

Increased Heterozygosity and Child Growth in an Isolated Subsistence Agricultural Community in the Valley of Oaxaca, Mexico

B.B. LITTLE, R.M. MALINA, AND P.H. BUSCHANG

Division of Clinical Genetics, Department of Obstetrics and Gynecology, Southwestern Medical School, The University of Texas Health Science Center at Dallas, Dallas, Texas 75235 (B.B.L.); Department of Anthropology, The University of Texas, Austin, Texas 78712 (R.M.M.); Centre de Recherche sur la Croissance Humaine, Université de Montreal, Montreal H3C 3J7, Canada (P.H.B.)

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ABSTRACT Gene flow and rate of inbreeding (ΔF) were calculated from demographic data for a community previously reported to be isolated from outside genetic influences of immigration. Significant child growth differences caused by gene flow among children born to native parents ($n = 287$) and offspring of native-immigrant matings ($n = 38$) were found in fatness (triceps skinfold), body proportions (sitting height ratio), and size (leg length). No differences were found between the two groups in height, weight, sitting height, and arm circumference. Variation in absolute and relative leg length in this population parallels previously reported differences in adult body size and proportion associated with increased heterozygosity caused by gene flow in other populations in southern Mexico.

Segregation of genetic effects in human populations is dependent, to a large extent, on the nature of the population and sample parameters available. In populations reported to be isolated and presumed closed to gene flow, endogenous factors are considered primary determinants of population genetic structure. Such populations are convenient for genetic analysis because boundaries for genetic and environmental influences are easily drawn. In populations of small size, inbreeding is a probable effect. If a population is not truly closed to outside genetic influences, however, low-level introduction of new genetic material i.e., gene flow, sufficiently increases heterozygosity to counter inbreeding effects and genetic divergence (Hartl, 1980). Thus, even small deviations from strict isolation can have a notable effect on population genetic structure and maintenance of genetic variation (i.e., heterozygosity).

Variation in population genetic structure can affect quantitative characteristics (Cavalli-Sforza and Bodmer, 1971). Intrapopulation analysis of a cohort of Jewish males,

for example, showed that adult morphology was positively correlated with heterozygosity (Kobyliansky and Arensburg, 1977; Kobyliansky and Livshits, 1983; Livshits and Kobyliansky, 1948a,b). Interpopulation analysis of adult morphological variation in southern Mexico found that higher levels of heterozygosity were associated with increased leg length, decreased trunk length (sitting height), and an overall increase in stature (Little and Malina, 1986). As inbreeding implies decreased heterozygosity, negative correlations of adult morphology and child growth status with inbreeding indicate a similar relationship between decreased heterozygosity and body size (Slatis and Hoene, 1961; Schull and Neel, 1963; Schork, 1964; Schreider, 1966; Adams and Neel, 1967; Murai and Fukuhara, 1968; Krieger, 1969; Komai and Tanaka, 1972; Neel et al., 1970).

This study analyzes child growth status and adult stature in a Zapotec Indian community reported to be endogamous. Off-

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spring of native parents are compared to children assumed to be more heterozygous because of outbreeding, i.e., having an immigrant parent.

MATERIALS AND METHODS

Children and adults in this study reside in a rural, subsistence-level farming community of about 1,700 people in the Valley of Oaxaca in southern Mexico. The community has been reported to be closed to immigration, and second-cousin marriage is preferred (Selby, 1966). Thus, inbreeding depression is an unknown possible influence on the small body size and delayed growth of the community's inhabitants (Little et al., 1986).

Subsistence-level agriculture with the assistance of oxen and burros is the primary occupation of 89% of village adults (Malina et al., 1985). Little irrigated land is available, and most food crops are produced on unirrigated land (Granskog, 1974; Little, 1983). Infant and childhood mortality in the community is 3 to 4 times the rate for Mexico (Malina et al., 1985). Adult statures of Zapotecs in the Valley of Oaxaca are short compared to other Indians in Mexico (Faulhaber, 1970) and adults in other countries. Child growth status is delayed by about 2 years, falling at or below the 5th percentile for reference data for well-nourished children (Malina et al., 1980; Buschang and Malina, 1983). Estimated growth rates between 6 to 13 years of age, however, are not as delayed as growth status (Buschang and Malina, 1983).

Secular change in size and maturity has not occurred in the Valley of Oaxaca over the past 80 years, with health and nutritional opportunities similar to those of Europe at the turn of the century (Malina et al., 1983a). Estimated nutrient intakes for children in the community (Amdurer, 1978) fall well below recommended daily allowances for Mexico (Hernandez et al., 1974). Chronic mild-to-moderate undernutrition is aggravated by a high infectious disease load and is compounded by the synergistic interaction of disease and undernutrition.

A community survey was conducted in the fall of 1978. It consisted of a census of each household and a series of anthropometric dimensions that were taken on 85% of the children and 25% of the adults. Socioeconomic information was collected as part of a com-

munity survey and included demographic data, information about land holdings, household goods (i.e., radios and other appliances), and occupation of the head of household (full-time farmer, part-time farmer, neither). Socioeconomic status was derived by ranking a sample of households based on ethnographic data, which included information on land holdings, household goods, etc., and community perception of wealth. A discriminant analysis was used to derive weights for SES. The weights were applied the entire sample to derive an SES index: $SES = .36 \cdot \text{household goods} + .47 \cdot \text{unirrigated land holdings} + .87 \cdot \text{occupation}$ (Malina et al., 1985).

Census data that indicated place of birth were used to calculate gene flow (Table 1). Inbreeding rates (ΔF) for the community were calculated from age- and sex-specific census data for the period between 1900 and 1980 (Table 2).

A sample of 267 adults (134 males, 133 females) in the community was also measured, and their ages were obtained through interview. Adult stature was adjusted for age-associated stature loss as indicated by Trotter and Gleser (1951): $\text{adjusted stature} = \text{stature} + [(\text{age} - 30) \cdot .06]$.

School children, aged 6–13 years, were measured as part of the community survey conducted in fall 1978. A subset of the measurements are considered here: height, sitting height, weight, arm circumference, and the triceps skinfold. Two dimensions and one ratio were computed: 1) estimated leg length = height – sitting height; estimated midarm muscle circumference = arm muscle circumference – $(\pi \cdot \text{triceps skinfold})$; sitting height ratio = sitting height/height $\cdot 100$. Measurement procedures and quality control have been described previously (Malina et al., 1980; Buschang and Malina, 1983; Malina and Buschang, 1985).

Using parents' place of birth, two groups of children were identified for analysis of variance (ANOVA): 1) children born of native parents ($n = 287$), and 2) children born of an immigrant and a native parent ($n = 39$). The second group is assumed to be more heterozygous because one-half their genes are from populations outside the community. Anthropometric data were available for 38 of the 39 children. Thus, the analysis compares 287 children born of native parents with 38 children born of immigrant-native matings.

TABLE 1. Frequency of individuals and genes by origin

Age group	Born inside community										Born outside community										Total population																			
	Native					I-N ¹ offspring ¹					Immigrants					Female					Male					Female					Male					Total ²				
	No. of genes		No. of genes			No. of genes		No. of genes			No. of genes		No. of genes			No. of genes		No. of genes			No. of genes		No. of genes			No. of genes		No. of genes			No. of genes		No. of genes							
	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New	n	Native	New				
	n		n			n		n			n		n			n		n			n		n			n		n			n		n			n		n		
0-4	128	256	0	110	220	0	15	15	12	12	12	12	12	12	12	0	0	0	1	0	2	143	271	15	5.24	123	232	14	5.69	266	503	29	5.45							
5-9	116	232	0	130	260	0	13	13	12	12	12	12	12	12	12	0	0	0	2	1	2	130	245	15	5.77	143	272	14	4.90	273	517	29	5.31							
10-14	130	260	0	91	182	0	6	6	8	8	8	8	8	8	8	1	0	0	2	1	2	137	266	8	2.92	100	190	10	5.00	237	456	18	3.80							
15-19	85	170	0	66	132	0	9	9	9	5	5	5	5	5	5	0	0	0	0	0	0	95	179	11	5.79	71	137	5	3.52	166	316	16	4.12							
20-24	44	88	0	58	116	0	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	48	90	8	8.16	64	118	10	7.81	113	208	18	7.96							
25-29	32	64	0	42	84	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	10	38	65	11	14.75	48	85	11	11.46	86	150	22	12.79						
30-34	33	66	0	23	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	34	66	2	2.94	25	46	4	8.00	59	112	6	5.36						
35-39	31	62	0	35	70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	31	62	0	41	76	6	7.32	72	138	6	4.35							
40-44	29	58	0	32	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	36	58	14	19.44	33	64	2	3.03	69	122	16	11.59						
45-49	33	66	0	24	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	33	66	0	0	25	48	2	0.4	58	114	2	1.72						
50-54	23	46	0	34	68	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	24	46	2	4.17	35	68	2	2.86	59	114	4	3.39						
55-59	28	56	0	13	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31	56	6	9.68	13	26	0	0	44	82	6	6.98						
60-64	8	16	0	13	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	16	0	0	13	26	0	0	21	42	0	0.00							
65-69	14	28	0	17	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	36	0	0	17	34	0	0	35	70	0	0.00							
70-74	14	28	0	16	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	28	0	0	17	32	2	5.88	31	60	2	3.23							
75-79	9	18	0	9	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	9	18	0	0	10	18	2	10.00	19	36	2	5.26						
80 +	3	6	0	9	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	6	0	0	4	8	0	0	7	14	0	0.00							
Total ²	764	1,528	0	720	1,440	0	46	46	46	40	40	40	40	40	40	44	833	1,574	92	5.32	782	1,480	84	5.37	1,615	3,054	176	5.45												

¹I-N is offspring of immigrant and native matings.

²Total census population in 1978.

TABLE 2. Breeding population and estimated rate of inbreeding

Year	N _e	ΔF
1900	391	.00128
1930	408	.00123
1940	396	.00126
1950	466	.00107
1960	473	.00106
1966	467	.00107
1970	568	.00088
1972	520	.00096
1978	623	.00080
1980	769	.00065

Raw data for adults and children were converted to z-scores: $z = (X_i - \bar{X})/SD$, where X_i is the measure X on the i th subject (child) and \bar{X} is the age- and sex-specific mean of measure X , and SD is the age- and sex-specific standard deviation. Sexes were pooled after z-score transformation among 1) children in order to make sample sizes large enough for analysis within the immigrant-native offspring category, and 2) adults in order to simplify the analysis. Additionally, SES and age were controlled by analysis of covariance (ANCOVA) in the ANOVA of child growth status.

Log (1/ΔF) is essentially an index of population potential for heterozygosity (increasing with higher values). Rate of inbreeding (ΔF) was calculated using standard formulae (Falconer, 1961) and breeding population sizes from 1900 to 1980 (Table 2). The breeding population is limited by the number of fecund females. The breeding population includes anyone from age 15 to 45 years. Although males > 45 years of age may potentially breed, males older than 45 years are not included because 1) 99% of women of reproductive age in the village are married, and 2) the correlation between spouses for age is high (0.96) (Malina et al., 1983b).

RESULTS

Gene flow appears to be relatively constant over time, although, because of small numbers in older age groups, estimates may not be reliable. This implies that certain levels of inbreeding could be cancelled on a population scale. Actual inbreeding, F , could not be calculated because the genealogical information has not been completely analyzed. Gene flow into the community over the past 80 years is, on the average, 5.45%, but ranged between 0 and 12.79% per age group (Table 1). The rate of inbreeding in the community

has decreased by about twofold since 1900 because of an increased number in the breeding population (Table 2). The adjusted adult stature z-scores regressed on birthdate and plotted with $\log(1/\Delta F)$ over time suggest a trend in the community for slightly increased stature over time with the decreased potential for random inbreeding (Fig. 1).

Increased heterozygosity is associated with significantly increased leg length, a decreased sitting height ratio (a relatively shorter trunk or conversely, relatively longer legs), and a thinner triceps skinfold ($P < .05$) (Table 3). Height was not appreciably different between the two groups, although legs were absolutely and relatively longer in more heterozygous children.

DISCUSSION

Increased leg length and a lower sitting height ratio in more heterozygous children in this study are consistent with an adult gain in leg length and loss in trunk length with increased heterozygosity among southern Mexico indigenous groups (Little and Malina, 1986). Stature, however, was not increased among the more heterozygous children in this study, contrary to findings in adults. Perhaps increased heterozygosity in the general population because of larger breeding populations over time is related to the lack of increased stature in more heterozygous children. Limited evidence suggests most of the effect of heterozygosity on morphological variance occurs with the first 10% increase (Little and Malina, 1986). Compared to Philadelphia black and white children, Zapotec school children have diminished growth in leg length (Buschang et al., 1986).

That the triceps skinfold is significantly thinner among more heterozygous children is probably due to environmental variation, though a genetic effect cannot be excluded. Because the community has existed since pre-Columbian times, it is possible that immigrant genes are less well adapted to the community's ecology than native genes. Growth status differences associated with increased heterozygosity in this study should be minimally affected by environmental variation because 1) both groups of children were reared in the same community; 2) SES variation between households within the community was statistically controlled; and 3) the sample of children was about equally distributed across SES.

Increased leg length and lower sitting height ratios are associated with African genetic heritage (Roberts, 1978). Based on historical and biochemical evidence, gene flow in the Tlaxacala area may contain African genetic material from at least two sources, Africans themselves and Spanish Moors (Crawford et al., 1979). Increased heterozygosity that is due to gene flow in southern Mexico affected craniofacial and postcranial anthropometrics in a way consistent with African influences (Little and Malina, 1986). In the community reported in this study, African influences in gene flow cannot be excluded, but the increase in heterozygosity is equally important.

Increased heterozygosity that is due to larger breeding populations in more recent times is similar to slight increases in adult stature (Figure 1). This is consistent with interpopulation trends in heterozygosity and adult stature (Little and Malina, 1986). Although it is not possible to assess inbreeding

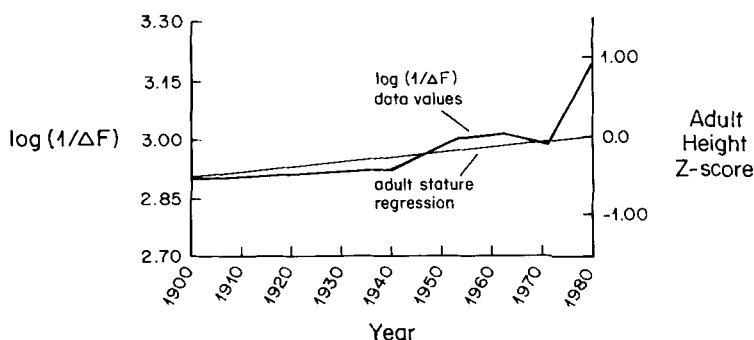


Fig. 1. Heterozygosity by census year and adult stature by year of birth.

TABLE 3. Comparison of growth status in school children aged 6 to 13 years among offspring of native parents and offspring of an immigrant and a native parent (I-N)

Variable	Unadjusted means				ANCOVA ¹ Adjusted means		ANOVA	
	Native (n = 287)		I-N (n = 38) ²		Native M	I-N ² M	F	Sig.
	M	SD	M	SD				
Z-scores ³								
Height	0.07	0.95	0.16	0.75	0.01	0.09	.14	.71
Sitting height	0.15	0.98	0.02	0.75	0.16	-0.13	1.69	.17
Leg length	-0.17	1.01	0.31	1.46	-0.16	0.30	3.60	.05
Sitting ht. ratio ⁴	0.14	0.99	-0.20	1.28	0.15	-0.28	3.65	.05
Weight	0.11	1.01	0.36	0.88	0.15	0.09	.08	.78
Arm circumference	-0.02	1.04	-0.09	1.10	0.01	-0.36	2.61	.11
Estimated arm muscle circumference ⁵	-0.07	0.98	0.00	1.26	0.00	-0.17	1.15	.29
Triceps skinfold	0.36	1.16	0.13	0.93	0.38	-0.09	3.96	.05

¹Age and SES were held constant.

²Immigrant-native offspring.

³z-score = $(X_i - \bar{X})/SD$ where X_i is individual observation and \bar{X} and SD are sex-specific mean and standard deviation, respectively.

⁴Sitting height ratio = (sitting height (cm)/height (cm)) \times 100.

⁵Estimated arm muscle circumference (cm) = arm circumference - (triceps skinfold (mm) \times 10 \times π).

effects directly, it is apparent that the potential for random inbreeding decreases over time in the community.

In this population, heterozygosity is increased by influences from at least two sources: 1) gene flow, and 2) a decreased rate of inbreeding. Increased heterozygosity because of gene flow affects child growth significantly, but the relationship between rate of inbreeding and child growth is not known. Decreased rates of inbreeding are, as a trend, similar to slight increases in adult stature over time (Figure 1), but the possible effect of gene flow on adult stature is not known. It is not clear that decreased ΔF is related to the slight increase in adult height, or whether the similarity is fortuitous. Nonetheless, it is clear that the population is influenced by two independent sources of genetic variation that affect morphological variation.

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