 %) of ahaptoglobinaemia, and thus some doubt as to the true frequencies of the haptoglobin genes. However, if the specimens without haptoglobin are disregarded, the gene frequency of Hp^{1} is 38 %, which is similar to the values found for other Ethiopian populations tested by Barnicot *et al.* (1962) and to European values, and distinctly lower than the 49 % found for the Beja, which approaches the typical Negroid range. In the present population no examples of the typical Negroid phenotype 2-1M was found.

The presence of a few examples of transferrin *CD* heterozygotes is common in samples of African populations; the two such cases found at Debarech contain the usual African TfD_1 variant.

Table 17. The MNS blood groups

phenotype	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
MMS	40	49	89	0.2834	0.2909	91.34
MsMs	19	26	45	0.1433	0.1478	46.41
MNS	39	31	70	0.2229	0.2132	66.94
MsNs	40	38	78	0.2484	0.2341	73.51
NNS	5	1	6	0.0191	0.0213	6.69
NsNs	13	13	26	0.0828	0.0927	29.11
totals	156	158	314	0.9999	1.0000	314.00

All specimens were tested with anti-S and none with anti-s. Of those found to be S-negative, 19 of the 156 from Adi-Arkai (including 10 MN) and 18 of the 158 from Debarech (including 11 MN) were tested with anti-U. Of these, only one negative was found, an MN from Debarech, who is therefore of genotype $MS^{u}NS^{u}$. In the gene frequency calculations MS^{u} and NS^{u} have not been distinguished from *Ms* and *Ns* respectively. Nine specimens were found to be Henshaw-positive, four (two from Adi-Arkai) were of type MMS and five (one from Adi-Arkai) of type MNS.

frequencies of gene complexes	
MS	0.2779
Ms	0.3845
NS	0.0332
Ns	0.3044
total	1.0000

Red cell enzymes (tables 26 to 30)

The only genetic system for which a conventionally significant difference was found between the highland and lowland populations was that of the 6-phosphogluconate dehydrogenase variant (tables 29 and 30). The difference is significant at the phenotypic level: $\chi^2 = 5.29$, so that, for 1 degree of freedom, P just exceeds 0.02. Since each phenotype represents a single genotype, the populations can be compared also in terms of genes, and at this level χ^2 is slightly increased to 5.81. When, as for these populations, comparisons are made for approximately 20 sets of parameters, it is to be expected that the difference will be 'significant' at the 1 in 20 level for

Table 18. The Rh blood groups

phenotype	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
CCDEE	0	0	0	0.0000	0.0001	0.02
CCDEe	0	0	0	0.0000	0.0028	0.88
CCDee	4	6	10	0.0318	0.0380	11.93
CCddee	0	0	0	0.0000	0.0013	0.41
CcDEE	0	0	0	0.0000	0.0006	0.19
CcDEeV	0	0	0	0.0000	0.0038	1.19
CcDEe(a)	0	2	2	0.0064	0.0071	2.23
CcDEe(b)	6	2	8	0.0255	0.0167	5.24
CcDeeV	22	16	38	0.1210	0.0986	30.96
CcDee	29	28	57	0.1815	0.1768	55.52
$CcD^{u}eeV$	0	0	0	0.0000	0.0012	0.38
$CcD^{u}ee$	0	0	0	0.0000	0.0036	1.13
CcddeeV	0	0	0	0.0000	0.0041	1.29
Ccddee	1	3	4	0.0127	0.0140	4.40
ccDEE	0	1	1	0.0032	0.0018	0.57
ccDEeV	4	1	5	0.0159	0.0221	6.94
ccDEe	6	8	14	0.0446	0.0414	13.00
ccDeeV	42	45	87	0.2771	0.2833	88.96
ccDee	27	29	56	0.1783	0.1793	56.30
$ccD^{u}eeV$	1	4	5	0.0159	0.0163	5.12
$ccD^{u}ee$	3	4	7	0.0223	0.0225	7.06
ccddeeV	4	4	8	0.0255	0.0261	8.20
ccddee	7	5	12	0.0382	0.0386	12.12
totals	156	158	314	0.9999	1.0001	314.04

All specimens were tested with anti-C, -c, -D, -E and -V. Those which were C−E+ were tested with anti-e (containing some anti-C). Each specimen positive for all the antigens C, c, D and E was tested with anti-Ce and anti-CE. It was thus possible to distinguish all the phenotypes that would have been distinguished by testing with anti-C, -c, -D, -E, -e and -V, and in addition, within the phenotype CcDEe, to separate the genotypes CDE/cDe, $CDE/cD^{u}e$ and CDE/cde on the one hand, from CDe/cDe and cDE/Cde on the other. The two phenotypes so distinguished are marked respectively CcDEe(a) and CcDEe(*b*). Phenotypes reacting for the antigen V have the symbol V added. This antigen is attributed to the simultaneous presence of the chromosome of the genes for c and e^{s}. No simple anti-e^{s} serum was available.

frequencies of gene complexes

CDE	(R_z)	0.0072
CDe	(R_1)	0.1627
Cde	(R')	0.0355
cDE	(R_2)	0.0422
cDeV	(cDe^{s}) (R_0^{s})	0.1876
cDe	(R_0)	0.2431
$cD^{u}eV$	$(cD^{u}e^{s})$ (R_0^{us})	0.0166
$cD^{u}e$	(R_0^{u})	0.0507
cdeV	(cde^{s}) (r^{s})	0.0579
cde	(r)	0.1965
	total	1.0000

one of these sets. The possibility must not, however, be neglected that this particular difference is the result of differential natural selection in the two contrasting environments. Although rare variants are known which differ quantitatively from the normal in their activity (Parr & Fitch 1967), the common variants detected electrophoretically are not known to show any such

TABLE 19. THE LEWIS BLOOD GROUPS

phenotype	no. observed: Adi-Arkai	Debarech	total	frequency observed
Le(a+)	14	13	27	0.1971
Le(a−)	67	43	110	0.8029
totals	81	56	137	1.0000

TABLE 20. THE KELL AND JS BLOOD GROUPS

phenotype	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
KK Js^bJs^b	0	0	0	0.0000	0.0010	0.30
Kk Js^a	0	0	0	0.0000	0.0033	1.00
Kk Js^bJs^b	9	10	19	0.0623	0.0570	17.38
kk Js^a	12	18	30	0.0984	0.0995	30.35
kk Js^bJs^b	131	125	256	0.8393	0.8393	255.99
totals	152	153	305	1.0000	1.0001	305.02

frequency of gene complexes	
$K\ Js^b$	0.0311
$k\ Js^a$	0.0528
$k\ Js^b$	0.9161
total	1.0000

TABLE 21. THE DUFFY BLOOD GROUPS

phenotype	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
Fy (a−b−)	27	31	58	0.3333	0.3123	54.34
Fy (a+b−)	22	27	49	0.2816	0.3066	53.35
Fy (a−b+)	15	30	45	0.2586	0.2839	49.40
Fy (a+b+)	11	11	22	0.1264	0.0972	16.91
totals	75	99	174	0.9999	1.0000	174.00

gene frequencies	
Fy^a	0.2279
Fy^b	0.2133
Fy	0.5588
total	1.0000

TABLE 22. SUNDRY BLOOD GROUPS

system	phenotype	no. observed: Adi-Arkai	Debarech	total	frequency observed	gene	gene frequency
P	P_1+	134	128	262	0.8344	P_1	0.5931
	P_1-	22	30	52	0.1656	$P_2(+p)$	0.4069
Lutheran	Lu (a+)	17	19	36	0.1146	Lu^a	0.0590
	Lu (a−)	139	139	278	0.8854	Lu^b	0.9410
Kidd	Jk (a+)	64	89	153	0.9107	Jk^a	0.7012
	Jk (a−)	6	9	15	0.0893	Jk^b	0.2988

differences, nor is there any obvious reason why this enzyme should have special significance in relation to the climatic and physiological environments concerned. It would, however, be desirable to test larger numbers of these two populations for this particular set of variants, possibly including quantitative tests on very fresh specimens, and it is important that such tests

Table 23. The Gm groups

phenotypes, Gm						no. observed			frequency observed	frequency expected	no. expected
1	2	4	5	10	11	Adi-Arkai	Debarech	total			
+	−	−	−	−	−	0	2	2	0.0117	0.0126	2.15
+	+	−	−	−	−	1	0	1	0 0058	0 0043	0.74
+	−	−	+	+	+	41	47	88	0.5146	0.5387	92.12
+	−	+	+	+	+	25	44	69	0.4035	0.3561	60.89
+	+	−	+	+	+	2	2	4	0.0234	0.0223	3.81
+	+	+	+	+	+	0	1	1	0.0058	0.0085	1.45
−	−	+	+	+	+	2	4	6	0.0351	0.0575	9.83
totals						71	100	171	0.9999	1.0000	170.99

frequencies of gene complexes

Gm^{1}	0.1121
$Gm^{1,2}$	0.0177
$Gm^{1,5,10,11}$	0.6304
$Gm^{4,5,10,11}$	0.2398
total	1.0000

Table 24. Haptoglobins

group	no. observed			frequency observed
	Adi-Arkai	Debarech	total	
1	16	22	38	0.1214
2–1	82	68	150	0.4792
2	47	59	106	0.3387
0	10	9	19	0.0607
totals	155	158	313	1.0000

Table 25. Transferrins

group	no. observed			frequency observed	frequency expected	no. expected
	Adi-Arkai	Debarech	total			
C	155	156	311	0.9936	0.9936	311
CD	0	2	2	0.0064	0.0064	2
D	0	0	0	0.0000	0.0000	0
totals	155	158	313	1.0000	1.0000	313

gene frequencies

Tf^{C}	0.9968
Tf^{D}	0.0032
total	1.0000

should be done on other comparable pairs of populations. The over-all frequency of 10 % of the PGD^{C} gene is consistent with the few African data available, and much higher than the European level.

Few surveys of the incidence of the adenylate kinase variants have been carried out. The AK^{1} gene is everywhere the most common, with AK^{2} reaching a frequency of 5 % in Europe but very rare or absent elsewhere. The frequency of AK^2 found in the present sample of Amhara (1 %) is similar to the 0.5 % of the Beja. Higher frequencies have recently been found in samples tested at the Serological Population Genetics Laboratory from a number of populations in the Near East.

The present series of Amhara show frequencies of the Acid Phosphatase variants (table 37) similar to those of other African populations so far tested, with a very high frequency of P^b,

TABLE 26. ADENYLATE KINASE VARIANTS

group	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
1	143	152	295	0.9736	0.9738	295.06
2–1	4	4	8	0.0264	0.0260	7.88
2	0	0	0	0.0000	0.0002	0.06
totals	147	156	303	1.0000	1.0000	303.00

gene frequencies	
AK^1	0.9868
AK^2	0.0132
total	1.0000

TABLE 27. ACID PHOSPHATASE VARIANTS

group	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
A	0	1	1	0.0060	0.0047	0.79
BA	7	14	21	0.1250	0.1276	21.44
B	61	85	146	0.8690	0.8677	145.77
totals	68	100	168	1.0000	1.0000	168.00

gene frequencies	
P^a	0.0685
P^b	0.9315
total	1.0000

TABLE 28. PHOSPHOGLUCOMUTASE (PGM^1) VARIANTS

group	no. observed: Adi-Arkai	Debarech	total	frequency observed	frequency expected	no. expected
1	27	53	80	0.4908	0.4848	79.02
2–1	30	35	65	0.3988	0.4143	67.52
2	7	9	16	0.0981	0.0885	14.43
6–1	1	1	2	0.0123	0.0086	1.40
6–2	0	0	0	0.0000	0.0037	0.59
6	0	0	0	0.0000	0.0000	0.00
totals	65	98	163	1.0000	0.9999	162.96

gene frequencies	
PGM_1^1	0.6963
PGM_1^2	0.2975
PGM_1^6	0.0062
total	1.0000

and with P^c absent. These frequencies are quite unlike those of Europeans but cannot yet be fitted into any clear African picture.

The number of known phosphoglucomutase variants is large, and products have been found of genes at three distinct loci. Most of the polymorphism is shown by the products of genes at the PGM_1 locus (table 28). The common genes at this locus are PGM_1^1 and PGM_1^2; with very rare exceptions the frequency of the latter lies between 16 and 33 %. Most of the values around and above 30 % are found in the Near East. The frequency in the Amhara, just under

Table 29. 6-Phosphogluconate dehydrogenase variants, Adi-Arkai

group	no. observed	frequency observed	frequency expected	no. expected
A	59	0.8939	0.8968	59.19
CA	7	0.1061	0.1004	6.63
C	0	0.0000	0.0028	0.18
totals	66	1.0000	1.0000	66.00

gene frequencies

PGD^A	0.9470
PGD^C	0.0530
total	1.0000

Table 30. 6-Phosphogluconate dehydrogenase variants, Debarech

group	no. observed	frequency observed	frequency expected	no. expected
A	75	0.7500	0.7482	74.82
CA	23	0.2300	0.2336	23.36
C	2	0.0200	0.0182	1.82
totals	100	1.0000	1.0000	100.0

gene frequencies

PGD^A	0.8650
PGD^C	0.1350
total	1.0000

Table 31. The glucose-6-phosphate dehydrogenase variants

type	no. observed: Adi-Arkai	Debarech	total	frequency observed
		males		
A+	1	2	3	0.0268
B+	49	60	109	0.9732
totals	50*	62	112	1.0000
		females		
A+	0	1	1	0.0192
AB+	0	2	2	0.0385
B+	15	34	49	0.9423
totals	15	37	52	1.0000

* omitting one enzyme-deficient sample.

gene frequencies

(calculated by gene counting, assuming the absence of heterozygotes for deficiency among the females)

Gd^A	0.0324
Gd^B	0.9676
total	1.0000

30 %, fits well into this picture, and may in particular be compared with the 27 % found in the Beja. Two examples of the rare heterozygote PGM_1^1/PGM_1^6 were found in the Amhara, but no examples of the typically African 'Atkinson' variant at the PGM_2 locus.

As already mentioned, only one doubtful example of glucose-6-phosphate dehydrogenase deficiency was found. Electrophoresis, however, showed the presence of several persons with the typical African A+ variant, in addition to the preponderant B+ type. As the genes concerned are X-linked it is necessary to tabulate males and females separately. An approximate gene frequency calculation has been performed by gene counting, disregarding the single doubtfully deficient male, and assuming that no females are heterozygous for a deficient gene. This gives a frequency of just over three per cent for the Gd^A gene. This has a variable frequency which in Africa can reach and even exceed ten per cent, but is extremely low in Europe where it is doubtful whether it anywhere reaches one per cent.

GENERAL DISCUSSION

Although this study can in many respects be regarded only as preliminary, since there are many aspects of the ecology which have not yet been considered, it does reveal a number of interesting features, not only about the ways in which Ethiopians adapt to altitudinal variation, but also about the general nature of environmental adaptation in man.

The Ethiopian situation is almost unique, since there can be few places in the world, whether in other mountain regions or elsewhere, where one finds, in heavily populated areas, such a dramatic change of environment in such a short geographical distance. This has ramifying implications, and, in particular, means that the populations in the two environments are likely to be closely related. In fact, as already stated, the blood groups and other marker frequencies, with one exception, do not differ significantly between the Adi-Arkai population, and the one highland population, at Debarech, which could be tested. Further, the estimated amount of migration between at least these two groups is so high that it would be most surprising to find genetic divergence for any system unless this could be explained either by selective migration, or by natural selection with respect to a gene highly favoured by one of the environments. Reference is made below to the absence of any indications of selection of the latter kind.

It must, however, be noted that ancestry could be playing a part in determining the distinctive features of the Geech population for which there is no gene marker information, and no evidence of gene flow from the demographic data. As already mentioned, the Geech population is entirely Mohammedan and probably represents the descendants of comparatively recent immigration into the area from the north. It is also a very small population and being apparently isolated might, by chance, have a distinctive gene pool. In most of the characters studied, however, the Geech population shows further development of the features which distinguish the Debarech population from the Adi-Arkai one, and it seems likely that this trend is directly due to the altitude gradient. On the other hand, it is worth pointing out that the Geech population, especially in the anthropometric study, displays charactersitics which do not fit such a trend.

Mohammedan groups also occur in the other two populations, but collecting blood samples from them was not easy and few were included in the marker analysis. However, the proportion of Mohammedans in the samples from these populations is very similar and their presence cannot account for the differences observed. It may, therefore, be safely concluded that these differences, and there are many, are mainly if not entirely due to the direct effect of the environment on growth, development and physiological state.

There are, of course, multiple components of the environment which differ in the highland and lowland regions besides barometric pressure. As already mentioned, the temperature régime varies also, and there is clear evidence that infectious diseases of most kinds are more common in the lowlands. No information was obtained in this study about the nutritional ecology of the area, but it seems likely, if only because of the climatic factors, that this will also differ considerably with altitude. And there are many other possible sources of variation. It is, therefore, not possible to ascribe with complete certainty any particular phenotypic modification to any particular environmental factor. Indeed, in most instances such modification will depend upon the interacting effect of all the varying components of the environment, and incidentally also upon the gene complexes which characterize the populations. Nevertheless in many cases, it is apparent that some particular environmental component is mainly responsible for causing a particular phenotypic difference. Thus, for instance, it seems reasonable to suppose that the variations in respiratory function, red cell count, and systolic blood pressure, are mainly functions of the differences in partial pressure of oxygen, whilst the differential white cell counts probably mainly reflect the varying patterns of disease incidence.

The situation with regard to the anthropometric study is more difficult to interpret. It is clear that there are many differences in physique between the highlanders and the lowlanders and with the exception of the measurements of thoracic size, which are obviously related to respiratory function variation, the cause for these differences is not immediately clear. Comparison of the two groups for which there is strong presumptive evidence of genetic similarity suggests that the highlanders tend to have a more robust physique than the lowlanders, with greater body weights, especially when this is related to their stature, and usually with greater circumferential dimensions and measurements which principally reflect skeletal development. The latter difference may be at least partly related to marrow hypertrophy associated with increased erythropoiesis. Other differences are probably attributable to nutritional factors; but it is possible that temperature variation is also playing a part, since it is known that thermal factors correspondingly affect the growth of experimental mammals (Harrison 1963). Certainly, whatever the cause, the variation is in conformity with the ecological rules of Bergmann and Allen, and the lowlanders, with their more linear physique, are better adapted, in this respect, for survival under the more continuous heat which characterizes their environment.

The study of the migrants also reinforces the view that the contrasting altitudinal environments profoundly affect the development of a number of characters. In all aspects of respiratory function, lowland migrants to the highlands resemble the native highlanders, and although there is evidence that migrants to the lowlands preserve some of their high altitude characteristics they tend to have lower respiratory capacity than highlanders. For reasons to be discussed later body weight shows closely correlated responses. There are two problems, however, in interpreting the analysis of the migrants. In the first place, it is possible that the observed pattern is due to selective migration, and is not due to environmentally produced changes following the migration. Unfortunately, the fact that migrants within the same broad environmental régime show no distinctive features does not preclude the possibilities of selective migration between the highlands and lowlands. The second problem concerns the developmental age at which migration occurred and this it was not possible to establish with any accuracy. So far as could be judged, most of the migrants were adult when they first moved, and if selective migration is not involved, this would indicate that respiratory capacity and the associated physique are modifiable after growth has ceased.

Whatever interpretation is made of the migrant situation it can, nevertheless, be generally concluded from the over-all study that variation in altitudinal environment produces marked developmental as well as physiological differences. It seems likely that most of these differences can be viewed as arising from phenotypic flexibility, and that the modifications directly caused by the environment facilitate survival in the environment that produced them. Some of the differences may, however, reflect aspects of comparative somatic fitness. It is difficult enough, even under experimental conditions, to distinguish between adaptive and fitness responses (Harrison 1963) and under natural conditions, when, even within the compass of single population, there is marked genetic and environmental variation, the problem cannot be rigorously analysed. However, when a particular difference occurs in the opposite direction to that expected from a hypothesis of adaptability, it is probably a component of differences in comparative fitness.

The low haemoglobin level in the highlanders, if real, is almost certainly of nutritional origin, and only indirectly due to altitude; nevertheless, presumably, it would indicate that in this component the highlanders are less fit than the lowlanders. Similarly, the decline in respiratory performance among adults, with increasing age, in both of the highland groups, which is probably due to the prevailing atmospheric pressures and temperatures in the mountains, is likewise indicative of greater environmental adversity.

The evidence of the vital statistics is also of some relevance. It is clear on the present evidence that hazards to survival during pregnancy are greater in the highlands than in the lowlands, and these no doubt arise in large part from the reduced barometric pressure. On the other hand, one would expect the higher levels of infectious disease in the lowlands to cause greater infant mortality, but there is no indication of this in the present data.

All the evidence, such as it is, therefore suggests that despite the marked adaptability which allows Ethiopians to survive in both of the very contrasting altitudinal environments studied, the more favourable conditions, at all stages of development, are provided by the subtropical lowlands. It is appreciated, however, that before a final judgement can be made much more data are required, and there is little doubt that Ethiopians themselves prefer to live in a highland environment.

Because of the technical difficulties described, it would seem unwise to comment further on the haematological results obtained in this study in comparison with those from other high altitude populations, but when one considers the other characters some interesting differences emerge, particularly in respiratory function.

Using an identical spirometer, Cotes & Ward (1966) and J. S. Haight, D. B. Rimmer & A. J. Boyce (personal communication) have made studies respectively on Bhutanese and Peruvian populations. By comparison with these, the measures of forced vital capacity and forced expiratory volume, even in the highland Ethiopian populations, are low, and this difference has been minimized by the fact that the other workers have used the mean of the best three performances in their tests. Indeed the values obtained for Ethiopians are less than those found in Europeans. However, this, of course, does not mean that the effective respiratory capacity is any poorer, since it is well known that measures of respiratory function are dependent upon body size, and, as has been shown, Ethiopians tend to be very light in body weight, though not particularly short in stature.

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It is interesting that, whereas other studies (Cotes 1965) have clearly indicated that stature variation shows the closest relationship with respiratory function, in Ethiopians it would appear that the prime correlations are with body weight. This apparently anomalous situation probably arises because of variation in body composition. Certainly all the Ethiopian groups have very low measures of subcutaneous fat, and if this reflects over-all fat levels, it seems probable that body weight is a better indicator of active biomass than stature or any function of stature.

In part, the greater weight of the highland groups must be due to thoracic hypertrophy; but conversely, because they are heavier than the lowlanders, one would expect them to have greater respiratory capacities, irrespective of the lower partial pressure of oxygen. The regression analysis, however, clearly shows that, whether stature or weight is taken as the measure of body size, the highlanders have a greater respiratory capacity than the lowlanders, independently of the size variation.

Little need be said from the comparative viewpoint about the anthropometric study itself, except to point out that it indicates that Ethiopians, whether in the lowlands or in the highlands, tend to have a very linear physique, unlike most mountain peoples. Some comment on the skin colour data seems justified in view of remarks that Ethiopians tend to be comparatively light coloured by African standards (Coon 1965). In actual fact, the levels of reflectance measured with the spectrophotometer are very low and at the shorter wavelengths the Ethiopian values are not distinguishable from Negro groups such as Yoruba and Ibo (Barnicot 1958). At longer wavelengths, where among dark-skinned peoples there is greater discrimination with the EEL spectrophotometer, the Ethiopians present higher values than these Nigerians and also Okavango Bantu, but they are darker than Khoisan populations, and darker even than Negroes living in Europe (Weiner, Harrison, Singer, Harris & Jopp 1964).

Finally, the blood group and other gene marker data indicate not only that the highland and lowland groups are not genetically differentiated from one another, but also that both are similar to other Ethiopian highland populations, among whom it has already been shown that genetic differences are small (Ikin & Mourant 1962). The comparatively high frequencies of *MS* and Fy^a suggest a rather higher proportion of Caucasoid ancestry than has been found in other Ethiopian populations tested, but this is not shown clearly, if at all, by the other genetic systems.

No examples of sickle-cell haemoglobin or thalassaemia were found in these populations and only one doubtful example of glucose-6-phosphate dehydrogenase deficiency. The genes for all of these tend to be associated with endemic malaria, which is present in the lowland area around Adi-Arkai, and there is evidence that all of them confer resistance to this disease. The situation, therefore, is very unlike the one that has been analysed in Sardinia (Carcassi, Ceppellini & Pitzus 1957; Adinolfi & Bernini 1960; Bernini *et al.* 1960), where highland and lowland populations have similar blood group frequencies but the lowland populations, which have been much more exposed to malaria, show considerably higher frequencies both of thalassaemia and of glucose-6-phosphate dehydrogenase deficiency than the highland ones. Because of the dramatic differences in environment, it is hard not to believe that natural selection is operating quite differently in these Ethiopian highlands and lowlands. However, even if the selection were operating differentially on the markers studied, and the samples were large, one would not expect to detect genetic differentiation when the migration rates are as high as they are, unless the selection was very strong.

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