
NATURAL VARIATION
IN HUMAN FECUNDITY

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Thomas Malthus has a secure place in the history of ideas. He sowed the seeds of the modern theory of evolution by natural selection in the minds of Charles Darwin and Alfred Wallace while at the same time helping to lay the foundations of the modern fields of demography, ecology, and political economics. Yet the same ideas that proved so inspiring also carried with them certain unrecognized, or at least unchallenged, assumptions which became firmly embedded in the way most scholars thought about human reproduction for the next two hundred years. Malthus's great contribution was the understanding that population growth tends to be exponential, that the number of people added to a population in a unit of time is a function of the number of people already in the population. At the same time he knew that population growth was the net result of two demographic processes: birth and death. Realizing that exponential growth cannot continue indefinitely, or even for very long, without outstripping necessary resources, he reasoned that some change in demographic dynamics must eventually limit the growth of any population. At this point he introduced a great dichotomy into Western thought, a dichotomy that has persisted to the present day, though current research is now calling it into question.

The dichotomy was embodied in the assertion that "natural" checks to population growth would occur through increases in mortality rates (e.g., via plagues, pestilence, famine, and war), while decreases in fertility would have to be the result of "moral restraint," or the action of social forces (e.g., marriage rules, religious prescriptions, sexual taboos, and individual abstinence). No evidence was required for this assertion; the superprolific nature of socially unrestrained human fertility was considered to be self-evident and without significant variation—certainly without any relationship to population size or resource abundance that might constitute a natural check on population growth.¹

The Malthusian assumption that significant variation in human fertility is socially, not biologically, determined has persisted to the present day, and not without reason. Certainly the dramatic decline in fertility rates that has occurred in conjunction with the rise of modern industrial economies in the West and that is occurring with increasing frequency throughout the developing world is a consequence of changing social forces molding individual reproductive behavior. Physiology has little, if anything, to do with it. Our hope for stabilizing the world population within the next century similarly lies clearly within the domain of moral restraint. Yet the degree of social control of human fertility that we

currently experience is a relatively recent phenomenon, and the unquestioning acceptance of Malthus's assumption may have blinded us to an understanding of the ways in which human fecundity (the biological *capacity* to bear offspring, as opposed to fertility, or the *fact* of having borne children) may also be subject to natural variation. Such natural variation in fecundity may have been an important part of our ecology in the distant and not so distant past, and may continue to influence patterns of fertility in the developing world today.

LOUIS HENRY AND THE IDEA OF VARIATION IN NATURAL FERTILITY

The first challenge to the Malthusian assumption came from the pen of French demographer Louis Henry in the middle of this century.² At that time considerable effort was focused on understanding the social causes of variation in human fertility in order to better “engineer” a rapid transition to lower fertility levels in the developing world. In a particularly influential article Kingsley Davis and Judith Blake identified two major determinants of fertility variation that were clearly within the social domain: marriage patterns (including ages at marriage, percent of women ever married, and rates of widowhood, divorce, and remarriage) and contraceptive use.³ Henry was interested in something else, however—the phenomenon he termed “natural fertility,” or fertility that showed no evidence of conscious efforts to limit family size. He could recognize such a fertility pattern in a population empirically when the probability of a woman having an additional child was largely independent of the number of children already born, also called *parity*. In such natural fertility populations the probability of having yet another child declines steadily with increasing parity, but without any abrupt drop. In contrast, Henry introduced the term “controlled fertility” to describe populations in which the probability of having another child drops precipitously after a target family size is reached. Henry collected data on populations that displayed the natural fertility pattern, considering only the fertility of married women, and made two quite surprising observations.

First, there was a great deal of variation in the level of fertility

that such populations displayed. The Malthusian assumption predicted that unrestrained human fertility would be high and relatively invariant near the maximum physiologically attainable. Yet Henry's populations varied in the number of children born to premenopausal women by nearly 100 percent from lowest to highest, a range that has only been increased by subsequent research. This variation was not a consequence of differences in marriage rates, since the comparison was only of married women. Nor was it a consequence of conscious family limitation, since fertility in all the populations was only weakly dependent on parity. Henry reasoned that the difference must lie in factors determining the average length of the time interval separating successive births. After considering and rejecting various possibilities, Henry suggested that variation in the effectiveness of lactation as a natural suppressor of ovulation might underlie the observed variation in levels of natural fertility between populations. He also explicitly noted that such a mechanism would be inherently physiological.

Henry's second observation was that the age pattern of female fertility was remarkably constant across different natural fertility populations, despite differences in the overall level of fertility. Fertility rates tended to rise until the mid-twenties and then to fall, slowly at first, more rapidly after age forty, until further offspring production ceased in all populations around age fifty. Not only did all populations show the same general parabolic rise and fall with age, the rate of change with age was proportionally very similar in all populations. This constant age pattern also seemed to Henry suggestive of physiological rather than sociological variation, though the mechanisms were more obscure.

Henry was careful not to confuse his definition of natural fertility with fecundity. It is quite possible, according to his definition, for couples in a natural fertility population to consciously manipulate their fertility, or even to use modern contraception, as long as they do so only to control the timing of their births, and not the number. Yet he clearly felt that the study of natural fertility was a first approach to the empirical study of variation in human fecundity. Far from closing the book, Henry's work opened a new and exciting chapter in our study of our own reproduction, underscoring human fertility as an area where biology and behavior are supremely interactive, and undermining the Malthusian dichotomy that had begun to constrict rather than aid our understanding.

*LACTATION, FECUNDITY,
AND THE "CHOREOGRAPHY"
OF BREASTFEEDING*

The question of the natural variability of human fertility has become a subject of interest to individuals from a broad array of disciplines, including demographers, sociologists, physicians, public health analysts, physiologists, and anthropologists. The interaction of social and biological perspectives in a field that was formerly considered a purely sociological domain has generated both excitement and controversy. Henry's two basic observations about natural fertility patterns continue to motivate current research even as new ideas are developed. Three decades of research have confirmed the fact that variation in the level of fertility between populations that do not practice parity-specific birth control is substantial, greater than the variation between populations that do practice family size limitation. It also remains true that variation in the level of fertility among natural fertility populations is a consequence of variation in inter-birth intervals, not in ages at first or last birth. The remarkable consistency in the age pattern of natural fertility, despite differences in level of fertility, has also been confirmed. The phenomena themselves are not in question, but their causes are. The search for these causes has focused more on the regulation of female reproductive capacity than on male, since female fertility is the primary limiting factor in human reproduction.

Henry suggested that the primary factor regulating birth interval lengths in natural fertility populations might be found by understanding the way breastfeeding delays the resumption of ovulation. It was already clear that women who never nurse their offspring, because of infant mortality or the use of bottles or wet-nurses, resume menstruation much earlier than women who nurse their offspring for any length of time. But among women who do breastfeed, the variation in timing of the resumption of cyclic ovarian function, as evidenced by the return of menstruation, is immense and not easily comprehensible. Some nursing women, Henry noted, resume menstruating right away, some only after a considerable time but before they wean their children, and others only after weaning. Since the practice of breastfeeding is prevalent

in most natural fertility populations, Henry suggested that we would go a long way toward understanding natural variation in interbirth intervals if we could understand why women fell into one or another of these categories.⁴

A breakthrough in unraveling this problem came from studies of the physiology of lactation. The hormone prolactin, which bears major responsibility for the maintenance of milk production in a lactating woman, was shown to respond episodically to each nursing event. Each time the baby begins nursing at its mother's breast, prolactin levels rise dramatically in the mother's blood. As soon as the baby stops nursing, prolactin levels begin a slower, exponential decline.⁵ Physiologically, this mechanism helps to regulate milk "supply" according to "demand": The frequency of the signal promoting milk production depends on the actual pattern of feeding. As the baby becomes less dependent on its mother's milk, the production of milk will taper off. However, because it was suspected that prolactin might also act to inhibit ovarian function, the same mechanism might work to regulate the return of female fecundity. The key variable, if this hypothesis were true, would not be the fact of breastfeeding, or even the total amount of time spent nursing in a day, but the *frequency* of nursing. Short episodes of nursing spread throughout the day at frequent intervals would result in higher average levels of prolactin than a few long, widely-separated episodes, such as the half-hour sessions at four hour intervals often recommended by American doctors of Dr. Benjamin Spock's generation.

Field studies of natural fertility populations began to confirm this hypothesis. Belgian workers in Zaire found that prolactin levels remained higher in women who reported nursing more frequently than in women who reported nursing less frequently throughout the first postpartum year, and that the less frequent nursers were more likely to resume menstruation in that time.⁶ Anthropologists Melvin Konner and Carol Worthman reported that !Kung San hunter-gatherers of Botswana continued to nurse their children at very high frequency for two to four years after birth, and that levels of ovarian steroid hormones indicative of ovarian function were more strongly correlated with nursing frequency than with infant's age.⁷ Evidence appeared to support the idea that the solution to Henry's problem lay in the temporal patterning of nursing behavior, the choreography of this most intimate relationship between mother and child.

The choreography of breastfeeding shows clearly the close relationship of social and biological influences regulating human

fertility. The mechanisms linking the frequency of suckling to the suppression of the mother's reproductive system are strictly physiological, the result of millions of years of evolution shaping this peculiarly mammalian pattern of maternal investment in offspring. The factors affecting the frequency of suckling itself, however, are largely social, and reflect the multiple constraints and demands that human mothers face. Anthropologist Catherine Panter-Brick has argued compellingly, on the basis of her studies of the Tamang of highland Nepal, that breastfeeding choreography is often structured more by opportunity than by demand. In the case of the Tamang, opportunity may be constrained by the mother's necessary participation in subsistence activities, such as transplanting rice, that separate her from her children for long stretches of time.⁸ Sara Nerlove reached a similar conclusion in a cross-cultural study of eighty-three societies, finding that supplemental foods are introduced into infants' diets at earlier ages in societies where women are heavily involved in subsistence work.⁹ Social attitudes and conventions about the "right" way to raise children, the availability of appropriate supplemental foods and alternative caretakers, competing demands on the mother's time and energy, and the advice of "experts" and friends can all influence the breastfeeding behavior of individual women and the typical patterns in individual societies. All of these social and environmental factors, acting through the agency of nursing frequency, could contribute to the variation in interbirth intervals observed among natural fertility populations. Indeed, data collected from a broad array of populations throughout the world indicate a strong correlation between the average duration of breastfeeding in a population and the average interbirth interval.¹⁰

Yet as compelling as this relationship between breastfeeding and interbirth intervals may be, it cannot be the whole story. Certain aspects of the relationship have been questioned in recent years. For example, it no longer seems that prolactin is directly involved in the suppression of ovarian function. Nor has the frequency of nursing always been found to correlate strongly with the duration of amenorrhea (absence of menstruation) either between individuals within a given population or between populations. Part of the answer to Henry's original question—why do some nursing women resume menstruation early and others late?—seems to involve variation in the temporal choreography of breastfeeding, but part of the answer may lie elsewhere, perhaps in the physical condition of the mother herself.¹¹

AGE AND FEMALE FECUNDITY

One important aspect of maternal condition is age. Declining fertility with advancing age, such as Henry described for natural fertility populations, has long been ascribed to a declining frequency of intercourse in older couples, and research on sexual behavior in Western societies has appeared to support this hypothesis. The increase in natural fertility with age among married women under twenty cannot be explained by the same mechanism, and is often either ignored or attributed to "adolescent sterility," a period of physiological sub-fecundity following the onset of menstruation characterized by irregular menstrual cycling. Recent re-evaluations of the data on declining frequency of intercourse with advancing age, however, challenge the idea that this mechanism alone can account for observed patterns of natural fertility decline.¹² Furthermore, even if declining frequency of intercourse were shown to be responsible for the age-related decline in natural fertility, we would still need to explain why age patterns of intercourse should be so consistent between different populations.

Once again, a possible answer to this question has come from the study of reproductive physiology. Until recently, the fact that menstrual patterns show little variation with age between the very earliest and very latest years of a woman's reproductive career was taken as evidence that her underlying pattern of fecundity was also quite constant. This notion crumbled when contrary evidence was presented from the realm of infertility research. Success in establishing pregnancies in women undergoing artificial insemination with donor semen (because their husbands had been found to be unable to produce viable sperm) has been shown to be strongly affected by a woman's age, with rates that begin to decline as early as age thirty.¹³ Subsequent studies provided evidence of similar age dependency in success rates of *in vitro* fertilization, ovulation induction, and ovum donation.¹⁴ The popular press quickly picked up on these reports and spread the notion of a "biological clock" within each woman determining her fecundity. The poignancy of this issue for women who might have delayed childbearing in order to pursue careers has been widely recognized and has given rise to numerous editorials in both newspapers and medical journals.

Investigating the causes of age-related declines in female fecundity requires sophisticated methods for monitoring a

woman's reproductive system. Many of these methods are highly invasive, uncomfortable, expensive, and difficult to perform outside of a hospital or clinical setting. One method that can shed some light on the issue and that avoids many of these drawbacks is the monitoring of ovarian steroid hormone levels in samples of saliva. Saliva samples can be collected easily and painlessly, can be collected by women themselves at home on a regular basis, and can be collected even under remote field conditions. The steroid hormones that can be measured in saliva provide important information on aspects of a woman's reproductive system that are crucial to her fecundity, including the maturation of the egg, the release of the egg at mid-cycle, the preparation of the uterus for the possible implantation of an embryo, and the support for the early stages of pregnancy if it occurs. For these reasons my colleagues and I have relied heavily on this method for more than a decade in our own studies of variation in female fecundity.¹⁵

Using salivary steroid measurements, we have been able to show that female ovarian function varies significantly with age, even in women who are menstruating regularly. Hormonal indices of ovarian function in regularly menstruating Boston women increase steadily with age until the mid-twenties, a decade or more after the onset of menstruation, and begin to decline by the early thirties, more than a decade in advance of menopause. This parabolic trajectory roughly parallels the trajectory of natural fertility observed by Henry, as well as the trajectory of declining female fecundity uncovered in infertility research.¹⁶

When the same methods are used to investigate age patterns of ovarian function in quite different populations, such as the Lese of Zaire's Ituri Forest and the Tamang of Nepal, the results are strongly reminiscent of Henry's original observations. The Lese are slash-and-burn horticulturalists who grow subsistence crops of cassava, dry rice, maize, and peanuts, supplemented with meat from wild game, much of which is acquired in trade with Efe pygmies.¹⁷ The Tamang are agro-pastoralists who grow wet rice, maize, millet, wheat, and barley, and tend mixed flocks of buffalo, oxen, cows, sheep, and goats at different elevations on the slopes of the Himalayas.¹⁸ Women in Zaire and Nepal show parabolic patterns of age variation in ovarian function virtually parallel to each other and to the patterns in Boston, but the average levels of ovarian function at any age differ significantly between the three populations. Salivary progesterone levels in Boston, for example, average 100 to 150 pmol/L higher than those in Zaire at all ages, while

levels in Zaire are 50 to 70 pmol/L higher than those in Nepal. The overall picture of age-patterns of ovarian function that are similar in shape but different in level is very reminiscent of Henry's original observation of a consistent age pattern to natural fertility, despite differences in level between populations.¹⁹

The factors contributing to age variation in female fecundity are likely to be multiple, but the age pattern of ovarian function, at least, appears to be a common feature of human reproductive biology, similar even in populations widely separated by geography, culture, and ecology. Unlike the variation in female fecundity associated with lactation, the variation in fecundity associated with age appears to be mediated by biology alone, providing a foundation on which other sources of variation, both social and biological, are elaborated. Some evidence suggests, for example, that lactational suppression of ovarian function may last longer in older women, even when their pattern of nursing is the same as that of younger women.²⁰ Interactions of this kind between different variables affecting natural fertility, such as age and lactation, constitute an important domain of future research.

ENERGETICS AND FEMALE FECUNDITY

Along with age, nutritional status is also a potentially important aspect of maternal condition that might affect fecundity. Reproduction requires a substantial investment of metabolic energy on a woman's part, and natural selection may have molded her reproductive physiology to be sensitive to her potential for successfully making that investment. Rose Frisch and her colleagues first drew attention to this possibility by noting that girls are unlikely to begin menstruating and that adult women often stop menstruating if they are excessively lean.²¹ Women athletes, especially those engaged in endurance sports, have also been found to be amenorrheic more often than the general population.²²

Once again, the ability to monitor ovarian function directly, rather than relying on indirect evidence such as the occurrence or regularity of menstruation, has provided additional insight into the relationship of energetic stress and female fecundity. Hormonal indices of ovarian function have been observed to decline in

American and German women who voluntarily lose only moderate amounts of weight by dieting, even when their weights remain in the normal range for their heights.²³ Similarly, women who jog for recreation have been found to have lower ovarian steroid levels than otherwise comparable but inactive women, even though their weights are well within the normal range.²⁴ In all these cases, menstrual patterns remain unchanged.

It is tempting to extrapolate from these results on exercise and dieting, athletes and anorexics, to the sorts of energetic stresses that women in traditional societies face, or that women might have faced regularly throughout our evolutionary past. Some have suggested, for example, that the long distances that hunter-gatherer women may travel in foraging for food could constitute an energetic stress similar to that faced by track and field athletes.²⁵ Hypotheses based on analogy alone are unsatisfactory, however. Evidence to support the idea that energetic stresses which arise from subsistence ecology, rather than from self-imposed regimes of exercise or diet, could affect ovarian function had to come from field studies of human populations.

Several such studies have now confirmed the fact that energy balance, the net of energy intake and energy expenditure, does affect ovarian function in a variety of populations. The Lese of Zaire show seasonal changes in ovarian function that parallel seasonal weight losses caused by regular food shortages. Conceptions are also less frequent during these periods of suppressed ovarian function.²⁶ Among the Tamang of Nepal, some women lose weight during the hard agricultural work of the monsoon season while others do not. Those who lose weight show lower indices of ovarian function than those who maintain or gain weight.²⁷ The Turkana of northern Kenya have also been studied in this regard by Michael Little, Paul Leslie, and their colleagues. The Turkana traditionally have relied on pastoral nomadism for their subsistence, maintaining herds of cattle in the arid regions of Kenya's northwestern plateau. In recent years some Turkana have turned to a settled, agricultural lifestyle. Settled Turkana have higher body weights for their heights and other indicators of lower energetic stress than nomadic Turkana. They also have hormonal patterns indicative of higher levels of ovarian function.²⁸

Interactions of nutritional status, energetic stress, and lactational suppression of ovarian function have also been reported. Peter Lunn, of the Dunn Nutrition Unit of the Medical Research Council of the UK, and colleagues have studied the effect of nutri-

tional supplements on the reproductive biology of women living by traditional agriculture in the Gambia. Baseline data revealed that the Gambian women were both chronically and seasonally undernourished. Caloric intake was below recommended levels even in the best of times, while seasonal food shortages resulted in regular periods of weight loss. Women in the study received substantial nutritional supplements during pregnancy and lactation, increasing their daily caloric intake by a quarter to a third. Birth weights were slightly increased, maternal weights and weight gains largely unaffected, and milk production unaltered by the supplements. However, average prolactin levels declined more quickly, menses resumed sooner, and birth intervals were shorter when women received the supplements than when they did not.²⁹

Like the age pattern of ovarian function, the responsiveness of ovarian function to energetic stress seems to be a general feature of human reproductive biology. A decline in hormonal indices of female fecundity can be observed under conditions of relative energetic stress in a wide range of populations differing dramatically in culture, ecology, and geography. The responses evoked by unavoidable ecological conditions are directly comparable to those evoked by voluntary behaviors. The responses are so consistent, and so graded in degree, that they are unlikely to be pathological. That is, the response of ovarian function to energetic stresses does not seem to indicate a system failing or breaking down with abrupt loss of function, but rather a system undergoing progressive adjustments to varying conditions. This responsiveness seems rather to be a beneficial aspect of the healthy functioning of the female reproductive system as will be discussed later.

ECOLOGY AND MALE REPRODUCTION

As noted earlier, most efforts to better understand natural variation in human fertility have focused on females, for the simple reason that the capacity of females to bear offspring is ultimately limiting on the fertility of any population. Yet it seems reasonable to ask whether male reproductive biology shows any of the same patterns of natural variation as described for females, or any unique patterns that might contribute to natural variation in human fertility.

Male testicular function shows evidence of progressive decreases with age, though studies differ as to the age at which this decline is first apparent. Certainly there is no evidence of an abrupt cessation of male testicular function in mid-life comparable to female menopause.³⁰ At least one study, among the Gainj of Papua New Guinea, a remote group of subsistence horticulturalists, indicates an earlier average onset of male reproductive senescence than normally observed in Western populations.³¹ It is not clear, however, whether this represents an atypical and possibly pathological variation, or whether male reproductive aging is generally more variable than female.

Males in several traditional societies, including the !Kung San of Botswana and Namibia, the Lese of Zaire, and the Turkana of Kenya, have been found to have lower levels of the testicular steroid testosterone than males in the United States and Europe, but the reasons for this difference are unclear.³² Extreme energetic stress, such as the starvation produced by dramatic famines or conditions of war, clearly decreases testicular function in males and can totally disrupt sperm production. But Lese males in Zaire and Tamang males in Nepal do not show an acute testicular responsiveness to energetic stress comparable to the ovarian response of females.³³ Chronic energetic stress, however, might still be responsible for chronic differences in testicular function between populations.

High environmental temperatures have also been suggested as having an adverse affect on sperm production in some populations. Seasonal variations in temperature have been associated with seasonal variations in the quantity and quality of sperm produced by men who work outside in hot climates, such as in New Orleans and San Antonio. Observations of comparable variations in the sperm production of men working in air-conditioned situations, however, have cast doubt on temperature as the important factor.³⁴

Interpretation of the evidence for variation in male reproductive function is complicated further by the lack of a clear relationship between those indicators that can be measured and male fecundity. For example, levels of hormones such as testosterone are at best only weakly correlated with sperm production. Sperm production in turn may be only weakly correlated with the ability to impregnate a fecund woman, as long as sperm counts are above some relatively low threshold.³⁵ In general, although there is evidence that male testicular function may vary, there is little evi-

dence for consistent patterns of natural variation that might contribute to patterns of natural variation in fertility among human populations.

THE ECOLOGY OF HUMAN REPRODUCTION

Contrary to Malthus's assumption, the results of current research, both in the clinic and in the field, indicate that many aspects of human fecundity show evidence of significant natural variability. Female ovarian function in particular appears to vary in response to age, lactation, and other energetic stresses. Rather than simply setting a biological maximum for the production of offspring with actual fertility being shaped by social constraints, natural variation in human fecundity appears to provide the foundation upon which the social regulation of fertility is elaborated. Many important features of achieved fertility patterns are the product of sociological and individual psychological factors, but others reflect variation in the underlying patterns of biological fecundity.

The patterns of variation that have been described for female ovarian function do not appear to be pathological. Rather they appear to represent calibrated responses of the organism to its environmental context. It is likely that these responses have been shaped by the action of natural selection in ways that benefit the lifetime reproductive success of the individual organism. For instance, young women characteristically have continuing energetic requirements for their own growth and maturation and greater potential for future reproduction than do older women. Hence natural selection may have molded female physiology to favor relatively more investment in continued growth and survival in young women, and more investment in reproduction in mature women. After a certain point, however, the probable success of new reproductive attempts begins to decline with age, either as a consequence of maternal condition or the quality of the eggs remaining in the ovary. Natural selection may have resulted in declining female fecundity in later reproductive ages as a result.

The reproductive response to varying energetic conditions may also be adaptive. An adult woman in a natural fertility popu-

lation can be thought of as alternating between two states: “metabolizing for one” when she is neither pregnant nor lactating, and “metabolizing for two” when she is pregnant or lactating. Pregnancy and lactation increase a woman’s energy requirements by a third to a half, and there is compelling evidence that under certain conditions women will divert energy from their own metabolic needs to meet those of gestation and milk production.³⁶ The ability to meet these energetic demands must have been the focus of intense natural selection during human evolution. Modulating fecundity in response to energetic stress probably represents one way in which the organism has been shaped to try to optimize its reproductive efforts. When energy is scarce and limiting, reducing fecundity increases the proportion of time a woman spends metabolizing for one relative to that spent metabolizing for two, thus helping her to maintain long term energy balance. When energy is abundant, increasing fecundity reduces the same ratio. If a woman’s physical condition is very poor her fecundity may drop to zero until she recovers to a point where a successful energetic investment in reproduction again becomes possible.

Understanding the underlying patterns of human fecundity helps us to make sense out of observed patterns of natural variation in human fertility, such as the consistency of the age pattern of fertility in natural fertility populations, the wide variation in fertility levels among populations with high rates of marriage and low usage of effective contraception, and patterns of seasonal reproduction in subsistence agricultural populations. The same insights shed light on the reproductive physiology of individuals in Western populations. Declining female fecundity with age after the mid-thirties is not an anomaly; menstrual irregularity in female athletes is not pathological; in some cases, simply gaining weight increases the probability of conception in women under treatment for infertility.³⁷ Broadening our view of the human condition and shedding unexamined assumptions about our biological heritage are keys to expanding our understanding of ourselves.

NOTES

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35. Emmet J. Lamb and Sean Bennett, "Epidemiologic Studies of Male Factors in Infertility," *Annals of the New York Academy of Sciences* 709 (1994): 165–178.
36. A. M. Prentice and R. G. Whitehead, "The Energetics of Human Reproduction," *Symposia of the Zoological Society of London* 57 (1987): 275–304.
37. G. W. Bates, S. R. Bates, and N. S. Whitworth, "Reproductive Failure in Women Who Practice Weight Control," *Fertility and Sterility* 37 (1982): 373–378; G. W. Bates, "Body Weight Control Practice as a Cause of Infertility," *Clinical Obstetrics and Gynecology* 28 (1985): 632–644.

SUGGESTED READINGS

The following are useful collections of conference papers combining physiological and demographic perspectives on human fertility:

Campbell, Kenneth L., and James W. Wood, eds. *Human Reproductive Ecology: Interactions of Environment, Fertility, and Behavior*. *Annals of the New York Academy of Sciences*, vol. 709 (1994)

Dunbar, Robin I., ed. *Human Reproductive Decisions: Biological and Social Perspectives*. London: Macmillan, 1994.

The following are slightly more detailed reviews of the topics covered in this chapter:

Ellison, Peter T. "Human Ovarian Function and Human Ecology: New Hypotheses." *American Anthropologist* 92 (1990): 933–952

Ellison, Peter T. "Reproductive Ecology and Human Fertility." In C. G. N. Mascie-Taylor and G. W. Lasker, eds. *Applications of Biological Anthropology to Human Affairs*. Cambridge, UK: Cambridge University Press, 1991.

Ellison, Peter T. "Advances in Human Reproductive Ecology." *Annual Review of Anthropology* 23 (1994): 255–275.

Research TOC

At the sociocultural level human reproductive decisions are exceedingly complex. Individual motivations are influenced and constrained by partners, peers and family, by religious values and legal... This paper will concern itself with a subset of these physiological decisions, those that are made in the form of natural variations in female ovarian function which in turn, modulate female fecundity. It will not consider the role of lactation in modulating human ovarian function, as that will be the subject of a separate paper in this volume. Rather it will only consider ovarian function in non-pregnant, non-lactating women. Human genetic variation is the genetic differences in and among populations. There may be multiple variants of any given gene in the human population (alleles), a situation called polymorphism. No two humans are genetically identical. There are at least three reasons why genetic variation exists between populations. Natural selection may confer an adaptive advantage to individuals in a specific environment if an allele provides a competitive advantage. Alleles under selection are likely to occur only in those geographic regions where they confer an advantage. Genetic variation is necessary in natural selection. In natural selection, organisms with environmentally selected traits are better able to adapt to the environment and pass on their genes. Major causes of variation include mutations, gene flow, and sexual reproduction. DNA mutation causes genetic variation by altering the genes of individuals in a population. Gene flow leads to genetic variation as new individuals with different gene combinations migrate into a population. Sexual reproduction promotes variable gene combinations in a population leading to genetic variation. Examples of geneti