J. biosoc. Sci. (2002) 34, 463–473
© 2002 Cambridge University Press Printed in the United Kingdom



REPRODUCTION IN HIGH ALTITUDE AYMARA: PHYSIOLOGICAL STRESS AND FERTILITY PLANNING?

E. CROGNIER*, M. VILLENA† AND E. VARGAS‡

*UMR 6578 CNRS – Université de la Méditerranée, Instituto Boliviano de Biologia de Altura and †Instituto Boliviano de Biologia de Altura, La Paz, Bolivia

Summary. Reproductive characteristics at high altitude are described based on the reproductive histories of 720 Aymara women, collected in 1998 and 1999 in a group of twelve peasant communities at a mean altitude of 4000 m in the Bolivian Altiplano. The reproductive pattern is shaped by a late onset of childbearing, associated with a rather short reproductive span and large birth intervals. Environmental conditions could explain the particularly late age at menarche of rural girls compared with their urban counterparts, whereas the age at first birth is likely to be under cultural control. The short reproductive span appears to result from a large mean interval between last birth and menopause, which is essentially determined by cultural decisions. The birth intervals, which are longer than in many traditional societies, could be the result of a slower restoration of postpartum fecundability induced by the hard way of life inherent in the Altiplano (including poor sanitary and nutritional conditions and high workload), perhaps aggravated by hypoxia. However, a secular trend in fertility is perceptible, towards earlier menarche, earlier age at first birth, increasing reproductive span and a slight increase in live births and surviving offspring, which is probably the result of a slow improvement in living conditions. The existence of birth control on the one hand, and a total fertility rate averaging six live births among the couples who do not practise contraception on the other, are other arguments against the hypothesis of a low natural fecundity in these Aymara groups.

Introduction

The relationship between human fertility and high altitude is a long-standing question which has been addressed by generations of investigators. However, since the International Biological Program of the 1960s and 70s, more systematic studies of reproductive patterns at altitude have been developed, in particular in the Andes (Baker, 1969; Baker & Dutt, 1972; Hoff & Abelson, 1976; Stinson, 1982, Gonzales, 1993) and in the Himalayas (Gupta, 1978; Bangham & Sacherer, 1980; Goldstein,

Tsarong & Beall, 1983; Laurenson et al., 1985). The absence of salient environmental contrasts other than altitude, and similar living conditions, suggested that the lower fertility of traditional groups living above 3000 m was a consequence of physiological impairment induced by hypoxia: depression of fecundability or incapacitation for a successful pregnancy (see James, 1966; Abelson, 1976; Hoff & Abelson, 1976; Weitz et al., 1978; Gupta, 1978, 1980; Bangham & Sacherer, 1980). However, later studies, which took into account the part played by behaviours, showed that fertility scores at high altitude, if ever ruled by physiology, were also, as anywhere else, under cultural control (Collins, 1983; Goldstein et al., 1983; Kashiwazaki, Suzuki & Takemoto, 1988).

The present work took the opportunity to make use of a survey developed in the Aymara ethnic group, remotely settled in the Bolivian Altiplano, to observe fertility patterns already analysed in the 1970s by Baker and colleagues in neighbouring Quechua populations.

Methods

A multipurpose survey, which was part of the National Program for the Study of Native Peoples of Bolivia, was developed by the Instituto de Biologia de Altura (La Paz), from August 1998 to December 1999 in twelve Aymara communities (Ayllu) located at altitudes varying from 3800 to 4100 m in the Altiplano, 30–60 km south-west of the city of La Paz.

Following the 1952 agrarian reform that dismantled the former *estancias* and *latifondias*, these communities make a network of small familial estates. Despite a sedentary lifestyle and a pronounced inclination to endogamic marriages, the lack of local mates and frequent short-range migrations maintained their genetic homogeneity.

A total of 868 nuclear families were studied with the purpose of creating a database of social, cultural and biological information about this society of still traditional agriculturists, remotely established at very high altitude. Censuses were conducted in each community, and individual data concerning members of each family were collected, including reproductive life histories of all women. Next, oral information was crossed with other sources (baptism and marriage registers, familial booklets, etc.) and checked with genealogical data when available.

Most information relating to individual chronology (date of birth, age or date of marriage, age of death) was fairly good. However, because there is a charge for inscription in the civil register and because this is not easily accessed, the information on infantile mortality depends essentially on memory and is the least reliable variable since the evocation of dead people is not trivial. Reproductive failures such as abortions are also under-reported, and in particular miscarriages before 4–5 months of pregnancy often fail to be mentioned.

The following analyses are based on a total of 720 reproductive histories, which were the data remaining after elimination of childless couples and families that had recently immigrated from other provinces of Bolivia. The analyses involving completed fertility were carried out on a subsample of 361 women aged 45 years or more. With the exception of the recalled age at menopause, all distributions were normal or normalized by transformation to decimal logarithms.

Table 1. Distribution of recalled ages at menarche among Aymara peasant women

Age classes	n	Min.	Max.	Mean ± SD
Age≤20	15	12	16	14·46 ± 1·19
$20 < age \le 30$	93	12	17	14.50 ± 1.19
30 <age≤40< td=""><td>173</td><td>11</td><td>17</td><td>15.11 ± 1.17</td></age≤40<>	173	11	17	15.11 ± 1.17
40 <age≤50< td=""><td>148</td><td>12</td><td>18</td><td>15.14 ± 1.17</td></age≤50<>	148	12	18	15.14 ± 1.17
$50 < age \le 60$	115	12	18	15.28 ± 1.15
Age≥60	118	12	20	15.68 ± 1.30
Total sample	662	11	20	15.23 ± 1.32

Results

Age at menarche

The mean recalled age at menarche obtained from 662 women of 15·2 years (range 11–20) is late. It does, however, vary with age class: from 15·7 years for the oldest class to 14·5 years for the younger group (Table 1), indicating a downward trend expressed by the following linear regression:

Age at menarche= $(0.0274 \times age) + 14.09$.

A very late age at menarche has frequently been observed in Asian populations living in high altitude. The mean estimate given by Pawson (1976) for Kathmandu (altitude 1460 m) was 16·1 years, and that for Sherpas living between 3475 and 4050 m was 18·1 years. Bangham & Sacherer (1980) found a mean recalled age of 16·3 years for Sherpa women in villages between 2000 and 3300 m in Nepal. Beall (1983) observed a mean age at menarche of 16·9 years (recalled) and 16·2 (status quo) in Nepalese women from villages above 3000 m, with a non-significant downward trend with decreasing age classes. However, Malik & Hauspie (1986) reported a median age at menarche (status quo) of 14·1 years for Bod girls living at 3500 m in Ladakh.

Data for Andean populations generally express earlier maturation rates: Gonzales, Villena & Ubilluz (1996) observed a median age at menarche (*status quo*) varying from 13·0 to 14·4 years among Quechua girls of low socioeconomic status, depending on their dwelling place either in Lima (sea level) or at an altitude of 4340 m. In the city of La Paz (mean altitude 3850 m), Bouloux (1968) found a mean of 13·6 years (recalled), Frisancho (1976, 1978) a median of 13·6 years (*status quo*) and Greksa (1990) a median of 13·4 years (*status quo*) for Aymara girls. These fairly converging values indicate a rather slow maturation rate, which besides living conditions (still not optimal among low- and middle-class residents), might possibly be affected by hypoxia in an unknown proportion. They contrast with the current data, whatever the age class. If subjects of the same generation, for example the age classes 40–50 and 50–60, in this sample are compared with Bouloux's data (i.e. subjects who experienced puberty in the late 1950s and early 1960s), a discrepancy of 18 months is seen between

Table 2. Estimated mean waiting time to first birth, mean age at first birth and menarche–first birth interval in the total sample of Aymara women, by age class

Variable	n	Mean \pm SD
Waiting time to first birth (months)	646	17.9 ± 6.7
Age at first birth (years)	0.10	177207
Age<30	107	20.1 ± 2.8
$30 < age \le 40$	188	23.1 ± 3.8
$40 < age \le 50$	187	23.7 ± 4.2
50 <age 60<="" td="" ≤=""><td>132</td><td>24.4 ± 5.1</td></age>	132	24.4 ± 5.1
60≤age	127	26.4 ± 5.8
Total sample	720	23.2 ± 4.1
Menarche-first birth interval		
Age<30	106	5.5 ± 2.5
$30 < age \le 40$	185	7.9 ± 3.7
$40 < age \le 50$	181	8.5 ± 4.3
50 <age 60<="" td="" ≤=""><td>128</td><td>8.9 ± 5.4</td></age>	128	8.9 ± 5.4
60≤age	120	10.5 ± 5.8
Total sample	720	8.3 ± 4.7

urban and rural samples. Similarly, comparison of the age class 20–30 years in Table 1 with Greksa's sample observed in 1986 (i.e. approximately the same birth cohort) shows that menarche still occurs more than 1 year later in the rural group. These differences cannot be ascribed to altitude, whereas the obvious contrast between the precarious living conditions of peasant groups of the Altiplano – lack of medical support, poor diet based on the potato as staple food, absence of hygiene, hard work – and the current conditions of life in the city, even among low income residents, would certainly explain a later maturation of peasant girls. This delay in maturation, added to an already slow maturation rate, would result in a very late menarche.

Age at first birth and menarche-first birth interval

Marriage as a frame built by society to enclose reproduction is not relevant to Aymara culture. Despite the influence of Christianity, many couples either live as concubines or finally marry when they have already had a family. The age at marriage is therefore a poor indicator of the onset of fertility, except for the youngest age classes who are integrating more and more occidental culture. The beginning of marital life not being precisely known, the waiting time to first birth is approximated, despite the subject's seemingly good knowledge of the time lag between the beginning of regular couple life and the first birth (Table 2).

The reliable variable is 'age at first birth', which averages 23·2 years (Table 2), a late beginning for childbearing considering the still traditional lifestyle of Aymara peasantry. The mean age at first birth estimated in a sample of 34 traditional societies from developing countries (McDonald, 1984) is 20·9 years, ranging from 18·0 years

Table 3. Distributions of the age at last birth, of the recalled age at menopause and of the last birth-menopause interval in the total sample of Aymara women, by age class

Variable	n	Mean \pm SD	Median
9			
Age at last birth (years)			
$50 \le age < 60$	127	39.1 ± 4.55	
60 ≤ age < 70	81	39.5 ± 4.39	
70≤age	42	41.0 ± 5.85	
Total sample	317	39.4 ± 4.63	
Age at menopause, recalled (years)			
50 ≤ age < 60	120	46.8 ± 3.04	48
60≤age<70	74	47.5 ± 3.34	49
70≤age	36	48.2 ± 2.92	49
Total sample	303	46.6 ± 3.33	48
Last birth-menopause interval (years)			
$40 \le age < 50$	66	9.25 ± 5.08	
$50 \le age < 60$	105	9.67 ± 6.10	
$60 \le age < 70$	64	10.4 ± 5.08	
70≤age	29	9.60 ± 6.91	
Total sample	264	9.73 ± 5.70	

(in Bangladesh) to 22·7 years (in Haiti). At altitude, Bangham & Sacherer (1980) estimated the mean age at first birth to be 22·0 years in Sherpa villages in Nepal (2200–2600 m). However, Weitz *et al.* (1978) cite a mean age at first pregnancy of 23·6 years for other Nepalese data at an altitude of 3500 m and Gonzales (1993) found a mean age of 24·2 years among Quechua in Cuzco.

The mean menarche-first birth interval of 8.3 years (Table 2) is also longer than that in most traditional peasant societies. It can be estimated at 7.0 ± 0.9 years (range 6.0-8.2) for nine populations mentioned in McDonald (1984), and in a society prone to early and universal marriage like Moroccan Berbers it falls to 2.9 years (Crognier, Baali & Hilali, 2001). In high altitude Nepalese Sherpas, Bangham & Sacherer (1980) found a mean menarche-first birth interval of 5.7 years; in Peru, Gonzales (1993) measured intervals of respectively 10.6 and 6.7 years among women in Cuzco (altitude 3400 m) and Cerro de Pasco (altitude 4340 m). Table 2 shows a trend towards a lower age at first birth and shorter menarche-first birth interval, probably reflecting a slow but general improvement in living conditions associated with behavioural changes.

Age at last birth, age at menopause and last birth-menopause interval

The age at last birth estimated from a subsample of 317 women aged 45 years or more was 39.4 ± 4.63 years (Table 3). The age at menopause (defined as the complete cessation of menses), obtained by *status quo* from women aged 40–60 years and estimated by probit analysis, gives a median age of 45.4 years (n=466).

In the total sample of women who declared themselves to be postmenopausal (as distinct from the preceding sample), the strongly skewed distribution of recalled age at menopause gave a mean value of 46·6 years (Table 5) and a median of 48 years. The same remark holds when recalled age at menopause is analysed by age classes, so that the apparent slight trend towards an earlier menopause that is expressed in the means becomes inconsistent when medians are considered. These evaluations indicate an earlier end of fecundity than observed in occidental industrial societies (e.g. median ages of 50·8 in England in 1965, 51·4 year in the Netherlands in 1969 and 51·4 years in the USA in 1981 and a mean age of 49·1 in Germany in 1972; Rahman & Menken, 1993). However, it is within the range of other traditional societies, either at low altitude (mean recalled age of 47·0 years in Berber peasants from Morocco, Crognier (1998a); and 48·4 years in Peru at sea level, Gonzales (1993)), or at high altitude (45·5 years in altitude, Gonzales (1993); 46·8 years by status quo and 45·9 by recall among women 50 years or more, in a high altitude Nepalese group, Beall (1983)), with no obvious relation between altitude and early menopause.

Despite large individual variation, the effective end of childbearing significantly precedes the physiological end of fecundity in every human population, in traditional societies as well as in industrialized nations (e.g. a mean interval of 11·7 years between last birth and menopause among Berber groups, Crognier (1998a)). The Aymara population is not exceptional in this matter, as shown in Table 3, with a mean interval close to 10 years. Variance analysis shows that the means of different age classes of postmenopausal women do not differ significantly (F=0·606, non-significant at p=0·05, for 3 and 260 df), thus refuting the existence of a behavioural change across generations. A positive correlation between first and last birth indicates that women would frequently pass a late age at menarche on to their age at last birth (r=0·44, p<0·0001), and hence a significant negative correlation between age at first birth and length of last birth—menopause interval (r= 0·39, p<0·0001). The main objective would consequently be more the accomplishment of a defined reproductive score, rather than a culturally defined age to stop childbearing.

Reproductive span, birth intervals and total fertility rate

The late menarche and the termination of childbearing before the end of biological fecundity determine a short reproductive span (interval between first and last birth) of only 13 years (Table 4), the change in the successive age classes not being significant (variance analysis: F=1.69, not significant at p=0.05). This span, compared with those of other traditional societies, is short. Estimates from the data of 34 traditional populations in McDonald (1984) give an average of 20.9 years and range from 18.0 years (Bangladesh) to 22.7 years (Haiti). In Moroccan Berbers, it varies from 18.6 to 21.0 years according to environment (Crognier, 1996), a short duration of 13 years only being associated with a close succession of pregnancies (Crognier, 1998b). The mean birth interval of 35.6 months (Table 4) is among the highest observed in this same sampling of 34 traditional societies: mean of 30.8 months, range of 26.7 (Jordan) to 37.8 months (Lesotho).

Table 4. Distributions of the reproductive span (first birth-last birth interval) and of mean birth interval in a sample of Aymara women aged 45 years or more

	n	$Mean \pm SD$
Reproductive span (years)		
45≤age<50	72	13.7 ± 6.15
50≤age<60	132	13.5 ± 6.04
60≤age<70	. 82	12.7 ± 6.44
70≤age	45	11.4 ± 6.24
Total sample	334	13.1 ± 6.21
Birth interval (months)*		
$45 \leq age < 50$	78	34.1 ± 7.76
$50 \le age < 60$	137	36.0 ± 7.44
60≤age<70	85	36.5 ± 7.51
70≤age	46	35.7 ± 6.43
Total sample	346	35.6 ± 7.43

^{*}Transformed to decimal logarithms.

Table 5. Distribution of the number of pregnancies, the number of live births and the number of offspring surviving to 15 years of age among Aymara women aged 45 years or more

Age class	n	No. pregnancies	No. live births	No. surviving to 15 years
				3
45≤age<50	79	6.0 ± 2.14	5.6 ± 2.34	4.6 ± 1.96
50≤age<60	143	5.9 ± 2.36	5.6 ± 2.35	4.8 ± 2.17
60≤age<70	88	5.4 ± 2.00	5.1 ± 2.06	4.3 ± 1.94
70≤age	51	5.3 ± 2.61	5.2 ± 2.60	4.2 ± 2.33
Total sample	361	5.7 ± 2.27	5.4 ± 2.30	4.5 ± 2.10

Despite the short reproductive span, the total fertility rate is not small. The mean number of live births computed from McDonald (1984) is 6.3 ± 0.80 so that Aymara fertility (total sample, Table 5) stands close beyond the limit of minus one standard deviation to the mean. Two features characterize Aymara fertility: a rather small proportion of pregnancy wastage (with the reservation imposed by the lack of reliability of corresponding data) and a good proportion of offspring surviving to sexual maturity (i.e. those who determine the parent's reproductive success).

Another characteristic of Aymara reproductive behaviour, already noted by Collins (1983), is the traditional practice of birth control, including in addition to the regulation of intercourse and withdrawal, abortive practices or casual infanticide. In the present case, 20% (n=70) of couples among the subsample of women aged

Table 6. Reproductive characteristics of Aymara women according to their eventual practice of contraception

Variable	Use contraceptives $(n=70)$ Mean \pm SD	Do not use contraceptives $(n=271)$ Mean \pm SD	p (t-test)
Age of woman ^a	57·4 ± 9·99	57·9 ± 9·18	ne
Age at first birth ^a	24.9 ± 4.96	24.2 ± 5.03	ns ns
Age at last birth ^a	35.0 ± 5.87	39.0 ± 5.71	***
Last birth-menopause interval ^a	13.6 ± 5.48	7.7 ± 5.95	***
Span of reproductive life ^a	11.7 ± 4.20	15.5 ± 5.64	***
Mean birth interval ^b	36.7 ± 7.60	35.3 ± 7.23	ns
Number of live births	3.96 ± 1.44	6.00 ± 2.16	***
Number of offspring≥15 years	2.84 ± 1.13	4.41 ± 1.88	***
Proportion of survivors	0.74 ± 0.22	0.75 ± 0.23	ns

^aYears; ^bmonths.

45 years or more claimed to have practised contraception and were consequently identified as a group, whatever the extent and means of their contraceptive practice may have been (Table 6).

Contraception was not used to postpone the onset of fertility, nor to increase the interval between births, but was used to end fertility. It shortened the reproductive span and lowered the number of live births and subsequently number of survivors to sexual maturity, without an apparent trade-off between number of progeny and survival rate. In the subsample which did not practise contraception, the total fertility rate averaged six live births, so Aymara fertility becomes very close to the average TFR computed from McDonald (1984).

Discussion

The elements of Aymara fertility presented in this article compose a reproductive pattern shaped by a late onset of fertility and a late beginning of childbearing, associated with a rather short reproductive span and large birth intervals. These characteristics could fit well with a scenario of physiological stress, in which poor conditions of health and nutrition, exacerbated by hypoxia, induce impairment of either fecundity or fertility processes. In particular, this could be the reason for the late age at menarche recorded among peasant girls. The huge discrepancy between the current observations and those of various other authors on adolescents living in the city of La Paz emphasizes the deep contrast in living conditions between rural and urban settlements, and the variety of environmental effects that are known to affect sexual maturation. This discrepancy cannot be explained by different levels of hypoxic stress, but the moderately late age at menarche among urban Aymara girls examined

by Greksa in 1986 (Greksa, 1990) is a sign of a possible influence of hypoxia on age at menarche. This urban Aymara sample was of low socioeconomic status; since 1996, it is probable that the trend towards an earlier maturation following the slow but general improvement of living conditions noted in the rural sample, has been paralleled by a similar trend in the low urban socioeconomic stratum. Greksa had already noted the existence of such a trend in the interval between the observations of Bouloux (1968) and his own, expressed not only by the fall in age at menarche but also by the increase in mean stature.

If the late beginning of childbearing were the consequence of an unusual protraction of anovulatory cycles following menarche, it could also result from a delaying action of an adverse environment. However, until demonstrated by hormonal investigation, such a slowing down of the rate of maturation remains hypothetical. Moreover, it is indirectly refuted by a particular mating behaviour: the inversion of the ages of spouses (32% of husbands are younger than their wives, 29% are the same age and only 39% are older). The greater the wife's age, the later the start of her reproduction. The regression of wife's age at first birth on spouses' age difference (age husband-age wife)

age at first birth = -0.293 (age husband – age wife) +24.09 years,

effectively shows that when a wife is 4 years older than her husband (8% of couples), her mean age at first birth will be delayed by more than 1 year compared with a counterpart born the same year as her husband. This tradition, which obviously aims at postponing the beginning of reproduction, would be pointless in circumstances in which biological fertility would be depressed. The absence of a relationship between age at menarche and age at first birth (Pearson's correlation coefficient r=0.11, not significant at p=0.05), is also a sign of the probable disconnection between the onset of childbearing and biological fertility. Considered in this context, the former expression of traditional behaviour displayed by the oldest age class (mean age at first birth=26.4 years, Table 2) would indicate a powerful cultural control of reproduction in the recent past.

In the absence of a strategy regulating birth spacing by contraception (see Table 6) and despite the traditional practice of breast-feeding (mean duration: $19\cdot 6 \pm 6\cdot 1$ months), the large birth intervals leave the possibility that fecundability could be affected by diverse factors. For example, Wiley (1998) noted the preponderance of sexually transmitted diseases (STDs) in Ladakh. No significant incidence of STDs was reported in the clinical examinations of individuals taking part in this survey. Another possible cause of the increase in length of birth intervals may be the slow recovery from physiological depletion following pregnancy and delivery, stressed by altitude and by poor nutrition. However, Vitzthum *et al.* (2000) have shown, from measures of salivary progesterone in Bolivian Quechua women, that ovarian function shows no sign of being impaired. If fecundability is not affected, the only other way in which altitude and poor living conditions could lead to an increase in the mean interval between live births would be the favouring of spontaneous abortions during the early stages of pregnancy. The poor quality of the current data on this precise point does not, unfortunately, allow this possibility to be estimated.

Conclusion

When considered successively, the various characteristics of the reproductive pattern – the delayed puberty and the extended birth intervals on one hand and the late beginning of childbearing and its early termination on the other – could respectively be explained by hard work, bad sanitary conditions, poor diet and cultural regulations. Fecundity between births does not seem to be depressed, and age at menopause appears to be normal; when contraception is not employed to shorten the reproductive span, the final reproductive score is not low compared with those observed in other traditional peasant societies.

However, the biological expression of stress on human beings in the hostile environment of high altitude is certainly not easy to separate from other factors, in particular if one considers that the Aymara have had plenty of time to 'work out' adaptive cultural responses to and cope efficiently with adverse conditions. Reproductive behaviours that seem designed to contain excessive fertility (e.g. late beginning of childbearing) could also (though not likely) be cultural acknowledgments of biological limitations.

References

- ABELSON, A. E. (1976) Altitude and fertility. Hum. Biol. 48, 83-92.
- BAKER, P. T. (1969) Human adaptation to high altitude. Science 163, 1149-1156.
- BAKER, P. T. & DUTT, J. S. (1972) Demographic variables as measures of biological adaptation: a case study of high altitude human populations. In: *The Structure of Human Populations*, pp. 352–378. Edited by G. A. Harrison & A. J. Boyce. Clarendon Press, Oxford.
- BANGHAM, C. R. M. & SACHERER, J. M. (1980) Fertility of Nepalese Sherpas at moderate altitudes: comparison with high-altitude data. *Ann. hum. Biol.* 7, 323–330.
- BEALL, C. M. (1983) Ages at menopause and menarche in a high-altitude Himalayan population. *Ann. hum. Biol.* 10, 365-370.
- BOULOUX, C. J. (1968) Contribution à l'Étude Biologique des Phénomènes Pubertaires en Très Haute Altitude (La Paz). Centre National de la Recherche Scientifique, Toulouse.
- Collins, J. L. (1983) Fertility determinants in a High Andes community. *Pop. Dev. Rev.* 9, 61–75.
- CROGNIER, E. (1996) Behavioral and environmental determinants of reproductive success in traditional Moroccan Berber groups. *Am. J. phys. Anthrop.* **100**, 181–190.
- CROGNIER, E. (1998a) Is the reduction of birth intervals an efficient reproductive strategy in traditional Morocco? *Ann. hum. Biol.* **25**, 479–487.
- Crognier, E. (1998b) Son los comportamientos reproductivos adaptativos? *Rev. Soc. Esp. Antrop. Biol.* **19**, 65–76.
- Crognier, E., Baali, M. & Hilali, M-K. (2001) Do 'helpers at the nest' improve their parents' reproductive success? *Am. J. hum. Biol.* 13, 365–373.
- Frisancho, A. R. (1976) Growth and morphology at high altitude. In: *Man in the Andes: A Multidisciplinary Study of High-Altitude Quechua*, pp. 180–207. Edited by P. T. Baker & M. A. Little. Dowden, Hutchinson and Ross, Stroudsburg, PA.
- Frisancho, A. R. (1978) Human growth and development among high-altitude populations. In: *The Biology of High-Altitude Populations*, pp. 117–191. Edited by P. T. Baker. Cambridge University Press, Cambridge.

- GOLDSTEIN, M. C., TSARONG, P. & BEALL, C. M. (1983) High altitude hypoxia, culture, and human fecundity/fertility: a comparative study. *Am. Anthrop.* **85**, 28–49.
- GONZALES, G. F. (1993) Reproducción Humana en la Altura. Publicación del Instituto de Investigaciones de la Altura, Universidad Peruana Cayetano Heredia y CONCYTEC, Lima, Peru
- Gonzales, G. F., Villena, A. & Ubilluz, M. (1996) Age at menarche in Peruvian girls at sea level and at high altitude: effect of ethnic background and socioeconomic status. *Am. J. hum. Biol.* **8**, 457–464.
- Greksa, L. P. (1990) Age at menarche in Bolivian girls of European and Aymara ancestry. *Ann. hum. Biol.* 17, 49–53.
- Gupta, R. (1978) A comparative demographic study of the Sherpas of Upper Khumbu (above 10000 ft), Nepal, and their migrant counterpart in Kalimpong sub-division (3000–6000 ft). *Indian stat. inst. Tech. Report* 11,1–11.
- GUPTA, R. (1980) Altitude and demography among the Sherpas. *J. biosoc. Sci.* **12**, 103–114. HOFF, C. J. & ABELSON, A. E. (1976) Fertility. In: *Man in the Andes*, pp. 128–146. Edited by P. T. Baker & M. A. Little. US/IBP Synthesis Series/1.
- James, W. H. (1966) The effect of high altitude on fertility in Andean countries. *Popul. Stud.* **20**, 87–101.
- Kashiwazaki, H., Suzuki, T. & Takemoto, T. (1988) Altitude and reproduction of the Japanese in Bolivia. *Hum. Biol.* **60**, 831–845.
- LAURENSON, I. F., BENTON, M. A., BISHOP, A. J. & MASCIE-TAYLOR, C. G. N. (1985) Fertility at low and high altitude in central Nepal. *Social Biol.* 32, 65–70.
- McDonald, P. (1984) Nuptiality and Completed Fertility: A Study of Starting, Stopping and Spacing Behaviour. World Fertility Survey Comparative Studies, No. 35.
- MALIK, S. L. & HAUSPIE, R. C. (1986) Age at menarche among high altitude Bods of Ladakh (India). *Hum. Biol.* **58**, 541–548.
- Pawson, I. G. (1976) Growth and development of high altitude populations: A review of Ethiopian, Peruvian and Nepalese studies. *Proc. Roy. Soc. B* **194**, 83–98.
- RAHMAN, O. & MENKEN, J. (1993) Age at menopause and fecundity preceding menopause. In: *Biomedical and Demographic Determinants of Reproduction*, pp. 65–84. Edited by R. Gray, H. Leridon & A. Spira. Clarendon Press, Oxford.
- STINSON, S. (1982) The interrelationship of mortality and fertility in rural Bolivia. *Hum. Biol.* **54**, 299–313.
- VITZTHUM, V. J., ELLISON, P. T., SUKALICH, S., CACERES, E. & SPIELVOGEL, H. (2000) Does hypoxia impair ovarian function in Bolivian women indigenous to high altitude? *High Altitude Med. Biol.* 1(1), 39–49.
- Weitz, C. A., Pawson, I. G., Weitz, M. V., Lang, S. D. R. & Lang, A. (1978) Cultural factors affecting the demographic structure of a high altitude Nepalese population. *Social Biol.* **25**, 179–195.
- WILEY, A. S. (1998) The ecology of low natural fertility in Ladakh. J. biosoc. Sci. 30, 457-480.