Instituto Boliviano de Biología de Altura
BIBLIOTECA DEL
— IBBA —
La Paz – Bolivia

AMERICAN JOURNAL OF HUMAN BIOLOGY 6:491–498 (1994)

Total Lung Capacity in Andean Highlanders

LAWRENCE P. GREKSA
Department of Anthropology, Case Western Reserve University, Cleveland, Ohio 44106

ABSTRACT Total lung capacity (TLC), residual volume (RV), and vital capacity (VC), as well as related measures of pulmonary function, were assessed in a sample of 39 male and 23 female native highlanders of Aymara ancestry (20.1–28.8 years) who were residing in La Paz, Bolivia (average altitude of about 3,600 m). After controlling for body and chest size, most measures of respiratory function were significantly larger in males than females ($P < .05$). Absolute TLC (1 BTPS) was significantly larger in the La Paz Aymara males than in highland Peruvian or Tibetan males ($P < .05$) but, after controlling for body size, TLC was only 1 and 4% larger in the La Paz Aymara than in highland Peruvians or Tibetans, respectively. Also, comparison of the body size-adjusted percentage increases in TLC, VC and RV above U.S. sea-level reference values in selected highland populations indicated that the enhanced TLCs of highlanders are primarily due to an enhancement of RV and secondarily due to an enhancement of VC. © 1994 Wiley-Liss, Inc.

The thorax and underlying pulmonary system of adult Andean highlanders tend to be larger than those of adult lowlanders (Greksa, 1991; Hurtado, 1964; Mueller et al., 1978; Velásquez, 1976). Hurtado (1964) argued that the functionally significant aspect of this unique highland respiratory pattern was an enhanced total lung capacity (TLC), which he demonstrated to be primarily due to an increase in residual volume (RV) and secondarily to an increase in vital capacity (VC). However, most studies of pulmonary function in Andean highlanders have measured only VC or chest dimensions (e.g., Boyce et al., 1974; Frisancho, 1969; Greksa et al., 1987; Hoff, 1974; Mueller et al., 1978). In addition, the few studies which assessed TLC in Andean highlanders did so only in adult males (Frisancho et al., 1973; Hurtado, 1964). The purpose of the present report is to provide such data for a sample of both male and female highland Andean adults of Aymara ancestry.

SUBJECTS AND METHODS

Subjects

The sample consisted of 39 male and 23 female young adults of Aymara ancestry (20.1–28.8 years) who were born and raised at high altitudes (> 2,500 m) and who were residing in La Paz, Bolivia (average altitude of about 3,600 m). The subjects were sampled from a school for physical education teachers and a sports club. The subjects thus tended to be moderately trained. However, although training affects some aspects of ventilation in adults, it does not influence static volumes (Åstrand and Rodahl, 1977).

Both the paternal and maternal surnames of 3.2% of the sample were Aymara, 21.0% had one Spanish and one Aymara surname, and 75.8% had two Spanish surnames. Significantly more males (43.6%) than females (17.4%) reported that they occasionally smoked cigarettes ($\chi^2 = 4.4$, $P < .05$). In particular, one male reported smoking 1 cigarette per day, three males reported smoking 2 cigarettes per day, and all other subjects stated that they only smoked at social events. Smokers and nonsmokers did not differ significantly in either anthropometry or respiratory function ($P > .05$).

Anthropometry and pulmonary function

The anthropometric dimensions utilized in this report are stature, weight, transverse chest diameter (chest width), and anterior–posterior chest diameter (chest depth).

Received May 7, 1993; accepted January 14, 1994.
Address reprint requests to L.P. Greksa.

© 1994 Wiley-Liss, Inc.

Chest width and chest depth were measured at the end of a normal expiration and at the level of the union of the 3rd and 4th sternebrae (Weiner and Lourie, 1981).

Pulmonary function was assessed with a 13.5-liter spirometer with an attached helium meter and blower (Warren Collins, Braintree, MA). The first maneuver performed by each subject was a maximum forced expiration following a maximal inspiration, which was used to determine vital capacity (VC) and forced expiratory volume in one second (FEV). The recorded volumes were based on the best of at least three efforts. After VC, inspiratory capacity (IC) and expiratory reserve volume (ERV) were assessed, with each based on the best of at least three efforts.

Next, functional residual capacity (FRC) was measured using a closed-circuit method with the rebreathing of helium. A similar method was used successfully at high altitude by Droma et al. (1991). First, the spirometer was flushed out and then approximately 3,200 ml of room air and 900 ml of 100% helium were added to the emptied spirometer, providing an initial helium concentration of approximately 10%. A nose clip was then applied to the subject, who began breathing room air through the spirometer's mouthpiece. After the helium and room air were thoroughly mixed and at the end of a normal expiration, the patient was switched into breathing the 10% helium mixture in the spirometer. At the same time, 100% oxygen was added into the spirometer at a rate necessary to maintain the baseline (i.e., end expiration point) of the kymograph as a horizontal line. The subject rebreathed for about 3 min, the time required to obtain a stable final helium concentration reading. The raw FRC determined from these data was adjusted in two ways. First, 100 ml was subtracted to account for the subject's absorption of helium. A second correction was necessary when the subject was not switched into the spirometer at exactly the end of a normal expiration. This switch in error was estimated by calculating the difference between a horizontal line describing the end expiration point and the line indicating when the subject was switched onto the spirometer. If the end-expiration line was below the start up line, then the difference was subtracted from the raw FRC and if the end-expiration line was above the start up line, then the difference was added to the raw FRC. Residual volume (RV) was then calculated as FRC minus ERV. Total lung capacity (TLC) was calculated as RV plus VC.

Population comparisons

Comparative high-altitude data on the three functionally most significant lung volumes, or TLC, VC, and RV, are only available for males. These measures were, therefore, compared between the La Paz males and those in the following samples: (1) 38 subjects of Andean Indian ancestry (mean age = 22.3 years) residing in Morococha, Peru at 4,540 m (Hurtado, 1964); (2) 22 males of Tibetan ancestry (mean age = 23.1 years) residing in Lhasa, Tibet at 3,658 m (Droma et al., 1991); (3) 6 males of European ancestry (mean age = 19.3 years) residing at Leadville, Colorado at 3,100 m (DeGraff et al., 1970); and (4) 60 Peruvians of unstated (probably mestizo) ancestry (mean age = 23.0 years) residing at sea level at Lima, Peru (Hurtado, 1964).

Since lung volumes are influenced by body size (Polgar and Weng, 1979) and there were significant differences in body size between some of these samples, both absolute and body size-adjusted lung volumes were compared between samples. Body size was controlled using the strategy suggested by Polgar and Weng (1979), or by calculating the ratio of each mean volume to the mean weight of the sample. In addition, in order to evaluate the relative importance of enhancements of RV and VC for explaining the enhanced TLCs of highlanders, the percentage increase in each lung volume above U.S. sea level reference values was estimated for each sample. This was accomplished by using body size-adjusted reference values for U.S. lowlanders provided by Polgar and Weng (1979): total lung capacity (82 ml/kg), vital capacity (66 ml/kg), and residual volume (16 ml/kg). The percentage increase in each lung volume over the low-altitude reference value was then calculated as:

$$\% \text{ increase} = [[\text{sample mean (ml/kg)} - \text{reference value (ml/kg)}]/[\text{reference value (ml/kg)}]] \times 100.$$

Thus, a sample with a percentage increase in TLC of 25% consists of individuals whose TLCs were 25% larger, on average, than those of U.S. lowlanders of the same body size.

TABLE 1. Age and anthropometry of 39 male and 23 female Aymara adults

	Males		Females			ANCOVA controlling for stature, chest width and chest depth		
	$\bar{X}$	SD	$\bar{X}$	SD	t	Male	Female	F
Age (yr)	24.0	1.9	22.9	1.5	2.6*	—	—	—
Stature (cm)	167.0	5.7	157.7	4.0	7.0***	—	—	—
Weight (kg)	61.2	6.5	57.2	5.8	2.4*	—	—	—
Chest depth (cm)	19.7	1.1	18.3	1.7	3.8***	—	—	—
Chest width (cm)	27.3	1.4	25.0	1.1	7.0***	—	—	—
Total lung capacity (TLC) (1 BTPS)	7.81	0.94	5.69	0.60	9.7***	7.27	6.24	15.3***
Vital capacity (VC) (1 BTPS)	5.42	0.65	4.15	0.46	8.2***	4.95	4.62	4.0
Residual volume (RV) (1 BTPS)	2.39	0.60	1.53	0.51	5.8***	2.31	1.61	10.1**
(RV/TLC) × 100	30.4	5.4	26.6	7.3	2.3*	31.8	25.3	7.4**
Functional residual capacity (FRC) (ml BTPS)	4.43	0.63	2.98	0.55	9.1***	4.28	3.24	21.9***
Inspiratory capacity (IC) (ml BTPS)	3.24	0.44	2.57	0.44	5.9***	2.98	2.84	0.9
Expiratory reserve volume (ERV) (ml BTPS)	2.04	0.28	1.45	0.11	9.5***	1.91	1.57	16.5***
Forced expiratory volume (FEV) (ml BTPS)	4.88	0.57	3.66	0.34	9.3***	4.51	4.03	10.8**
(FEV/VC) × 100	91.1	3.3	90.1	2.9	1.3	91.1	87.4	6.8*

*$P < .05$.
**$P < .01$.
***$P < .001$.

Statistical analyses

Since all of the pulmonary function variables are interrelated, comparisons between males and females were first made with a multivariate analysis of covariance, controlling for anthropometric dimensions which are known to influence lung volumes, or stature, chest depth, and chest width (Polgar and Weng, 1979). Respiratory function may be influenced by age (Polgar and Weng, 1979), but age did not exert a significant effect in the present sample. Therefore, only the analyses in which the anthropometric dimensions were controlled are reported. The anthropometric covariates for these analyses were identified as follows. First, multiple regressions in which stature, stature^2, and stature^3 were the independent variables were performed, using an alpha inclusion level of 0.05. Next, separate regressions were performed for chest width and chest depth, in which the significant stature variables identified in the initial regressions were entered first, followed by a chest dimension and it's square. Once again, an alpha inclusion level of 0.05 was utilized. All anthropometric variables which were entered into at least one regression (stature, chest width, and chest depth) were used as covariates. This method resulted in redundant control of the same variation in some pulmonary function variables but ensured that all possible anthropometry-related variation was controlled prior to comparing pulmonary function between sexes.

The relationship between chest size and pulmonary function is an issue of interest in high-altitude pulmonary function studies. The strength of this relationship was determined by calculating the partial correlations of each pulmonary function measure with both chest depth and chest width, after controlling for body size (as assessed by the stature terms identified with the regressions described earlier). All statistical analyses were performed with SPSSPC+, Version 3.0.

RESULTS

All measures of body and chest size, and most measures of respiratory function, were significantly larger in male than in female Aymara adults in the sample (Table 1, $P < .05$). Since males tend to have larger body and chest sizes than females and since pulmonary function volumes are influenced by both body and chest size, comparisons were also made between males and females after controlling for stature, chest depth, and chest width. A multivariate analysis of covariance controlling for anthropometry indicated that there were significant differ-

TABLE 2. Results of regressions of pulmonary function measures on stature (S) and partial correlations of pulmonary function measures with chest depth and chest width, after controlling for stature-related variation[1]

	Males				Females			
	Regressions with stature		Partial correlation controlling for stature		Regressions with stature		Partial correlation controlling for stature	
	Variable entered	*r*	Chest depth (cm)	Chest width (cm)	Variable entered	*r*	Chest depth (cm)	Chest width (cm)
TLC	S	0.71^{+++}	0.26	0.30	S	0.16	0.22	0.19
VC	S	0.64^{+++}	0.46^{**}	0.54^{***}	S	0.55^{++}	0.10	0.20
RV	S	0.42^{++}	−0.11	−0.13	S	0.32	0.20	0.07
RV/TLC	S	0.11	−0.26	−0.31	S	0.44^{+}	0.14	0.01
FRC	S	0.62^{+++}	−0.09	0.02	S	0.26	0.22	0.02
IC	S	0.45^{++}	0.49^{**}	0.44^{**}	S	0.44^{+}	0.11	0.14
ERV	S	0.48^{++}	0.05	0.32^{*}	S	0.18	0.20	−0.21
FEV	S	0.62^{+++}	0.36^{*}	0.41^{*}	S	0.55^{++}	0.27	0.16
FEV/VC	S	0.06	−0.23	−0.29	S	0.21	0.30	−0.13

[1] See Table 1 for abbreviations.

Measure significantly related to stature: $^{+}P < .05$, $^{++}P < .01$, $^{+++}P < .001$.

Measure significantly related to chest dimension, after controlling for stature: $^{*}P < .05$, $^{**}P < .01$, $^{***}P < .001$.

TABLE 3. Total lung capacity (TLC), vital capacity (VC), and residual volume (RV) in selected populations of adult males

	TLC (1 BTPS)		VC (1 BTPS)		RV (1 BTPS)		Estimated mean (ml BTPS/kg weight)		
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	TLC	VC	RV
La Paz Aymara	7.81	0.94	5.42	0.65	2.39	0.60	127.7	88.6	39.1
Peru (high-altitude)	6.96	0.74	4.88	0.68	2.07	0.37	126.1	88.4	37.5
Tibet	6.80	0.89	5.00	0.50	1.86	0.56	123.2	90.6	33.7
Leadville	6.41	1.04	4.68	0.65	1.73	0.57	97.2	70.8	26.4
Peru (low-altitude)	6.50	0.62	5.00	0.54	1.50	0.23	103.5	79.6	23.9

ences between males and females in respiratory function ($F = 4.9$, $P < .001$). Analyses of covariance indicated that, after controlling for body and chest size, all measures with the exception of VC and IC were significantly larger in males than in females (Table 1, $P < .05$), although VC approached significance ($P = .051$). The greatest difference between males and females was in RV, which was about 43% larger in males than in females, after controlling for body and chest size (Table 1).

The results of regressions of each pulmonary function measure against stature are included in Table 2. With the exception of RV/TLC and FEV/VC, all variables were significantly and positively related to stature in males ($P < .05$). All variables were also positively related to stature in females but only the relationships with VC, RV/TLC, IC, and FEV were significant ($P < .05$). All of these relationships were linear. Examination of the coefficient of correlation (*r*) indicates that, with the exception of RV/TLC and FEV/VC, all relationships were stronger in males than in females.

Partial correlations of chest depth and chest width with each measure of lung function, while controlling for stature, are also presented in Table 2. After controlling for stature, only VC, IC, and FEV were significantly related to chest depth in males while these same measures plus ERV were significantly related to chest width in males ($P < .05$). None of the partial correlations were statistically significant in females ($P > .05$).

Absolute TLC, VC, and RV (e.g., expressed in 1 BTPS) in the La Paz males and in selected comparison samples are included in Table 3. Absolute TLC, VC, and RV were all significantly greater in the La Paz males than in all of the comparison samples (*t*s of 2.6–8.9, $P < .05$). For example, TLC (1 BTPS) in the La Paz males was about 12% larger than in highland Peruvians and

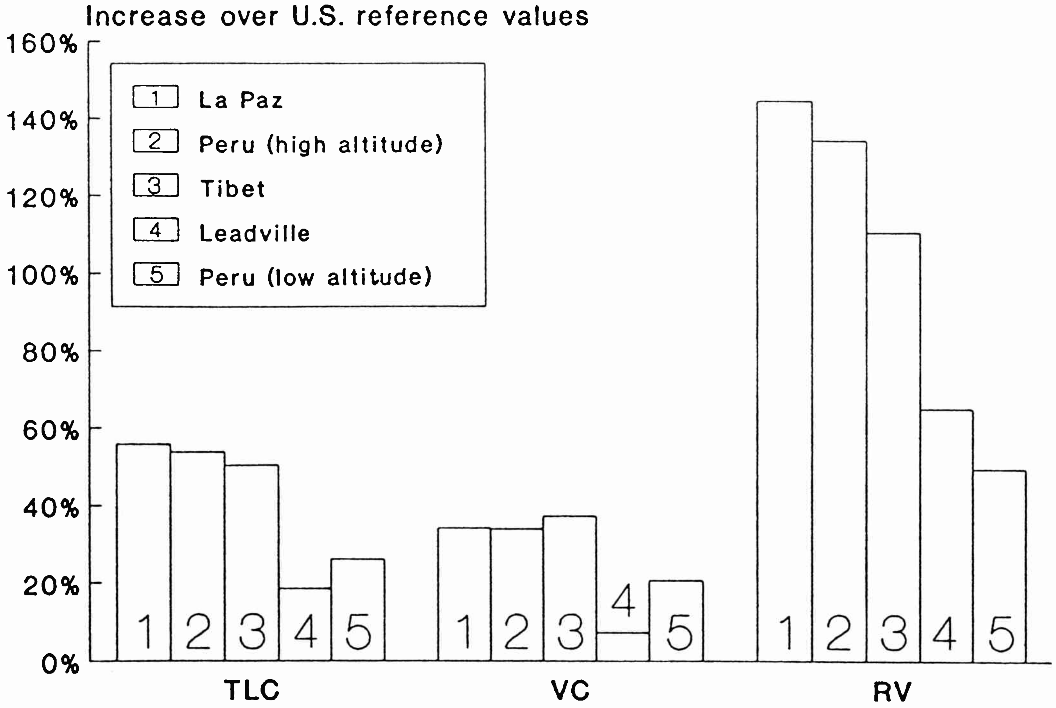

Fig. 1. Percentage increases in TLC, VC, and RV above U.S. low-altitude reference values.

about 15% larger than in Tibetans ($P < .05$). However, there were substantial body size differences between samples and, as noted earlier, lung volumes are influenced by body size. Estimated means of each measure after controlling for body weight are, therefore, also included in Table 3. Since these values were estimated from published means, statistical comparisons were not possible. Nevertheless, it is clear that the differences between the three samples of native highlanders (La Paz Aymara, Peruvian highlanders, and Tibetans) are considerably reduced once body weight is controlled. For example, body size adjusted TLC is only about 1 and 4% larger, respectively, in the La Paz Aymara than in the highland Peruvians and Tibetans. On the other hand, control of body size tends to amplify the magnitude of the difference between the three samples of native highlanders and the Leadville Caucasians. For example, absolute TLC is about 22% larger in the La Paz Aymara than in Leadville Caucasians while body size adjusted TLC is 31% larger in the La Paz Aymara. In addition, the increases in TLC, VC, and RV relative to U.S. lowlanders were all larger in lowland Peruvians than in the sample of high-altitude Leadville Caucasians.

Finally, Figure 1 describes the percentage increases in TLC, VC, and RV above U.S. low-altitude reference values, after controlling for body size. Several points are noteworthy. First, the enhanced TLCs of all groups were primarily due to an enhancement of RV and secondarily due to an enhancement of VC above those of U.S. lowlanders. Second, the percentage increases in both TLC and VC relative to U.S. lowlanders were fairly similar in the three groups with a long history of residence at high altitudes (La Paz Aymara, Peruvian highlanders, and Tibetans). However, after controlling for body size, the La Paz Aymara displayed a relative increase in RV above reference values for U.S. lowlanders of about 145%, as compared to 134% in the Morococha Quechua and only 111% in the Lhasa Tibetans. For the reason given earlier, it cannot be determined whether or not these differences are statistically significant.

DISCUSSION

Stature, weight, chest depth, and chest width were all significantly larger in the young adult males than in the young adult females in the present study (Table 1). This finding is consistent with expectation (Greksa and Beall, 1989). In addition, males were significantly older, by 1.1 years on average, than females ($P < .05$). However, although respiratory function is influenced by age, the older age of the male sample did not influence the analyses reported here, probably because of the relatively small age range of the sample. After controlling for stature-, chest depth-, and chest width-related variation, there were a number of significant differences in respiratory function between the young adult males and females in the present study, including in TLC and RV (Table 1). Respiratory function has not been reported for both adult males and females in any other study of highlanders but similar sex differences have been reported in lowlanders (Åstrand and Rodahl, 1977).

Stature was more likely to be significantly related to measures of respiratory function in males than in females (Table 2). For example, TLC, RV, and VC were all significantly related to stature in males while, of these three measures, only VC was significantly related to stature in females. The greater tendency for respiratory function measures to be significantly related to stature in males may simply reflect the greater stature variation in the male sample (Table 1).

Several studies have found significant relationships between measures of chest size and FVC (e.g., VC) in adult male highlanders (Droma et al., 1991; Frisancho et al., 1973; Hurtado, 1932; Mueller et al., 1978). After controlling for stature, VC (but not TLC or RV) was also significantly related to chest size in Aymara males (Table 2). In the one study of FVC in adult female highlanders, Mueller et al. (1978) found that FVC was significantly related to maximum chest circumference in adult female Aymara, after controlling for stature. However, in the present study, none of the measures of respiratory function, including VC, RV, and TLC, were significantly related to chest size in adult female Aymara, after controlling for stature (Table 2). The Mueller et al. (1978) sample included adults ranging in age from 20 to 80 years while the present study included females between the ages of 20 and 30 years. Thus, the differing results of these two studies may be a consequence of the wider age range of the Mueller et al. (1978) sample.

Highlanders have long been noted for their enhanced lung volumes, generally as assessed by FVC, relative to lowlanders (Greksa and Beall, 1989). As noted earlier, Hurtado (1964) hypothesized that the functionally significant aspect of these enhanced lung volumes was an enhanced TLC, and particularly the RV subcomponent, which he demonstrated to be primarily responsible for the enhanced TLC of Quechua highlanders. The present study was not designed to test this hypothesis but the results presented in Figure 1 are consistent with expectation. In particular, the enhancement of TLC in male Aymara, Peruvian, Tibetan, and Caucasian highlanders is primarily due to enhancements in RV and secondarily to enhancements in VC. For example, RV in Aymara males displayed an average increase over U.S. low-altitude reference values of about 145% while VC displayed an average increase of only about 34%.

There has been some discussion in the literature as to whether or not lung volumes (particularly TLC), as well as their associated chest dimensions, differ between Andean and Tibetan highlanders (Beall, 1982; Droma et al., 1991; Greksa and Beall, 1989). The absolute value of TLC was in fact significantly larger in the La Paz Aymara than in Tibetans (Table 3, $P < .05$). However, after controlling for body size, TLC was only about 4% larger in the La Paz Aymara than in Tibetans. Also, the average percentage increase in TLC over U.S. low-altitude reference values was only slightly lower in Tibetans than in the two Andean samples, while the average percentage increase in VC over U.S. low-altitude reference values was only slightly greater in Tibetans (Fig. 1). On the other hand, the average percentage increase in RV over U.S. low-altitude reference values was substantially less in Tibetan (111%) than in Aymara (145%) highlanders. However, since TLC is calculated by summing VC and RV and since the average percentage increases in both TLC and VC over U.S. low-altitude reference values were very similar in these highland populations, it is not clear if these data reflect true differences between samples or if they are simply an artifact of the statistical procedure. Thus, it seems reasonable to conclude that, after controlling for body size, there are only minor differences between Tibetan and Andean highlanders in at least TLC and VC, and possibly in RV.

Finally, although body size-adjusted TLC is similar between these Andean and Himalayan samples, it should be noted that this does not necessarily imply that the magnitude of enhancement in TLC over and above what it would be in a lowlander of similar ancestry (e.g., as an assessment of the effect of chronic hypobaric hypoxia on lung volumes) is similar in Andean and Himalayan natives. In reality, the magnitude of the enhancement of TLC cannot be accurately quantified for either Andean or Himalayan natives, due to difficulty in locating comparable lowland samples in both locales. The percentage increases in TLC, VC, and RV above U.S. sea level reference values allows evaluation of the relative importance of enhancements in RV and VC for explaining the enhanced TLCs of highlanders but they should not be viewed as accurate estimates of the effect of chronic hypobaric hypoxia on lung volumes. For example, if one assumes that Hurtado's (1964) low- and high-altitude samples are comparable (or at least that his low-altitude sample is a more appropriate standard than U.S. reference values), then the effect of chronic hypobaric hypoxia on TLC in Peruvian highlanders (e.g., TLC in Peruvian highlanders minus TLC in Peruvian lowlanders) is considerably less than the percentage increase in TLC above U.S. sea level reference values in Peruvian highlanders (Fig. 1). The fact that lung volumes differ between Peruvian and U.S. lowlanders (Fig. 1) is not surprising. The existence of such ethnic variability in the lung volumes of lowlanders is well documented (Binder et al., 1976; Hsu et al., 1979; Schoenberg et al., 1978). In other words, given the absence of comparable Andean and Tibetan lowland samples and given the existence of ethnic variability in the lung volumes of lowlanders, sufficiently accurate estimates of the effect of chronic hypobaric hypoxia on lung volumes in Andean and Tibetan highland natives to allow determination of whether or not both groups exhibit similar enhancements of TLC as a result of exposure to a hypobaric hypoxic environment is not possible at the present time.

ACKNOWLEDGMENTS

This study was made possible by the cooperation and assistance of the Instituto Boliviano de Biología de Altura, Instituto Nacional Superior de Educación Física, and Club Pilcomayo. The assistance of Dr. H. Spielvogel, Dr. Luis Paredes-Fernanadez, and E. Caceres, as well as the constructive suggestions of the anonymous reviewers, is especially appreciated. This research was supported by Grant BNS 8506788 from the National Science Foundation and by a grant from the Wenner-Gren Foundation for Anthropological Research.

LITERATURE CITED

Åstrand P-O, and Rodahl K (1977) Textbook of Work Physiology, 2nd ed. New York: McGraw-Hill.

Beall CM (1982) Comparison of chest morphology in high altitude Asian and Andean populations. Hum. Biol. *54*:145–163.

Binder RE, Mitchell CA, Schoenberg JB, and Bouhuys A (1976) Lung function among Black and White children. Am. Rev. Respir. Dis. *14*:955–959.

Boyce AJ, Haight JSJ, Rimmer DB, and Harrison GA (1974) Respiratory function in Peruvian Quechua Indians. Ann. Hum. Biol. *1*:137–148.

DeGraff AC Jr, Grover RF, Johnson RL Jr, Hammon MW Jr, and Miller JM (1970) Diffusing capacity of the lung in Caucasians native to 3,100 m. J. Appl. Physiol. *29*:71–76.

Droma T, McCullough RG, McCullough RE, Zhuang J, Cymerman A, Shinfu S, Sutton JR, and Moore LG (1991) Increased vital and total lung capacities in Tibetan compared to Han residents of Lhasa (3,658 m). Am. J. Phys. Anthropol. *86*:341–351.

Frisancho AR (1969) Human growth and pulmonary function of a high altitude Peruvian Quechua population. Hum. Biol. *41*:365–379.

Frisancho AR, Velásquez T, and Sanchez J (1973) Influence of developmental adaptation on lung function at high altitude. Hum. Biol. *45*:583–594.

Greksa LP (1991) Human physiological adaptation to high-altitude environments. In GW Lasker and CGN Mascie-Taylor (eds.): Applications of Biological Anthropology to Human Affairs. Cambridge: Cambridge University Press, pp. 117–142.

Greksa LP, and Beall CM (1989) Development of chest size and lung function at high altitude. In MA Little and JD Haas (eds.): Human Population Biology: A Transdisciplinary Science. New York: Oxford Univ. Press, pp. 222–238.

Greksa LP, Spielvogel H, Caceres E, and Paredes-Fernandez L (1987) Lung function of young Aymara highlanders. Ann. Hum. Biol. *14*:533–542.

Hoff C (1974) Altitudinal variations in the physical growth and development of Peruvian Quechua. Homo *24:*87–99.

Hsu KHK, Jenkins DE, Hsi BP, Bourhofer E, Thompson V, Tanakawa N, and Hsieh GSJ (1979) Ventilatory functions of normal children and young adults—Mexican-American, White, and Black. I. Spirometry. J. Pediatr. *95:*14–23.

Hurtado A (1932) Respiratory adaptation in the Indian natives of the Peruvian Andes: Studies at high altitude. Am. J. Phys. Anthropol. *17:*137–165.

Hurtado A (1964) Animals in high altitudes: Resident man. In DB Dill, EF Adolph, and CG Wilber (eds.): Handbook of Physiology. Section 4: Adaptation to the Environment. Washington, D.C.: American Physiological Society, pp. 843–868.

Mueller WH, Yen F, Rothhammer F, and Schull WJ (1978) A multinational Andean genetic and health program. VI. Physiological measurements of lung function in an hypoxic environment. Hum. Biol. *50:* 489–513.

Polgar G, and Weng TR (1979) The functional development of the respiratory system from the period of gestation to adulthood. Am. Rev. Resp. Dis. *120:*625–695.

Schoenberg JB, Beck GJ, and Bouhuys A (1978) Growth and decay of pulmonary function in healthy Blacks and Whites. Resp. Physiol. *33:*367–393.

Velásquez T (1976) Pulmonary function and oxygen transport. In PT Baker and MA Little (eds.): Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua. Stroudsburg: Dowden, Hutchinson and Ross, pp. 237–260.

Weiner JS, and Lourie JA (1981) Practical Human Biology. New York: Academic Press.