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The home team advantage: reproduction in women indigenous to high altitude

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Summary

Although there is substantial evidence that environmental conditions disrupt reproductive function among newcomers to hypoxic settings, it is not certain that low oxygen pressure reduces fertility among those indigenous to high altitude. Even when fertility does appear to be relatively lower, numerous behavioral and sociocultural factors may be responsible. These are best examined within demographic frameworks that delineate a finite list of the proximate determinants of fertility. The findings presented here are based on several studies of indigenous Andean populations (Peruvian Quechua at 4000 m, Bolivian Quechua at 3100 m, Bolivian Aymara at 4000 m). Data on ovarian function suggest that neither progesterone levels nor menstrual cycle length or regularity are significantly different from those of women at lower altitudes. Data on two behavioral factors that determine fertility levels, coital frequency and infant feeding practices, suggest that the former is not likely to be of significance in co-habitating couples, but that variation in breastfeeding patterns has probably made a substantial contribution to differences in fertility among at least some populations at high altitude.

Key words: ovarian function, menstrual cycle length, coital frequency, breastfeeding, proximate determinants of fertility.

Introduction

Centuries of anecdotes and documentation suggest that colonizers and transients from the lowlands, whether human or otherwise, experience changes in reproductive functioning and reductions in fertility while residing at higher altitudes. The 16th century missionary Father Cobo wrote of the first colonial Peruvian capital, situated at high altitude, ‘that it was sterile and horses, pigs and cows could not be raised’ (Cobo, 1897). The historian Antonio de la Calancha (de la Calancha, 1639) claimed that it was 53 years from the founding of Potosi (4000 m altitude) till the birth of the first child of Spanish parents. These and other observations, along with evidence that normal functioning is typically restored upon retreat to lower altitudes, led Monge (Monge, 1948) to propose that low oxygen pressure reduces fertility (number of live births), perhaps by reducing fecundity (capacity to conceive) and/or increasing fetal loss. Later evidence, principally drawn from animal experiments, suggested that environmental conditions at high altitude, including cold as well as hypoxia, can have a direct and negative bearing on at least some aspects of reproductive functioning (Heath and Williams, 1989).

Nevertheless, it is not certain that those indigenous to high altitude suffer comparable disruptions of normal reproductive functioning as a result of hypoxia. That ontogenetic adaptation of the reproductive system to hypoxia is likely demonstrated by Father Cobo’s observation (Cobo, 1897) that ‘…the Indians are healthiest and where they multiply the most prolifically is in these same cold air-tempers, which is quite the reverse of what happens to the children of the Spaniards, most of whom when born in such regions do not survive’. Hence, rather than considering changes in function amongst those new to the hypoxic environment – an approach that can make significant contributions to understanding physiological mechanisms – the focus here is on variation in reproductive functioning among women indigenous to high altitude, a perspective that emphasizes the dynamic evolutionary history of the organism in its environment.

Observed fertility levels in Andean populations

The first analyses in the Andes of fertility differences among humans according to ethnicity and/or altitude relied upon national-level census data. Stycos (Stycos, 1963) argued that an apparently lower fertility in Indian-speaking populations of Peru was due to greater marital instability and a concomitant lower exposure to the risk of conception. Heer (Heer, 1964) proposed that the purported lower fertility resulted from increased levels of abortion or infanticide. In contrast to these behavioral explanations, James (James, 1966) argued that the physiological effects of altitude were responsible for a seemingly lower fertility among indigenous populations. Unfortunately, causal hypotheses aside, none of these early studies adequately demonstrated the existence of any consistent fertility differential according to either ethnicity or altitude. National surveys at the time were not infrequently biased by poor interviewer/interviewee communication (Chen and Murray, 1976), perhaps especially as regards personal reproductive histories, often subject to purposeful or unconscious omission of miscarriages, stillbirths and dead offspring. Other than this difficulty, the measures of fertility used in these early analyses were probably biased. As suggested by James (James, 1966) and Whitehead (Whitehead, 1968), and later confirmed by Dutt (Dutt, 1980), the ratio of the number of children under 5 years of age to the number of women aged 15–49 (a common index of fertility used in early studies) is downwardly biased by the greater infant and child mortality known to exist in higher regions. Similarly, at higher elevations, the average number of children ever born to women aged 45–49 is disproportionately biased downwards by the omission in reporting infants dying shortly after birth.

Recognizing these limitations, later studies in the Andes concentrated on community-level estimates of fertility. In a review of the literature, Baker and Dutt (Baker and Dutt, 1972) argued that '…the present evidence suggests that the fecundity and ability of human populations to produce live offspring should be lower at high altitude' but concluded that 'How much loss in fertility or whether it is lower at all [at high altitude] cannot be judged at present simply because there is no appropriate material'. Subsequently, Hoff and Abelson (Hoff and Abelson, 1976) compared populations at high (Nuñoa, Peru) and low (Tambo Valley, Peru) altitude, in particular noting an increased fertility in high-altitude natives that had migrated to low altitude, and concluded that the data '…provide evidence that the stress of hypoxia does act to reduce fertility at high altitude'. Later evaluations of available data questioned whether hypoxia had been demonstrated to have any effect on fertility (Goldstein et al., 1983). More recently, Schull et al. (Schull et al., 1990) found no clear support for a relationship between hypoxia and fertility among Chilean mestizos and Aymara.

Table 1 presents available data on fertility in several Andean populations and low-altitude populations with which they have been compared. For example, in Peruvian Quechua/mestizo at high and low altitude, the completed fertility rate (CFR, which is the average total number of children ever born to women over 45 years old) is 6.7 and 8.3, respectively, suggesting that hypoxia may reduce fertility (Hoff, 1968; Abelson, 1976). However, when examining all studies collectively, the CFR for high- and low-altitude populations in these studies ranges from 5.8 to 9.1 and from 4.6 to 8.3, respectively. Similarly, crude birth rate (CBR, which is the annual number of live births per 1000 population) ranges from 51 to 82 in high-altitude populations, from 46 to 56 in populations at middle altitudes, and is as low as 48 in a low-altitude sample. Clearly, fertility levels vary considerably at any altitude, and one cannot help but agree with Baker (Baker, 1978) that 'the fertility data on high-altitude peoples present a complex picture from which obvious conclusions do not emerge'.

The proximate determinants of fertility

In addition to environmental factors, social and cultural factors in humans may also underlie any apparently lowered production of offspring at high altitude. Marriage, labor and migration patterns as well as prolonged lactation and sterility from sexually transmitted diseases have all been implicated (Stycos, 1963; Heer, 1964; Weitz et al., 1978; Goldstein et al.,

Table 1. *Fertility measures for Andean samples*

	High altitude		Middle altitude		Low altitude		
Sample	CFR	CBR	CFR	CBR	CFR	CBR	Source
Aymara (Chile)	7.3	82			6.4	48	Cruz-Coke et al., 1966
	8.5				7.2		Cruz-Coke et al., 1966
	5.8						Cruz-Coke et al., 1966
			7.1				Schull et al., 1990
Mestizo (Chile)	6.9		6.7		4.6		Schull et al., 1990
Quechua/mestizo (Peru)	6.7						Hoff, 1968
	9.1*				8		Way, 1972
					8.3		Abelson, 1976
		49					Baker and Dutt, 1972
		54					Baker and Dutt, 1972
				46			Alers, 1971
				56			Alers, 1971
Aymara (Bolivia)	5.9		7.2		6.9		Dutt, 1976; Dutt, 1980
			5.3		5.4		Dutt, 1976; Dutt, 1980
Quechua (Bolivia)		51		46			Godoy, 1984

CFR, completed fertility rate=average total number of live births for women over 45 years old.
CBR, crude birth rate=annual number of live births per 1000 population.
*Number of pregnancies.

Table 2. *The proximate determinants of fertility (Bongaarts and Potter, 1983)*

1. Natural fecundability (the monthly probability of conception):
   - *p1*=probability of an ovulatory cycle
   - *p2*=probability of insemination during the mid-cycle fertile period
   - *p3*=probability that insemination during the fertile period leads to fertilization
   - *p4*=probability that fertilization results in a recognizable conception
2. Marriage and marital disruption
3. Onset of permanent sterility
4. Spontaneous intrauterine mortality (fetal loss)
5. Induced abortion
6. Post-partum infecundability (including lactational subfecundity)
7. The use and effectiveness of contraception

Table 3. *Proximate determinants of natural fertility (Wood, 1994)*

I. Exposure factors
1. Age at marriage or entry into sexual union
2. Age at menarche
3. Age at menopause
4. Age at onset of pathological sterility

II. Susceptibility factors
5. Duration of lactational infecundability
6. Duration of the fecund waiting time to conception, determined by:
   a. frequency of insemination
   b. length of ovarian cycles
   c. proportion of cycles that are ovulatory
   d. duration of the fertile period, given ovulation
   e. probability of conception from a single insemination in the fertile period
7. Probability of fetal loss
8. Length of the nonsusceptible period following fetal loss
9. Length of gestation resulting in a live birth

1983; Kashiwazaki et al., 1988; Vitzthum, 1989; Wiley, 1998). Hence, the demonstration of relatively fewer live births at greater elevations, even if well substantiated, is not, in and of itself, evidence of the influence of hypoxia. Conversely, similarity in fertility among populations at different altitudes does not disprove hypoxic effects because other factors may compensate for physiological changes caused by varying oxygen pressure.

The numerous environmental, behavioral and sociocultural factors that may influence fertility levels can be evaluated within a demographic framework (developed by Bongaarts and Potter, 1983) that delineates the proximate determinants of fertility. Refining a model originally proposed by Davis and Blake (Davis and Blake, 1956), they identified a complete set of seven proximate determinants through which any and all socioeconomic and environmental factors can affect fertility (Table 2). Recently, Wood (Wood, 1994) has reformulated the model to consider more specifically the biological determinants of natural fertility and to construct a framework more tractable for quantitative analyses (Table 3).

Examined within these frameworks, hypoxia is most often hypothesized to affect fertility by increasing fetal loss and/or reducing fecundability by impairing fecundity. However, fecundity in women indigenous to high altitude (and in many other settings) has not been measured directly. Rather, reduced fecundity has often been inferred for a high-altitude population if fertility appears to be reduced, especially if fetal loss does not appear to be increased. However, because relatively little attention in studies of high-altitude populations has been given to the other proximate determinants of fertility, which may or may not be influenced by hypoxia, a conclusion of impaired fecundity due to hypoxia is premature.

Not surprisingly, given the extraordinary demands of such an effort, there have been no studies of a high-altitude population in which all the proximate determinants of fertility have been studied simultaneously. However, an evaluation of the range of variation in these determinants among high-altitude populations, and how this variation compares with that of other populations, can afford some insight into the possible significance of hypoxic conditions for human reproduction. In addition, a recently completed longitudinal study of an *altiplano* Aymara population, Project REPA (Reproduction and Ecology in Provincía Aroma; see below), has gathered a large body of comprehensive data on the reproductive patterns, hormonal profiles and outcomes of conceptions among women indigenous to high altitude. Findings from this investigation as well as published data are presented below to provide better information about reproduction among high-altitude populations. Specifically, the focus here is on the length of ovarian cycles, progesterone levels during the ovarian cycle, the probability of insemination, and breastfeeding patterns.

Materials and methods

Setting

Project REPA is a multidisciplinary longitudinal study of reproductive functioning and health among rural Aymara families indigenous to the Bolivian *altiplano*. Participants are drawn from 30 communities scattered over approximately 200 km^2 situated at 4000 m approximately half-way between La Paz and Oruro. Preliminary studies began in 1989, with more than 2 years of continuous fieldwork from 1995 to 1997 and additional data collection through 1999. All study protocols were approved by the IRB at the University of California, Riverside.

Altiplano farms commonly comprise a cluster of small adobe buildings with one to several separate quarters for sleeping and another for cooking and eating. Such clusters are scattered over the landscape, separated by farming and grazing lands, and organized into politically recognized communities with locally elected leaders, more or less centered around a primary grade school or small church that serves for monthly community meetings and other activities. Subsistence is based upon agropastoralism – sheep, cattle, potatoes, barley, onions, carrots – augmented to varying extents by cash income generated principally through males laboring outside the household and the selling of farm products (e.g. wool, potatoes, milk) in the regional markets or to 'middlemen'.

Sample

Representing more than 80 % of the eligible participants, 316 women, 19–40 years of age and currently in stable sexual unions, were recruited during 12 months beginning in November 1995. Of these, 125 were pregnant and/or lactating/non-cycling throughout the study's duration. Of the remaining 191 menstruating women, 98 were and 93 were not breastfeeding at the time of the first observed menstruation (Vitzthum et al., 1998; Vitzthum et al., 2000b).

Data collection

Throughout participation, menstruating women were visited every other day by a bilingual (Aymara/Spanish) female *promotora* (research team member) to record menstrual status and collect a saliva sample for later assays of progesterone and estradiol levels (Vitzthum et al., 1998). Beginning at cycle day 24/25, a urine sample was collected to detect human chorionic gonadotrophin (hCG), evidence of a conception, using StanBio QuPID kit (sensitive at 25 mi.u. ml^{-1} hCG; i.u.=international units). Sample collection continued until the next menses or, if positive, until evidence of a fetal loss (two sequential negative tests) or the sixth month of gestation. One to eight menstrual initiations were observed for each participant. The results of hCG urine tests allowed menstrual segments to be classified into eight types (Table 4) (Vitzthum et al., 2000b). Women who were lactating but non-cycling at the time of initial recruitment were visited weekly until the first post-partum menses, then followed as described above.

Following protocols previously established by studies in Peru and Bolivia (Vitzthum, 1989; Vitzthum, 1992; Vitzthum, 1994), data on infant feeding practices (including breastfeeding) were obtained through structured interviews of currently nursing mothers and observation of actual practices. Questions on coital frequency were part of a structured interview on health practices and family-size preferences, administered several months after initial recruitment, by a REPA *promotora* very familiar to the participant.

Table 4. *Segment types based on hCG tests*

Type	Description	Code	*N*
1	Non-conception/non-post-fetal-loss	NC/NPFL	612
2	Likely post-fetal-loss	LPFL	13
3	Post-fetal-loss	PFL	5
4	Likely conception+likely fetal loss	LC	20
5	Conception+fetal loss	CFL	10
6	Conception+term birth	CT	23
7	Conception+induced abortion	CA	1
8	Conception+unknown outcome	CU	13

N=697.
hCG, human chorionic gonadotropin.

Analyses

Adopting World Health Organization (WHO) guidelines (Snowden, 1983), menstrual intervals are referred to as 'segments' rather than cycles to avoid the presumption of normal cycling, and segment length is defined as the first day of menses up to and including the day before the subsequent menses. Following Burkhart et al. (Burkhart et al., 1999), 'regular' is defined as having all a woman's observed segments of length 26–32 days inclusive. 'Predictable' is defined (Vitzthum et al., 2000b) as having no more than a single observed segment (of 3–5 segments observed per woman) outside the range 26–32 days. For comparison with previous studies, descriptive statistics (Table 5) are given for a sample comprising all individual segments. However, the inclusion of multiple segments from women who did not conceive during the study may bias the sample towards women of lower fecundity and, perhaps, aberrant segments. Furthermore, within such a sample, not all data points are independent, confounding statistical analyses. Therefore, the correct units of analyses for statistical comparisons are the mean or median of each woman's segments. Statistical analyses of menstrual segments, coital frequency, and infant feeding practices were carried out using SPSS for Windows (Version 10.0).

Results

Reproductive history

For the sample of 191 menstruating women (665 non-truncated menstrual segments observed), mean age was 29.3 years and all but nine women were between 22 and 36 years of age, a period during which the probability of an ovulatory cycle is relatively high and constant (Lipson and Ellison, 1992). Mean recalled age at menarche was 14.1 years, a value roughly midway in the ranges reported for other samples from high altitude (Greksa, 1990). Mean age at first birth was 20.0 years, and mean parity was four, so women averaged four live births in the first 9 years of childbearing.

Ovarian segment length and regularity

For those segments in which a conception did not occur and that did not follow a fetal loss (type 1 segment), length averaged 28.5 and 29.1 days, respectively, for the all-segments and individual-means samples (Vitzthum et al., 2000b). Table 5 lists those populations for which roughly comparable data on segment length are available in the literature. Despite the differences of ecology, lifestyle and nutritional status, this Aymara sample falls neither particularly low nor high in the

Table 5. *Segment lengths in several populations*

Sample description		Number of cycles[1]	Number of women[1]	Segment length (days)			Source
				Median	Mean	S.D.	
Project REPA:	20–38 years	*612*		28	28.5	4.8	Vitzthum et al., 2000b
Project REPA:	20–38 years		*159*	28	29.1	4.4	Vitzthum et al., 2000b
Canada/U.S.:	20–24 years	3320	*257*		30.5	3.99	Chiazze et al., 1968
	25–29 years	3412	*266*		29.4	6.34	
	30–34 years	6691	*505*		28.8	6.53	
Denmark:	20–35 years	*1061*	295	29			Kolstad et al., 1999
Denmark:	25–34 years		*434*		28.4	2.6	Münster et al., 1992
Guatemala:	18–39 years	*880*	301		30.4	3.97	Burkhart et al., 1999
India (Bengal):	Adult	*782*	110		30.1		Datta, 1960
South India:	20–24 years		*583*		32.3	4.9	Jeyaseelan and Rao, 1993
	25–29 years		*699*		31.2	3.9	
	30–34 years		*413*		31.1	4.0	
Mali:	15–53 years	400	*54*	28.5			Strassmann, 1997
New Guinea:	18–44 years	37	*36*	36			Johnson et al., 1987
Switzerland:	20–40 years	*31 644*		27.8[2]			Vollman et al., 1977
UK:	21–25 years	*2606*		29	29.3	4.15	Monari and Montanari, 1998
	26–30 years	*4387*		28	28.8	3.94	
	31–35 years	*5224*		28	28.4	3.92	
UK:	20–24 years	*1494*			29.2	3.69	Bailey and Marshall, 1970[3]
	25–29 years	*3078*			28.7	3.57	
	30–34 years	*3762*			27.9	3.55	

[1]Units of analysis are italicized.
[2]Mean of medians for all cycles at each year of age.
[3]Earlier subset of Monari and Montanari (1998).

range of observed segment lengths, suggesting that if hypoxia does affect ovarian cycle length, the effect is insignificant.

Despite an average cycle length falling well within the range of other populations, it may be that cycle irregularity is greater at high altitude. In Project REPA, 109 women were observed for at least three type 1 segments, 78 for at least four, and 61 for at least five. In each of these subsamples, only approximately one-third (35–38 %) of the women can be considered regular, and 59–78 % (depending upon the number of segments observed) of the women meet the criterion of predictability (Vitzthum et al., 2000b). Given the widespread myth of regular cycles being the norm, these may appear to be low levels of regularity and predictability but, in fact, are comparable with those found among Maya women (Burkhart et al., 1999).

Progesterone profiles

Progesterone has a characteristic profile during the menstrual cycle, levels being relatively low and flat during the follicular (pre-ovulatory) phase, then rising and peaking approximately half-way through the luteal (post-ovulatory) phase before returning to basal levels, signaled by the onset of menstrual bleeding. Because the absence or reduction of a rise and peak in progesterone is considered indicative of subfecundity, progesterone levels are an excellent proxy for measuring fecundity.

In 1992, to test the hypothesis that fecundity is reduced in women at high altitude, salivary progesterone levels were measured in a sample of Quechua women residing at 3100 m (Vitzthum et al., 2000a). The observed mean mid-luteal progesterone level was 243 pmol l^{-1} (Table 6), a value much lower than that of a Boston sample (333 pmol l^{-1}) and somewhat lower than a sample of Polish women during the post-harvest season (283 pmol l^{-1}) but considerably higher than the samples of agriculturalists from Zaire (167 pmol l^{-1}) and Nepal (138 pmol l^{-1}) in the winter season, a period of relatively less work and greater food resources (as was the case for the period during which the Bolivia data were collected; in the monsoon season, this Nepal sample averaged only 85 pmol l^{-1}). In other words, the high-altitude Bolivian sample falls within the range of progesterone levels observed for several low-altitude populations and is substantially higher than the Nepal sample, drawn from a population residing at only 1870 m.

Because progesterone levels are known to vary with age, and the age distributions of these five samples are not identical, progesterone levels were examined for mid-aged (25–35 years old) women separately. In adjusting for age, the mean mid-luteal progesterone levels are more similar among the samples, and the relative rankings change somewhat. The two higher-altitude samples (Bolivia and winter Nepal) are nearly identical (251 pmol l^{-1} and 253 pmol l^{-1} respectively) and substantially

Table 6. *Salivary progesterone levels in five populations*

	N	Mean mid-luteal progesterone level ($pmol\,l^{-1}$) All ages	25–35 years old	Data source
Bolivia	20	243±21.0	251±17.1	Vitzthum et al., 2000a
Poland				G. Jasienska, personal communication
Post-harvest	20	283±16.9	299±19.6	
Harvest	20	224±12.5	237±14.7	
Nepal				Panter-Brick et al., 1993
Winter	21	138±21.0	253±53.0	
Monsoon	20	85±8.0	124±19.0	
Zaire	56	167±6.5	201	P. T. Ellison, personal communication
Boston	124	333	373	Lipson and Ellison, 1992

Values are mean ± S.E.M.

higher than the low-altitude Zaire sample ($201\,pmol\,l^{-1}$). Interestingly, while lower than that of Polish women ($299\,pmol\,l^{-1}$) during the post-harvest season (a period roughly comparable with the seasons during which the winter Nepal and Bolivia data were collected), these samples from higher altitudes display progesterone levels greater than that of the low-altitude (700 m) sample of Polish women during the peak of harvesting ($237\,pmol\,l^{-1}$). The lowest value ($124\,pmol\,l^{-1}$) is seen in the Nepal sample during the monsoon season, a period of far greater energetic stress than characterizes the seasons when data for the other samples were collected.

Unfortunately, all the field studies listed in Table 6 were characterized by methodological limitations that may have biased the findings. To eliminate such biases, Project REPA collected data on progesterone levels longitudinally as women made the transition from lactating/non-menstruating to lactating/menstruating to non-lactating/menstruating (Vitzthum et al., 1997; Vitzthum et al., 1998). Simultaneously, urine samples taken to detect hCG allowed progesterone levels to be correlated with conception events. In brief, the data clearly indicate that conceptions typically occur at progesterone levels far lower than those observed in samples of women from industrialized countries, suggesting that the relatively lower progesterone levels are not pathological but normal and natural in this and other populations in developing countries. To summarize, although the findings of these various hormonal studies are not conclusive, it does not appear that the progesterone level observed in the high-altitude Bolivian sample is unusual or suggestive of an effect of hypoxia on ovarian function.

A model of flexible responsiveness to environmental conditions

These data suggest that characteristics of the ovarian cycle that determine fecundability are not disrupted by hypoxia in women indigenous to high altitude. Given that colonists and transients do experience such disruptions, how is it that these women do not appear to have a negative response to the stressors of high altitude? One explanation could be genetic adaptation, but this seems unlikely given that Bolivian women of varying levels of European and indigenous admixture have comparable ovarian cycle lengths and progesterone levels. Rather, I would argue that adjustments during the developmental period (analogous to those seen in adaptations of the respiratory system to hypoxia) are occurring such that successful reproduction occurs in the face of any chronic, but not debilitating, stressor.

Integrating known attributes of mammalian physiology and the changing probabilities of successful reproduction in different conditions, I have proposed a Flexible Response Model (FRM) that considers the specific conditions under which a reduction in reproductive effort decreases or increases Darwinian fitness (Vitzthum, 1990; Vitzthum, 1997; Vitzthum, 2001). The FRM delineates the evolution and attributes of a reproductive system that can respond flexibly to ecological conditions, incorporates the role of individual life history, and offers predictions regarding the life history parameters and econiche characteristics of species that have evolved a flexibly responsive reproductive system. The FRM predicts that Andean women are adapted to the conditions in which they were born and developed, and that successful reproduction is to be expected even when such conditions would be prohibitive for newcomers. Project REPA was designed to test some of the predictions of the FRM, and to date, the findings have been consistent with this hypothesis.

Having considered two of the routes by which hypoxia may affect fertility and finding the evidence less than compelling, it remains to be determined which factors may be responsible for relatively lowered fertility in some high-altitude populations. To address this issue further, two behavioral determinants are considered next.

Probability of insemination

In the proximate determinants model as developed by Bongaarts and Potter (Bongaarts and Potter, 1983), variation in natural fecundability (the monthly probability of

Table 7. *Reported frequency of weekly marital intercourse (Project REPA)*

	Mean	Median	Mode	Minimum	Maximum	*N*
How many times per week do you think women in your community have sexual relations?	3.08	3	2	1	7	120
How many times per week do you have sexual relations?	2.17	2	1	0	7	167

conception) is largely the result of variation in the frequency and timing of intercourse. In the model of Wood (Wood, 1994), fecundability is acknowledged to be determined by several physiological factors but, of course, the probability of insemination remains an essential, if not sufficient, component. Despite the importance of this determinant, there are few reliable data regarding coital patterns amongst human populations.

Because of polyandry and/or migration patterns related to traditional, colonial and contemporary labor practices, at high altitude some average population-level coital frequencies may be less than that of residents at lower altitudes (Goldstein et al., 1983). But what has yet to be examined is whether coital frequency among co-habitating monogamous partners in any high-altitude population varies significantly from that of other populations. If significantly lower, for whatever reason, then fertility levels could be relatively reduced.

To estimate coital frequency (Table 7), women participants in Project REPA were asked two questions, both of which they could decline to answer. (i) In your opinion, how many times per week do the women of your community have sexual relations? (ii) How many times per week do you have sexual relations? The findings are noteworthy only for their ordinariness. On average, women reported that they had sexual relations about twice a week, and that the members of their community were having sex more frequently (about three times per week). In comparison with other data (Table 8), the monthly rates are neither very low nor high, suggesting that in comparison with other populations there is no reason to suspect that the probability of insemination is especially atypical in this Andean population.

Infant feeding practices and fecundity in Andean women

Although it is well known that birth is followed by a period of subfecundity principally attributable to breastfeeding (WHO, 1995), and that Andean women practice extended breastfeeding (T. Baker, 1976), it is only relatively recently that these two observations have been explicitely linked to explain variation in fertility levels in Andean populations (Vitzthum, 1989; Vitzthum, 1992).

In the absence of breastfeeding, the average return of fecundity is approximately 6 weeks post-partum (Wood, 1994). According to the 1998 Demographic and Health Survey (DHS) for Bolivia, the nationwide median duration of breastfeeding is 17.6 months and that of post-partum amenorrhea is 10.2 months (Table 9). In other words, as much as 9 months on average have been added to the birth interval as a result of lactation. All other determinants being equal, those with longer interbirth intervals will have a lower average life-time fertility. It was even argued (Short, 1976) that breastfeeding had prevented more births than all modern contraceptives combined (an observation that may not be quite accurate today given the intervening 25 years of family planning efforts worldwide).

Regionally, Bolivian women in rural areas breastfeed longer than urban women (19.1 *versus* 16.4 months) and, by ecological zone, women in the *altiplano* nurse longer than those of the lowlands (19.5 *versus* 14.5 months). As would be expected from the breastfeeding patterns, rural women have longer durations of post-partum amenorrhea than do urban women (10.9 *versus* 8.6 months), as do women at high altitude compared with the lowlands (11.0 *versus* 8.2 months). Although the data are not presented in the DHS report, it can be inferred that rural high-altitude women breastfeed the longest and have the lengthiest

Table 8. *Reported monthly frequency of marital intercourse (Udry et al., 1982)*

Population	Mean	*N*
Belgium 1975	10.3	3987
Japan 1975	8.3	617
Thailand 1969	6.4	795
USA 1965	6.9	3512
USA 1970	8.5	4560
USA 1974	9.5	1633
Project REPA	8.7	167

Table 9. *Breastfeeding and fecundity in selected Andean populations*

	Duration of breastfeeding (months)	Duration of post-partum amenorrhea (months)
Bolivia (1998 DHS)	17.6	10.2
Urban	16.4	8.6
Rural	19.1	10.9
Lowlands	14.5	8.2
Altiplano	19.5	11.0
Peru (1997 DHS)	20	8
Nuñoa	21.1	18.8
Nuñoa, mid-SES	16.6	8.8
Nuñoa, low-SES	23.6	21.6

SES, socioeconomic subsample.

durations of amenorrhea and, hence, interbirth intervals. This inference is supported by four community-level studies in Nuñoa, Peru and Patacamaya, Bolivia, both at approximately 4000 m altitude, and Cocapata and Rinconada, Bolivia, at approximately 3100 m altitude.

Nuñoa, Peru, is the well-known site of several classic studies on human adaptation to high-altitude conditions (Baker and Little, 1976). In 1985, 30 women currently with a child less than 3 years old were interviewed in Quechua on their reproductive histories and infant feeding practices (Vitzthum, 1989; Vitzthum, 1992). The mean duration of reported daytime breastfeeding was 21.1 months, somewhat longer than the national median of 20 months reported in the most recent DHS. The duration of amenorrhea (based on probit analysis of current status), however, was 18.8 months, far longer than the national median of 8 months (DHS). Given the roughly comparable durations of breastfeeding, one might be tempted to attribute the longer amenorrhea in Nuñoa women to hypoxia. Closer inspection of the data suggested otherwise.

On the basis of several criteria, the sample was partitioned into two relative socioeconomic subsamples (SES) (low- and mid-SES). Heads of mid-SES families generally had steady cash-based employment, while those of low-SES households were day laborers, agropastoralists or unemployed. These differences translated into greater access to the market economy, greater use of bottle-feeding, and the feeding of better foods among mid-SES families, all of which contributed to differences in durations of breastfeeding and post-partum amenorrhea. Among poor women, the mean duration of daytime breastfeeding was 23.6 months *versus* 16.6 months in mid-SES women.

Even more striking, the median duration of amenorrhea among the poorer SES is 21.6 months but among the mid-SES is only 8.8 months, a value very comparable with the national median. (The relationship between durations of breastfeeding and post-partum amenorrhea is not linear because of variations in how women breastfeed, what else is fed to the infant, and a woman's own nutritional status, all of which reflect cultural values and economic conditions.) Hence, the extended median duration of amenorrhea of Nuñoa women, which can be expected to contribute to longer birth intervals and relatively reduced fertility, is better attributed to prolonged breastfeeding than to ecological conditions at high altitude (unless one argues that poverty, itself a determinant of breastfeeding duration, is an ecological condition common to high altitude).

The infant feeding practices observed in Nuñoa are not, however, 'the Andean pattern', as demonstrated by studies of three high-altitude Bolivian communities. In Rinconada and Cocapata, two small rural Quechua communities, breastfeeding generally ends rather abruptly at only 1 year of age, the belief being that to continue to nurse when a child is beginning to walk will prevent her/him from ever walking properly. Menses typically returns shortly thereafter, although if menstruation should return while still breastfeeding it is interpreted as a signal to wean. Although Cocapata lies along a dirt road at least a full day's travel by truck north of Cochabamba, and Rinconada is approximately an additional hour's walk in the adjacent valley, several women in both communities disapprovingly noted that women '*del campo*' ('in the countryside', waving at some distant point while speaking) did breastfeed for 2 years.

Even in these small communities, however, socioeconomic variation was apparent and influenced infant feeding practices much as it had in Nuñoa. However, as the virtual absence of a local market economy meant a near absence of bottle-feeding by anyone, more important was the quality of the foods given to infants. In all Andean communities observed in these studies, infants are fed 'the foods of the house' rather than any diet specifically earmarked for them (except in the rare case where bottles and formula may be used). Hence, household resources translated directly into dietary quantity and quality for infants, thereby affecting infant growth, suckling patterns and maternal fertility.

Cultural preferences may also interact in unpredictable ways with economic resources. In both Cocapata and Rinconada, goats provide milk to the family larder, but only in Rinconada is it given to infants. In neither community is the readily available cow's milk given to infants. Asked for the reasons behind these feeding decisions, most simply shrugged and said 'that's the way it is' (*asi es*). However, in these rural regions, drinking an animal's milk is a rarity for adults as well; usually it is made into cheese. Hence, Rinconada's practice is a local innovation the likes of which may crop up in any setting, influencing breastfeeding and generating variation in maternal fertility no matter the altitude.

Although Patacamaya, the largest community in Project REPA, lies at the intersection of Bolivia's two major highways, in 1997 most of the inhabitants in this and the surrounding smaller communities were without electricity or water/sanitation systems, and most relied principally or solely upon agropastorialism for subsistence. However, every Sunday the impressively extensive market affords opportunities to sell farm goods and garner at least some cash income, essential for purchasing many household items (e.g. kerosene) and some foods (e.g. cooking oil).

In comparing the infant feeding practices of this principally Aymara population with those of the three Quechua communities discussed above, there are some interesting similiarities and striking differences. In all regions, breastfeeding is not initiated until approximately 24 h after birth, and other liquids (typically herbal tea) are given instead. Post-partum amenorrhea averages approximately 1 year in the Patacamaya region, and breastfeeding is also prolonged, averaging approximately 2 years. Thus, the women in this region exhibit the longest overlap of menstruating while lactating, and many continue to breastfeed in the first few weeks of a new pregnancy, a pattern not observed in the other Andean communities. There are also marked differences in the timing of the introduction of solid foods, being much earlier in all the Bolivian communities (approximately 4 months) than in Nuñoa (approximately 13 months). In these and probably other communities, it is likely that the substantial variation in many aspects of infant feeding practices has generated variation in fecundity and fertility among Andean populations irrespective of whatever contribution there may be from hypoxia.

Concluding remarks

The data presented here suggest that at least two physiological determinants of fertility, probability of ovulation as inferred from progesterone levels and length of ovarian cycle, are not significantly different among women indigenous to high altitude compared with women in other populations. Hence, even if fertility levels are shown to be lower among some high-altitude populations, it is not likely that hypoxia is influencing reproductive patterns through either of these mechanisms. These findings are consistent with the Flexible Response Model, which predicts that Andean women would reproduce successfully even under conditions that are prohibitive to newcomers. However, other physiological mechanisms that may reflect the operation of hypoxia, such as an increase in fetal loss, remain to be examined. The data also suggest that coital frequency, which determines the probability of insemination, does not differ among co-habitating couples in at least the population sampled by Project REPA, but that there is much variation in infant feeding practices among Andean populations. Because of the well-documented effect of lactation on fecundity, it is likely that the prolonged breastfeeding common to Andean women contributes substantially to any observed reduction in fertility. Infant feeding repertoires themselves reflect differences in ecological and economic conditions, some unique to the Andes, others characterizing impoverished populations in any locale. Recognizing the different sources of these variations in infant feeding practices can lead to better-informed interventions designed to improve the health of Andean women and their children.

Through more than 10 years as my principal collaborator, Doctora Hilde Spielvogel, Director of Bioenergetics, Bolivian Institute of High Altitude Biology (IBBA), La Paz, has been instrumental in the design and implementation of the research projects in the Bolivian Andes discussed here. ‘Thank you’ cannot suffice. The labor of many able assistants, most notably Esperanza Caceres, Head Biotechnician, Department of Bioenergetics, IBBA, made these investigations possible. Funding was provided for different aspects of this longitudinal research by, chronologically, the University of Michigan, the Hewlett Foundation, the University of California, the University Research Expeditions Program, the National Science Foundation, and Binghamton University, SUNY. And finally, I express my unwavering appreciation to the Andean women whose decisions to participate were acts of courage undertaken in the hope of improving the lives of themselves and their families.

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