# DISSOCIATING BIOLOGICAL FROM SOCIAL DETERMINANTS OF FERTILITY IN NON-CONTRACEPTING POPULATIONS: HIMALAYAN WORKLOADS, LACTATION, AND REPRODUCTIVE ECOLOGY

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*Introduction: Fecundity or Fertility Variation?*

REPRODUCTIVE ecology is the study of reproduction as an aspect of human biology that varies with ecology (the environmental context). This field of research has gained great impetus from the ability we now have to measure population variation in the hormones that underpin human fecundity. We can do this non-invasively, from minute samples of saliva or blood, for populations living far away from a research laboratory. From these biological samples, we can ascertain whether specific hormones (chemical messengers produced from the brain to control ovarian or testicular function) vary for individuals who maintain high energy expenditure, experience food shortages, or breast-feed infants intensively, relative to contexts where physical activity is undemanding, food intake sufficient, and lactation periods short.

Why has this proved so important? For the first time, we have the means to dissociate the biological mechanisms underpinning variation in human *fecundity* from the social variables influencing variation in human *fertility*. Let us not confuse fecundity with fertility. The former refers to one's *ability* to reproduce, while the latter designates *actual* reproductive success (number of live births). Thus sterility caused by sexually transmitted infections, the risk of conception failure (failure of the fertilized egg to implant), intra-uterine mortality (foetal loss) and

post-partum infecundability (with breast-feeding) are all variables which affect fertility via fecundity. Age at marriage and frequency of sexual intercourse affect fertility but not fecundity. Demographers call the six variables listed above 'proximate determinants of natural fertility', where natural fertility designates re-production subject to natural causes (i.e. unaffected by contraception) (Bongaarts 1993). *All* the variables we can think of (socio-economic practices, subsistence strategies, gender relations, nutritional status, and nursing patterns) which might influence birth rates in natural fertility populations do so through the proximate determinants named above. The challenge is to identify which determinants are the key ones for a given population.

Fecundity, Wood noted (1994: 100), 'is considered by many demographers to be little more than a nuisance, an annoying creature whose sole aim in life is to confound analyses of the social factors affecting fertility.' However, for concep-tual clarity it is important to dissociate biological determinants of reproduction from social ones.[1] Moreover, the reasons underlying variation in fecundity have proved to tell a fascinating story.

In this article, I shall use my own field experience in Nepal to illustrate a part of this story, which concerns the impact of working and breast-feeding behaviours on fecundity. I raise the following four issues:

(1) Do very heavy workloads affect women's reproductive ability?
(2) Does temporary infecundity matter for actual fertility?
(3) Do men show a different sensitivity to energetic constraints?
(4) To what extent do differences in nursing schedules affect fecundity?

*Issues in reproductive ecology*

I first outline some of the theoretical and empirical background that framed the Nepal study.

What triggers low fecundity?

Research in the field of reproductive ecology has focused on variation in fecun-dity, namely the reproductive ability of non-contracepting individuals in their ha-bitual environment.

In developing countries, it had been commonly observed that many non-contracepting populations are characterized by low fertility, extremely long intervals

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[1] This is not easy. In his list of proximate determinants, Bongaarts (1993) classified the duration of post-partum infecundability as a behavioural, not a biological factor, because it depends on breast-feeding; yet the mechanism underlying post-partum infecundability, which is triggered by breast-feeding, is undoubtedly physiological.

between births, and birth seasonality. Bongaarts (1993: 12) indicated that the total fertility rate for a 'typical traditional developing country' is only 7 births, compared with a theoretical maximum biological fertility for a woman of 35 births. Indeed, the *Guinness Book of Records* reported one woman having given birth to 69 children from 27 pregnancies (Harrison 1992). What could explain the fact that women who are not contracepting experience far fewer births than this biological maximum? Low fecundity was surely related to poor nutritional status in populations such as rural Gambia and Bangladesh—but then why did poorly nourished women manage to give birth at all (Prentice and Prentice 1988)? It was thought that long intervals between births were related to prolonged lactation, but how long or how intense does breast-feeding have to be? Furthermore, the causes of birth seasonality were poorly under-stood: there were a number of known possible biological and social influences, but which had prime importance?

Competing theoretical models

In Western populations, the observation that menstrual disturbances were preva-lent among thin, dieting, or exercising women had already generated a heated de-bate. Rose Frisch and colleagues had put forward a powerful model, based on Western data, which saw fecundity as being dependent upon critical *thresholds* of weight-for-height (representing fat stores, i.e. energy, that were able to govern the onset of menses and also maintain reproductive function; Frisch and McArthur 1974). It was argued that amenorrhoea is common among athletes, ballet dancers, and slimmers, and could be caused by a loss of 10–15% of body weight, equiva-lent to a loss of about 30% of body fat (Frisch 1982, 1988). This powerful hy-pothesis came in for considerable criticism (see, for example, Bongaarts 1982), and the ensuing debate has been most recently summarized by Peter Ellison (2001). Ellison and his colleagues proposed instead a model of human reproductive function that allowed for a more dynamic and sensitive response to environmental cues (see Ellison 1990). Instead of a threshold model based on critical percentages of body weight or fat, this model proposed a *continuum* of reproductive function, with several grades of reproductive suppression (from fully competent menstrual cycles to frank amenorrhoea, via the suppression of specific sex hormones which lead to ovula-tory failure or failed implantation). The argument was that 'rather than acting as an "off/on switch", ovarian function responds to many ecological, behavioural, and con-stitutional factors in the manner of a "rheostat"' (Ellison, Panter-Brick *et al.* 1994: 2249). These factors include a woman's energy balance, breast-feeding practices and constitutional age, all of which demonstrably affect fecundity variation.

What triggers ovulation failure?

The mechanisms identified in either 'switch' or 'rheostat' models are hormonal. In brief, the cascade of hormonal events that leads to ovulation and egg implantation is controlled by gonadotropin-releasing hormone (GnRH) produced in the hypothalamus of the brain. GnRH stimulates the nearby pituitary gland to release follicle-stimulating hormone (FHS), which promotes the development of eggs inside the ovary, and luteinizing hormone (LH), which helps time an egg's release from the follicle (known as ovulation). Meanwhile in the ovary, the growing follicule secretes the hormone oestrogen, which regulates LH through a feedback loop to the pituitary and helps prepare the uterine lining for possible implantation. After ovulation, the remaining cells in the follicle become the corpus luteum, a gland that secretes progesterone to help maintain the lining of the uterus in preparation for implantation (Figure 1). Thus if GnRH pulses are disrupted, production of FHS and LH hormones may be low and ovulation may fail. If this happens, oestrogen levels will be low in the first 12–15 days of the menstrual cycle (follicular phase), while in the second (luteal) phase of the cycle, progesterone levels will also fail to rise.

What disrupts GnRH is the key question, of course. It could be low energy reserves (measured by body mass index), negative energy balance (weight loss per se), intense exercise (without weight loss), the stimulus of lactation, early immaturity or late senescence, poor fat availability or excess fibre in vegetarian diets, psychosocial stress, or a combination of these. Measures of hormone levels in a population will not tell us the 'why', but they can tell us whether fecundity is suppressed in an individual woman.

Given this background, some questions come to mind regarding the variables that might affect the hormonal control of reproduction in non-Western populations. Does 'exercise' affect the reproductive ability of women who assume heavy workloads in subsistence? Is 'dieting' comparable to energy restriction during seasonal food shortages? And what about the impact of long periods of lactation? It was a methodological breakthrough, namely the ability to assay hormones from minute saliva and blood samples, which opened up the field of reproductive ecology to anthropologists working with remote populations. Figure 2 shows a Nepali woman dropping a 2.5 ml saliva sample in a collection tube, which I then sent to Ellison's laboratory at Harvard University for assay of reproductive hormones.

*Himalayan Populations*

In many ways, Nepal provides an extraordinary opportunity for research in reproductive ecology. There is a stark contrast between seasons, which affects patterns of energy expenditure and dietary intake, making it possible to study the same in-
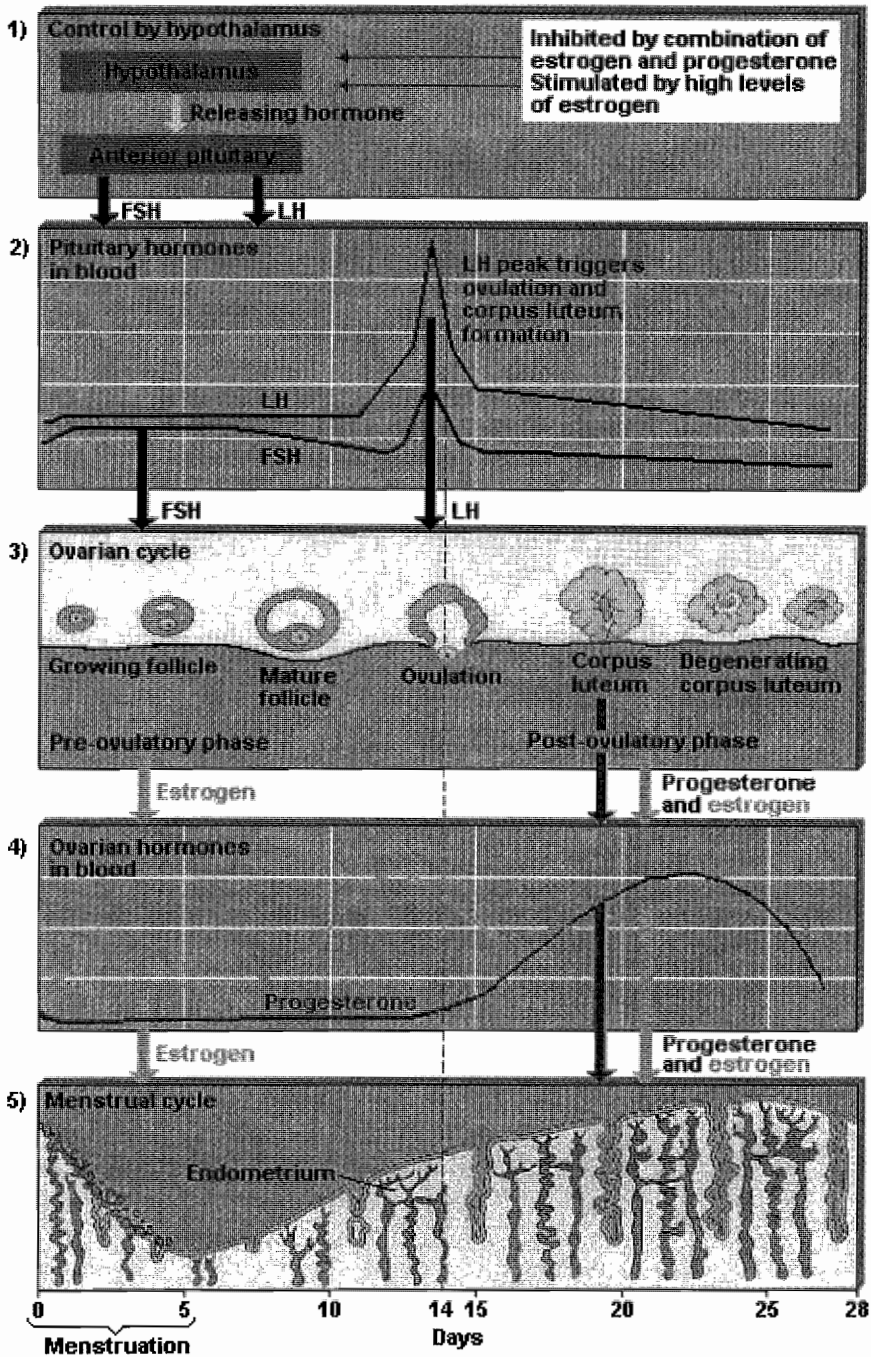
FIG. 1. *A schema of the major events associated with the menstrual cycle* (from http://www.people.virginia.EDU/~rjh9u/menscyc3.html, accessed 4/02/04); image modified by Robert J. Huskey from Cecie Starr and Beverly McMillan, *Human Biology* (2nd edition, Wadsworth 1997) and reprinted with permission
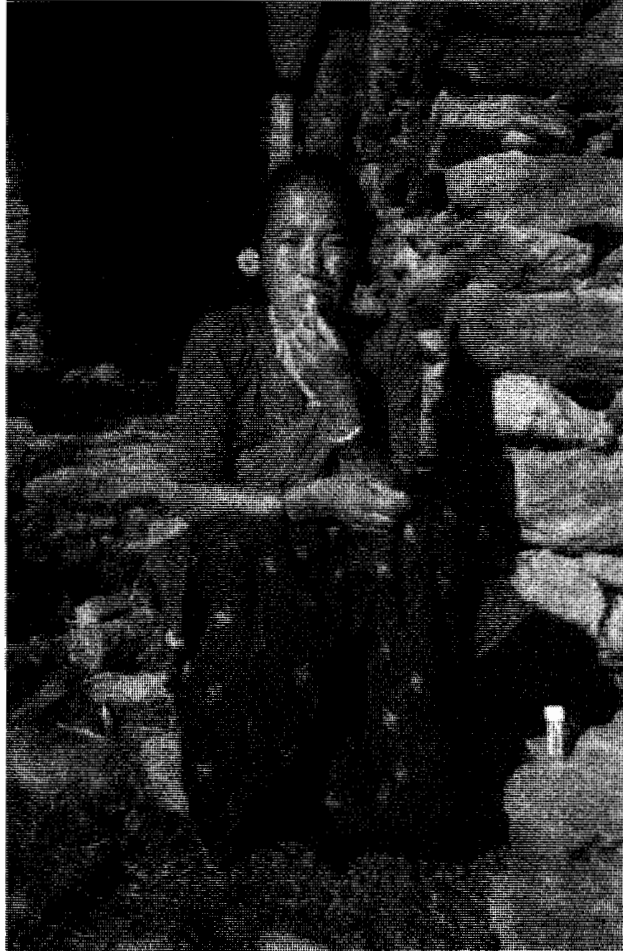
FIG. 2. *Nepali woman donating a saliva sample for this hormonal study*

dividuals under different circumstances, each person acting as their own control. There are a number of caste/ethnic groups, culturally distinct yet co-existing in a given location, and exhibiting radically different reproductive histories. And as elsewhere, men and women differ in subsistence responsibilities, reproductive commitments, and constitutional characteristics. Such variability by season, caste/ethnic group, and sex offers research opportunities for investigating how reproduction varies with ecology, behaviour, and biology.

Caste/ethnic contrasts

My original fieldwork focused on two populations, who live in the same village in the foothills of the Himalaya (1870 metres) in Nuwakot District, central Nepal, in an area without roads or electricity. The Tamang population are agro-pastoralists of Tibeto-Burmese descent, while the Kami group are blacksmiths, a low-caste of Indo-Aryan descent, who recently migrated into the foothills. The Tamang and Kami groups differ dramatically in their socio-economic and cultural profiles. Among the Tamang, men and women work in subsistence responsibilities (agriculture, husbandry, forest work), exploiting a very large mountainside for land, pasture, and forest resources. Because of this diversified resource base, the work of Tamang women is absolutely essential for household subsistence: even while they are pregnant and lactating, mothers successfully combine productive and reproductive responsibilities, carrying young children with them to meet their multiple work requirements. Traditional Tamang society is fundamentally egalitarian, committed to relationships of reciprocal exchange (Fricke 1986) and work schedules characterized by a lack of a rigid sexual division of labour. By contrast, among the Kami, the men work in the smithy supplying the Tamang with agricultural and household implements, and the economic responsibilities of the women (looking after a few plots or animals) are very much secondary. Kami women are less mobile, and the expression of their social status is to remain at home with the children. In essence, the Tamang woman is valued for her work, whereas the Kami woman is first and foremost a wife and mother (Acharya and Bennett 1981; Panter-Brick 1992a).

The demographic profiles of the two groups are also contrasted (Table 1). The completed fertility rate for women over 45 years of age is much lower for the Tamang, whose intervals between births average more than 3 years, and who breast-feed for about 3 years. Post-partum amenorrhoea (estimated from data on the resumption of menses after birth) is on average 9 months longer for the Tamang. In matters of reproduction and sexual activity, Tamang women exercise more autonomy than the Kami: they are able to marry late, to divorce and remarry, and to return to their parent's home for long periods of time. Their lower fertility and longer birth intervals relative to Kami women could well be explained in terms of more intense workloads and prolonged lactation, but also in terms of frequent spousal separation.

TABLE 1. Demographic characteristics of two caste/ethnic groups in the village under study in Nepal (based on fieldwork in 1982–83)

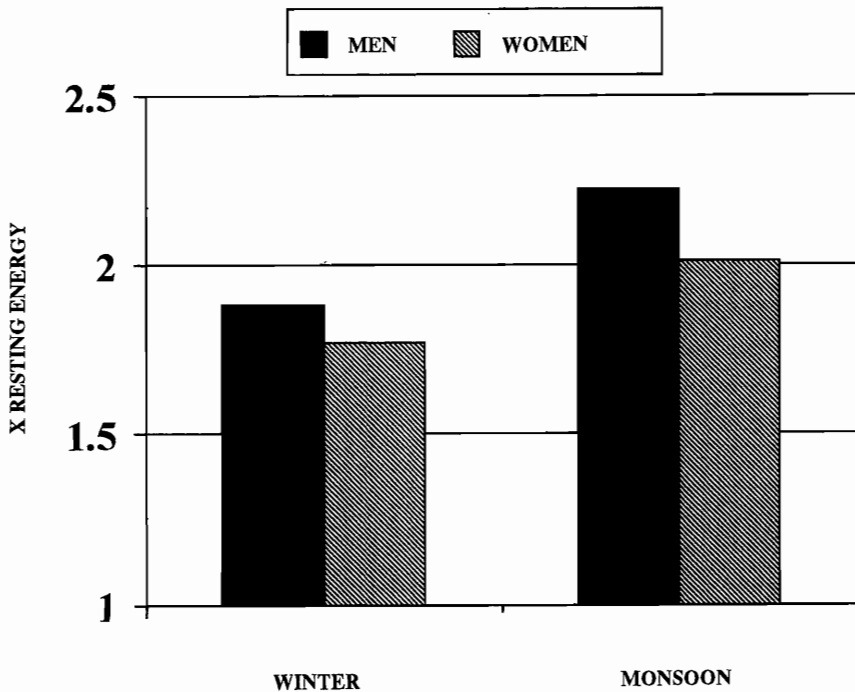|  | Tamang agro-pastoralists Mean | Kami blacksmiths Mean |
|---|---|---|
| Completed Fertility Rate (births) | 5.6 | 7.9 |
| Birth interval (months) | 37.7 | 29.4 |
| Length of lactation (months) | 35 | 25 |
| Post-partum amennorhea (months) | 18.9 | 10.2 |



FIG. 3. *Physical activity levels for men and women in Nepal, in two seasons of the year (expressed as multiples of resting energy). These are moderate in the winter and heavy in the monsoon*

Seasonality

The workloads of the Tamang show significant seasonal variation[2] (Figure 3). In the winter, physical activity levels (PAL)[3] were moderate for both Tamang men
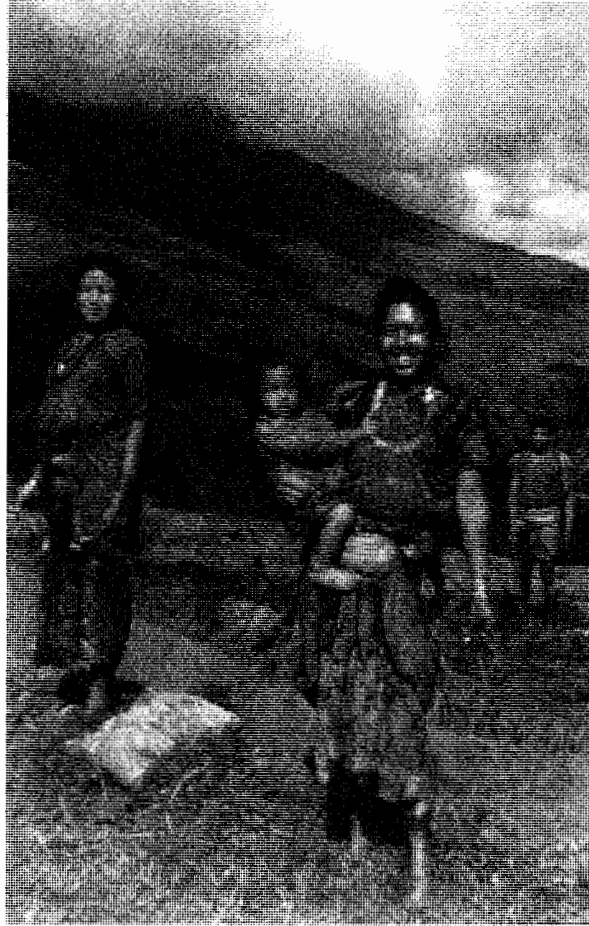


FIG. 4. *Work of Tamang women in the monsoon: transplanting finger-millet*

[2] Workloads were measured from the direct observation of daily activities (entailing over 3600 hours of direct minute-by-minute observation, 6.00 a.m. to 7.00 p.m., throughout one calendar year in 1982–83) and estimates of energy expenditure (measured by oxygen uptake in specific tasks).

[3] Physical activity levels (PAL, measured as 24-hr energy expenditure) are best expressed as multiples of resting energy, to enable comparisons across men and women of different body sizes. By international conventions, a PAL of 1.55 times resting energy corresponds to a light workload, say that of a clerk; a PAL of 1.7 is moderate, and one above 1.8 is heavy.

and women. In the monsoon, by contrast, PAL were very heavy: this was the time to plant millet and rice on the many small plots terraced on the mountainside (Figure 4). Interestingly, PAL were no different for pregnant and lactating women relative to non-pregnant, non-lactating women during the monsoon: all women worked equally hard. And because dietary intakes fluctuated with energy expenditure (there was no 'hungry season'), men and women sustained only small losses of body weight from winter to monsoon: 1.5 kg for men and 1 kg for women (3% and 2% of initial body weight).

## *Issue 1: Do heavy workloads affect women's reproductive ability?*

My first task was to measure hormonal variation in relation to seasonal changes in energy balance. To this end, over 3000 saliva samples were collected in both winter and monsoon seasons (in 1990–91) to measure levels of progesterone (for 24 non-pregnant, non-lactating women) and testosterone (for 43 men). Only healthy, normally menstruating women were included in this part of the study, to ascertain how fecundity changed with seasonality (no Kami were recruited, as all were either pregnant or lactating). Women gave one saliva sample every two days, during one menstrual cycle; the hormonal levels were subsequently aligned relative to day 0 of menstrual onset, when data collection stopped.

### Hormonal suppression

Figure 5 shows these progesterone (P) profiles over one menstrual cycle for the 24 healthy, regularly menstruating Tamang women. The P values are significantly suppressed in the monsoon season relative to the winter ($p<0.05$), namely in the season of hard physical work. One would expect a peak progesterone output in the mid-luteal phase of the menstrual cycle (days –9 to –5, retrospectively aligned on day 0, the beginning of menses). In this phase, mean P values fell by 38% from winter to monsoon (from 138 to 85 pmol/l, $p<0.01$). The flat P profiles indicate that many women experienced anovulatory cycles (they menstruated, but did not ovulate). The proportion of ovulatory cycles was 71% in the winter, but only 38% in the monsoon (Panter-Brick, Lotstein *et al.* 1993).

### Associations with weight loss

This hormonal suppression was significantly associated with changes in body weight ($p<0.01$). Most women lost weight in the monsoon: in the weight-loss group, P values were significantly depressed. Other women managed to gain weight: in the weight-gain group, P values show no suppression. Given that body

mass index was no different for these two groups of women, hormonal responses were not dependent on nutritional status per se. Rather, dynamic changes in weight (weight loss following negative energy balance) suppressed reproductive function independently from nutritional status (current energy reserves, or body mass index). Interestingly, the weight loss involved was relatively minor (-1 kg or 2% body weight for the cohort). Changes in fecundity were best understood as 'sensitive' responses to environmental cues, as described by Ellison, Panter-Brick *et al.* (1994).
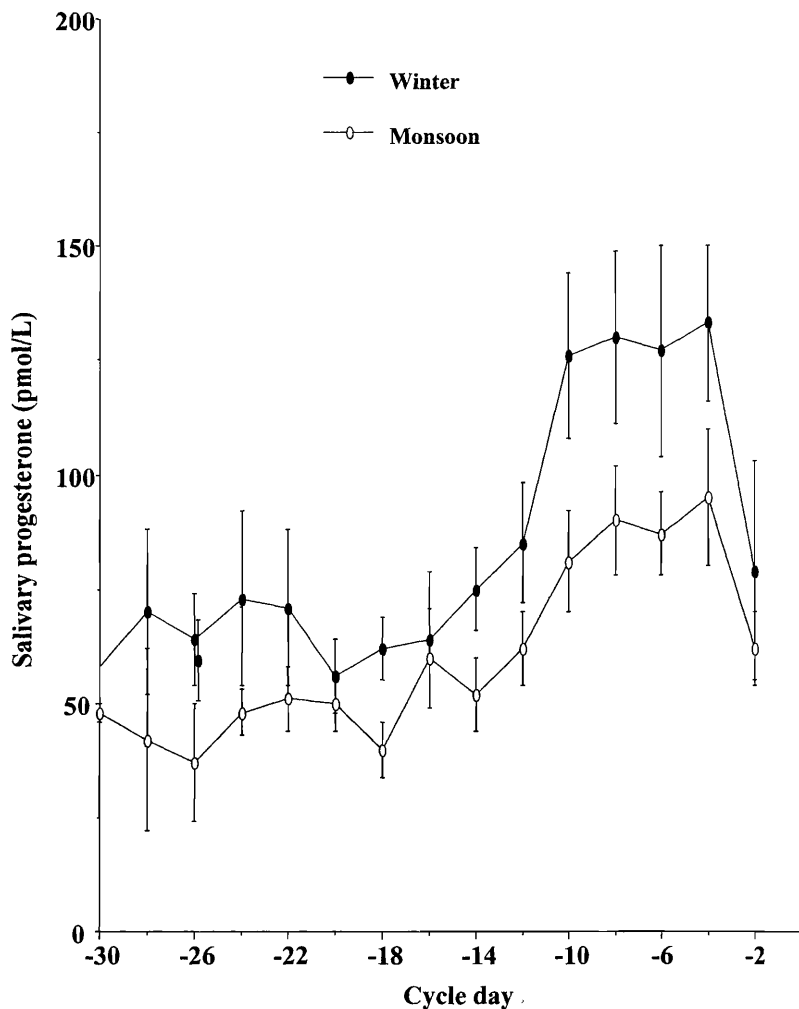
FIG. 5. *Seasonal suppression of progesterone levels (mean values, standard error) in regularly menstruating Tamang women. The flatter profile in the winter season shows increased risk of ovulatory failure (a temporary suppression of fecundity)*

Inter-population comparisons

The progesterone profiles for the Tamang were also considerably lower than other populations sampled by exactly the same methodology. Figure 6 shows data collected for several populations from industrialized and developing countries. Women working in simple farming subsistence economies, such as the Congo (formerly Zaire) and Nepal, have significantly lower progesterone profile than affluent middle-class women in the USA. Intermediate profiles are shown for the Quechua of highland Bolivia (who have light workloads and limited food intake) and rural Polish farm workers (who average heavy workloads with unconstrained food supply). These data are evaluated in greater depth in Panter-Brick and Pollard (1999: 147–52). The fact that levels of progesterone vary across populations has notable implications for understanding the population-specific riskes of cancer and appropriate dosages of hormonal contraceptives (Ellison 1999, Vitzthum *et al.* 2002).
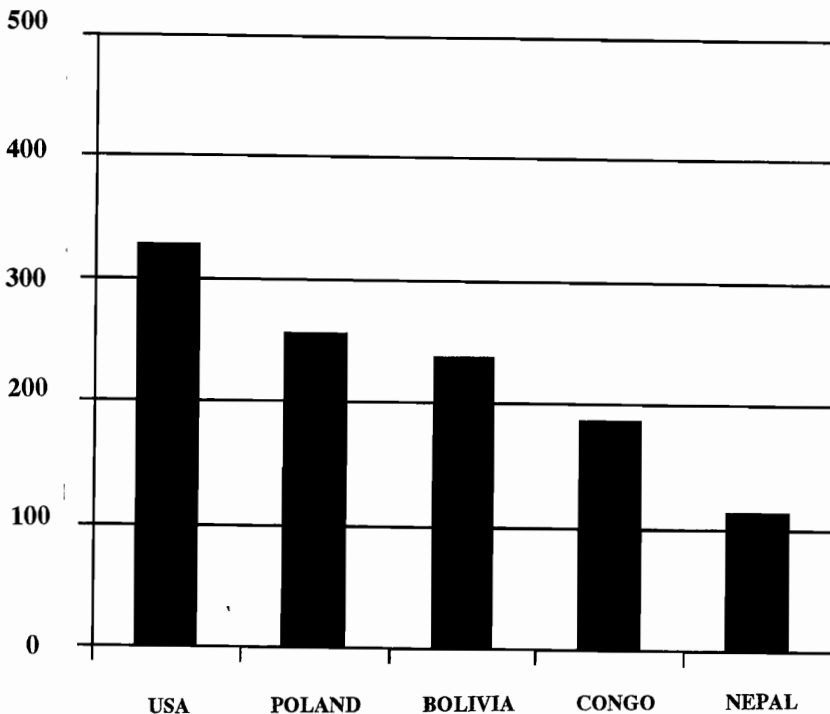


FIG. 6. *Population differences in progesterone values (luteal phase) reflecting variation in reproductive ability*

*Issue 2: Does temporary infecundity matter for actual fertility?*

To what extent does temporary infecundity matter for actual fertility? In other words, does seasonal infecundability in the monsoon explain the birth seasonality observed for the Tamang population? Which of the biological and cultural variables explain most of the variation in actual fertility, as reflected in the monthly distribution of births or conceptions?

Figure 7 shows the monthly conception rates for Tamang women exposed to the risk of pregnancy, using a life-table analysis for 1,829 live births, and focusing on a cohort who gave birth in the most recent five-year period (Panter-Brick 1996). There are two troughs of conception, one in mid-winter (month 2, February) and one in mid-monsoon (month 8, August). The magnitude of seasonal variation (98% for the peak of conception in July relative to February) is just below that reported for the Matlab area of Bangladesh (130%). It is worth emphasizing that the Tamang could accurately report birth dates in years and months (relative to the
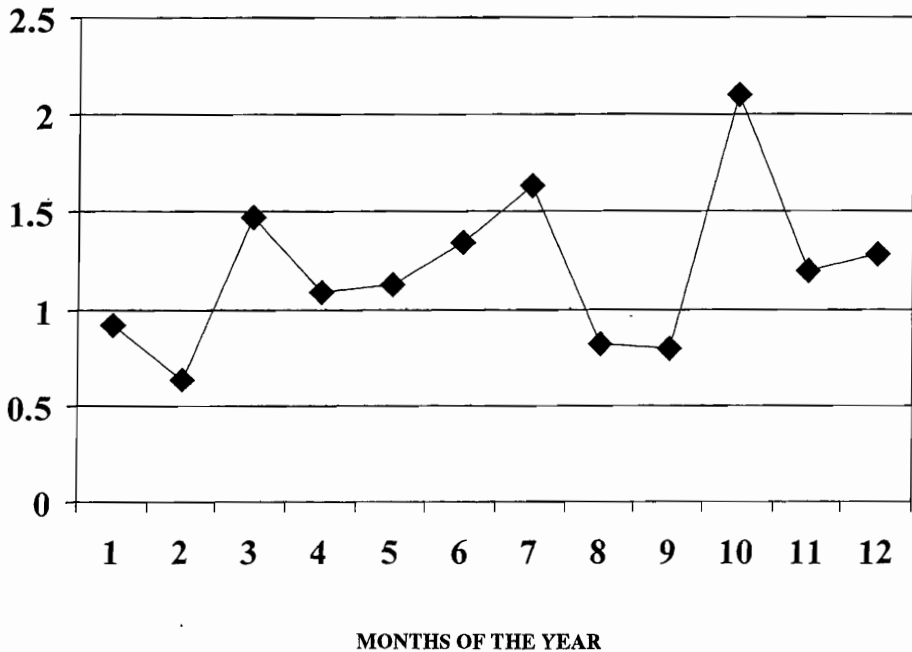


MONTHS OF THE YEAR

FIG. 7. *Monthly conception rates for women at risk of pregnancy*

Hindu and Tibetan calendar), as it is unusual for a non-literate population to remember births in such detail.

The first trough is unlikely to result from biological variation in fecundity, since maximum body weight is gained in the winter. A more likely explanation is

the out-migration of men for wage labour, albeit limited in the population. By contrast, the second trough is consistent with hormonal data indicating suppressed ovarian function, triggered by weight loss and intense agricultural workloads in August.[4] As for the peaks of conception (months 7 and 10), they can tentatively be assigned to behavioural variables that affect the frequency of intercourse, because there is no evidence for underlying biological variation.

There can be no simple, single explanation for birth seasonality. However, this study does suggest that the mid-winter trough is likely to be associated with behavioural variables, such as the separation of spouses (e.g. to meet work responsibilities), while the monsoon trough is likely to reflect biological variables, namely a temporary suppression of fecundity.

## Issue 3: Do men show a different sensitivity to ecological constraints?

The Nepal fieldwork also illustrated a stark contrast between men and women. Let us recall that Tamang men assumed higher workloads, similar seasonality and larger weight losses than women. However, assays of their saliva samples indicated no detectable impact of seasonality on male testosterone levels. In contrast to women, men follow different cues tracking environment, biology or behaviour when it comes to modulating their reproductive function. Male reproduction is less sensitive to moderate energy stress compared to female reproduction, where producing the actual baby is relatively energetically expensive. It would pay for women to be responsive to energetic conditions in order to maximize the probability of a successful outcome (Ellison and Panter-Brick 1996; Panter-Brick and Pollard 1999). What accounts for population variation in men's testosterone levels, however, is still a matter for debate (ibid.: 152; Bribiescas 2001).

## Issue 4: To what extent do differences in nursing schedules affect fecundity?

Finally, the field study attempted to sort out some of the possible reasons why the Tamang and Kami caste groups showed such a stark contrast in demographic characteristics (Table 1). Here the focus of attention was on the duration of breast-feeding and post-partum amenorrhoea, with complementary information on day-to-day nursing intensity and food supplementation. Hormonal data were sought, this time from blood spots to determine the hormone prolactin (after a protocol devised by Carol Worthman of Emory University). I recruited both Tamang

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[4] It cannot be an artefact of the peak of conceptions in July (life-table analysis considers only women exposed to actual risk to pregnancy, removing them from consideration for the period of pregnancy and post-partum amenorrhoea).

and Kami lactating women (while saliva sampling had raised no difficulty, it took some convincing to make finger-prick blood samples acceptable).

Nursing and hormonal responses

Prolactin is the hormone that helps a woman produce more milk, and is triggered by the frequency of her infant's feeds. It does not cause amenorrhoea, but has been used as a proxy to measure the breast-feeding intensity associated with post-partum amenorrhoea. The study showed that, in the Tamang case, prolactin levels were sustained at high levels, whereas among the Kami, prolactin levels quickly declined after a nursing feed. This is consonant with the observation that Kami women experienced a shorter period of post-partum amenorrhoea: Kami women breast-fed for a shorter period, their hormonal levels indexing the intensity of lactation fell quickly to base line, they resumed full reproductive function more quickly after birth, and they became pregnant again relatively sooner. Interestingly, the differences in nursing behaviour are related to differences in the cultural and socio-economic characteristics of these communities: Kami housewives, who are less mobile than Tamang women engaged in agro-pastoral tasks on the mountainside, have more opportunity to provide children with supplementary foods cooked at home (Panter-Brick 1991, 1992b, 1993).

Current literature shows, however, that nursing schedules alone cannot explain the duration of post-partum amenorrhoea. To give two examples, the Amele of lowland Papua New Guinea and the Toba of Argentina breast-feed very intensively, yet resume menses quickly after birth. One hypothesis under investigation is that intensive lactation fails to suppress fecundity because these women show very good nutritional status, such that frequent nursing does not represent for them a significant energy drain or metabolic load (Ellison 2001: 119; Panter-Brick and Pollard 1999).

Competing hypotheses

The exact mechanisms explaining the contraceptive effects of lactation—linking nursing behavior to suppressed reproductive function—are still being debated in the current literature. There have been two competing hypotheses—the *nursing frequency* hypothesis and *the relative metabolic load* hypothesis—disputing the relative influence of the intensity of nursing schedules versus the intensity of energetic stress in triggering longer periods of post-partum amenorrhoea (Lunn 1996; Ellison 2001: 106–26). Lactation and nutrition/energy have been pitted as social versus biological reasons for explaining temporary changes in fecundity or reproductive ability. In truth, they are not mutually exclusive.

## Conclusions

At least in principle, it is possible for research to distinguish between the biological and social variables that influence birth rates. For studies of birth seasonality in a given population, this should help us move beyond the dangers of 'ecological fallacy', whereby birth rates are simply correlated with a myriad of different variables without a strict causal basis. As Wood (1994: 534) noted, 'everything varies seasonally (temperature, rainfall, hormones). Some of these variables may have direct causal links to birth seasonality, but many do not'. If only for conceptual clarity, it is fruitful to tease apart which are the most important variables among those that govern fertility (the proximate determinants).

The 'social' and 'biological' perspectives on reproduction are often treated as if they are polarised. Yet in reality they intersect. For instance, explanations for post-partum amenorrhoea may favour lactation, a socio-cultural behaviour with physiological consequences, or nutritional status, a biological variable where socio-cultural and economic context has prime importance. Ellison (2002: 123) recently noted, 'there has been something very comforting to social scientists in the notion that human fertility is, pathology aside, simply a function of human behavior'. Yet it is evident that even natural fertility in non-contracepting populations is not just a function of behaviour: it is also a function of biology responding to changing cues from the environment. The challenge is to find how behaviour intersects with biology in producing observed variation in human fertility.

Hormonal data have been obtained for different populations world-wide, but they do not tell a single story: women and their babies may spontaneously adopt very different nursing schedules, which are superimposed on different levels of energetic stress arising through workload and diet. What is emerging is a fuller picture of the relationships between human behaviour, human biology, and human ecology, which affords much scope for refining models of fecundity and fertility variation.

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