

Energetics and Reproductive Effort

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ABSTRACT Natural selection favors the optimal allocation of energy and other limiting resources to reproduction. Human reproductive physiology displays characteristic patterns that can be viewed as mechanisms that help optimize reproductive effort in the face of environmental energetic constraints. Female ovarian function is particularly sensitive to energy balance and energy flux, resulting in a synchronization of conception with favorable energetic conditions. Reproductive effort during gestation is highly buffered from environmental energetic constraints, but the duration of gestation and final birthweight are both very sensitive to maternal energy availability. Milk production during lactation is relatively buffered from maternal energetic constraints as well, but the duration of lactational amenorrhea is sensitive to the relative metabolic load of lactation. Male gamete production is very insensitive to energetic constraints, but variation in testosterone production in response to both age and longer-lasting energetic conditions contributes to the modulation of somatic and behavioral aspects of male reproductive effort, aspects that are more energetically costly for a male. There is also new evidence that testosterone may also help to modulate the trade-off between male parenting and mating effort. *Am. J. Hum. Biol.* 15:342–351, 2003. © 2003 Wiley-Liss, Inc.

Human life histories, like those of other organisms, can be formalized as strategies to optimize reproductive effort, or the allocation of resources to reproduction. Necessary constraints on the allocation of resources generate unavoidable trade-offs between investment in self and investment in offspring and between finer categories of allocation. A life history strategy is composed of a set of allocation priorities that results in characteristic patterns of growth, mortality, and fertility across the lifespan of the organism. Those strategies that result in higher inclusive fitness are favored by natural selection over others and come to characterize the biology of a species.

A key aspect of life histories is the partitioning of resources to reproduction, or reproductive effort (Stearns, 1992). Greater reproductive effort implies a reduction in resources available to other allocation categories (such as growth, immune function, tissue repair, etc.) and therefore implies costs to survivorship or future fertility. In addition, there may be necessary trade-offs between subcategories of reproductive effort, such as the investment in current vs. new offspring. While reproductive effort is not the only aspect of life histories that contributes to overall fitness, other life history features, such as increased survival, only come to have fitness value insofar as they eventually result in increased reproduction. Thus, the optimization of reproductive

effort can be viewed as the cornerstone of successful life history strategies. Indeed, this cornerstone often becomes the central focus of analysis, referred to as reproductive strategy.

The allocation of reproductive effort is mediated at many different levels. Behavioral mediation is particularly appropriate for responding to evanescent social contexts and to the strategies pursued by conspecifics. The field of behavioral ecology has flourished with the development of increasingly sophisticated theory and methodology for the analysis of reproductive strategies at the behavioral level. But reproductive effort is also modulated at the physiological level, particularly in response to more persistent ecological contexts (e.g., chronic energy scarcity) and predictable life-stages (e.g., adolescence, reproductive maturity, reproductive senescence). Several authors have noted that the endocrine system plays an important role in shaping life histories at the physiological level by mediating metabolic allocation to competing domains (Finch and Rose, 1995; Bribiescas, 2001).

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Received 16 August 2002; Accepted 9 December 2002

Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/ajhb.10152

The physiological regulation of reproductive effort is manifested primarily in the allocation of metabolic energy to reproduction. Both the amount of energy allocated and the temporal pattern of allocation have profound consequences for ultimate reproductive success, both through their impact on fertility and through their impact on mortality. Although energy is not the only limiting resource to be considered in optimizing reproductive effort, it is certainly the principal one for humans as for other organisms (Ellison, 2001a). Indeed, in the crudest sense a living organism can be thought of as a system that captures energy from the environment for the purpose of replicating itself. The efficiency with which it carries out that task is the ultimate measure of its fitness.

The purpose of this review is to outline several of the chief ways in which human physiology effectively modulates reproductive effort in response to variation in the availability of metabolic energy. The development of minimally invasive sampling techniques (Ellison, 1988; Ellison et al., 1989; Campbell, 1994; Leslie et al., 1996; Worthman and Stallings, 1997; Holman et al., 1998) has led to an increase in field studies of human reproductive physiology. These studies have led to a greater appreciation of the range of human variation in this important domain of our biology (Campbell and Wood, 1988; Ellison et al., 1993a,b; Ellison, 1994, 2001a,b). Consistent patterns of variation have emerged in some areas that are amenable to functional interpretation. Other areas have only recently become the focus of systematic study. Yet as the field of human reproductive ecology continues to develop, the role of energetics as an important unifying principal has already become clear.

MODULATION OF THE PROBABILITY OF CONCEPTION

For women the principal form of reproductive effort is parenting effort, or direct investment in offspring. Gestation and lactation represent intensive periods of investment, when a substantial portion of a mother's total metabolic budget is allocated to the support of her offspring with no direct benefit, and often substantial cost, to the mother's survival or subsequent fertility. Maternal parenting effort must also be allocated in large quanta of both energy

and time in order to realize any benefit. Diversion of energy to parenting effort begins almost immediately upon conception, even though the metabolic demands of a developing offspring are negligible at first. Stored energy accumulated early in gestation provides a crucial resource for meeting the rising metabolic demands of late gestation and early lactation (Villar et al., 1992).

Physiological modulation of reproductive effort in human females begins with mechanisms that adjust the probability of conception in response to maternal energy availability. Three aspects of maternal energetics can be distinguished as potential correlates of conception probability. Those are: 1) energy status, or the amount of stored energy that can be mobilized as reproductive effort; 2) energy balance, or the net residual of energy intake minus energy expenditure that can be potentially allocated to reproductive effort; and 3) energy flux, or the absolute level of energy turnover independent of energy balance. Although often correlated, these three aspects of human energetics are logically separable and can vary independently. High energy status, for example, is usually associated with a recent history of positive energy balance. But two individuals can have the same amount of stored energy at a given point in time and yet be characterized by very different energy balance, one losing weight while the other is gaining weight. Similarly, low levels of stored energy (low energy status) can occur in individuals characterized by very different energy flux, low flux in the case of starvation, high flux in the case of high-intensity athletic training. Both energy status and energy balance are expected to have monotonically positive relationships to the availability of energy for reproduction. Under conditions of neutral energy balance, however, energy flux is expected to have a curvilinear relationship to the availability of energy for reproduction. Low energy flux in the context of neutral energy balance usually results from reduced energy expenditure to accommodate constrained low energy intake. High energy flux in the context of neutral energy balance usually results from increased energy intake to accommodate constrained high energy expenditure. In either case, the constraints that force energy flux to one extreme or the other also constrain the organism's ability to allocate energy to reproduction.

Ovarian function in adult, nonpregnant, nonlactating women shows a consistent pattern of variation in association with indices of energetic conditions. Variation in ovarian function is sometimes manifest as variation in menstrual frequency and regularity, and such variation has clear implications for the monthly probability of conception. But more subtle variation in ovarian function, manifested as variation in ovarian steroid levels, has also been demonstrated to occur in the absence of observable variation in menstrual patterns and that variation, too, has been linked to variation in the probability of conception (Lipson and Ellison, 1996). This has led to the concept of a continuum of ovarian function reflected in quantitative variation in the principal ovarian steroid hormones, estradiol and progesterone, which also represents a continuum of female fecundity (Ellison, 1990).

Many of the patterns of variation in ovarian function associated with energetics were first observed as variation in menstrual regularity associated with pathological or otherwise rather extreme conditions. For instance, anorexia nervosa, a pathological condition associated with restricted food intake and emaciation, is often associated with amenorrhea (Warren, 1983). Frisch and MacArthur (1974) noted that treatment resulting in weight gain often also leads to the resumption of menses. The association of amenorrhea with other states of emaciation has led some to propose a more general category of "starvation amenorrhea" to characterize the association (VandeWeile, 1977). Frisch and MacArthur (1974) originally argued that the amenorrhea of anorexia nervosa sufferers is a consequence of low energy status (low fat stores). The resumption of menstruation after weight gain was attributed to the reattainment of a threshold energy status. Frisch (1984) later extended the same argument to athletic amenorrhea as well. However, it is not possible in these cases to discriminate the effects of variation in energy status from those of variation in energy balance and energy flux. Anorexia nervosa patients and other sufferers from starvation amenorrhea are characterized by very low energy flux as well as by low energy status. The resumption of menses after weight gain is associated with both increases in energy flux and with positive energy balance. Similarly, athletic amenorrhea is associated with high energy flux more reliably

than with low energy status (Sanborn et al., 1987). Bullen and colleagues (Bullen et al., 1985; Williams et al., 1999) attempted to separate high energy flux from negative energy balance by studying a group of women undertaking an intensive exercise regime while adjusting the caloric intake of half of the group to maintain body weight. Their results indicated that high energy flux by itself can be associated with disruption of ovarian function.

Studies of Western women subject to more moderate energetic stresses and using more sensitive measures suggest that ovarian function is more sensitive to energy balance and energy flux than to energy status. For example, among 24 regularly menstruating Boston women there was no correlation between weight or body mass index and salivary estradiol levels in the follicular phase of the cycle. However, there is a significant positive correlation between change in weight and change in mid-follicular estradiol levels (Lipson and Ellison, 1996). Similarly, among eight Boston women voluntarily restricting caloric intake to lose weight, an average weight loss of 1.9 kg/month is associated with significantly lower progesterone levels compared to stable weight controls (Lager and Ellison, 1990). Moderate exercise, such as recreational jogging for 12.5 miles/week, has also been associated with significantly lower salivary progesterone profiles compared to nonexercising controls, even in the absence of any change in weight (Ellison and Lager, 1986). Similar results have been reported for German women (Pirke et al., 1985; Schweiger et al., 1988).

Variation in ovarian function is also observed to occur in association with energetic stresses that arise from the subsistence ecology among a broad range of human populations. Among Lese horticulturalists in the Ituri Forest of the Democratic Republic of the Congo, nearly universal weight loss is a common feature of the pre-harvest season. In Lese women this weight loss is accompanied by lower levels of salivary progesterone and estradiol, longer intermenstrual intervals, and shorter durations of menstrual bleeding. All these trends are reversed after the harvest as positive energy balance is established. Over time this seasonal variation in ovarian function is reflected in a statistically significant seasonal pattern of conceptions (Bailey et al., 1992; Ellison et al., 1989). Among

Tamang agriculturalists in central Nepal, weight loss associated with seasonally heavy workloads is associated with suppression of salivary progesterone profiles (Panter-Brick et al., 1993). Similarly, among Polish farm women there is a significant negative correlation between workload during the agricultural season and salivary progesterone levels. In these subjects the suppression of progesterone profiles appears to be a correlate of energy flux, not energy balance, since there is no correlation with change in weight or fat reserves (Jasienska and Ellison, 1998).

In summary, the available evidence indicates that ovarian function varies in relation to energetic conditions prior to and at the time of a potential conception. It further suggests that a woman's ability to partition energy to reproduction on an ongoing basis is a more significant correlate of ovarian function than the accumulated store of energy. There are two possible functional interpretations of these facts that are not mutually exclusive. The first is that the ability of a woman to divert metabolic energy towards reproduction in the early gestation period is a significant factor in the success of that pregnancy. Indeed, even though the direct energetic costs of the embryo and placenta are minimal in the first few months of gestation, significant fat accumulation occurs during this period (Hyttén and Chamberlain, 1981; Villar et al., 1992). These stores are later drawn upon to meet the high costs of late gestation and early lactation. The efficiency of fat storage is increased in early pregnancy in direct proportion to estrogen levels (O'Sullivan et al., 2001). The high metabolic priority accorded this early fat accumulation may also be supported by the suppression of basal metabolic rate observed in early pregnancy among women with restricted energy intake (Prentice and Whitehead, 1987; Poppitt et al., 1994).

The second implication is that successful reproduction depends on a continuous diversion of energy from a woman's current metabolic budget. It is the potential for sustaining an ongoing investment that matters most. Net energy balance is the best indicator of that potential. Extremes of energy flux indicate the presence of important constraints on potential allocation. Energy status is the least reliable indicator of the potential for ongoing investment since energy stores

may already be being mobilized to meet an energy budget that is highly constrained.

There are a number of intriguing problems that arise from the tension between empirical observations on the environmental sensitivity of ovarian function and a general adaptive theory of human reproductive ecology. For example, why should female fecundity vary in a continuous, rather than a discrete, way with energy availability? Why are energy balance and energy flux better predictors of reproductive success than energy status? Lengthier treatments of these questions are available to interested readers in Ellison (2001a) and Jasienska (2001).

It appears that natural selection has molded human physiology to make conception more likely under conditions that predict an ability to sustain an ongoing energetic investment in an ensuing pregnancy. This results in a correlation of favorable energetic conditions with conception and not necessarily with birth, lactation, or other points in the reproductive process. This pattern does not imply that energetic conditions at later periods are of no consequence for reproductive success. Rather, it may be that formative environmental conditions were sufficiently unpredictable that mechanisms to synchronize conception with current energetic conditions were favored by natural selection over mechanisms to optimize energetic conditions at some point in the future (Ellison, 2001a).

MODULATION OF THE DURATION OF GESTATION

The establishment of a pregnancy is sensitive to energetic conditions. Once established, however, the continuation of a pregnancy appears to be highly buffered from variation in energetic conditions. There is very little difference, for example, between rates of early embryonic loss determined from sensitive assays of human chorionic gonadotropin in women living in North Carolina compared to women living under conditions of chronic energy shortage in Bangladesh (Holman, 1996; Wilcox et al., 1989). Nor do periods of extreme restriction of energy intake during pregnancy, such as experienced in the Dutch "hunger winter" during the German occupation in World War II, result in increased rates of spontaneous abortion (Stein et al., 1975).

Energetic conditions during pregnancy can, however, affect both the birthweight of the resulting offspring and the duration of gestation. Restricted energy availability can have a particularly negative effect on fetal fat accumulation and resulting birthweight (Villar et al., 1992; King et al., 1994). Since birthweight itself is a powerful determinate of infant mortality risk, one might imagine that natural selection would have produced an association between low energy availability and longer duration of gestation in order to buffer birthweight to some degree (Peacock, 1991). There is no temporal constraint on placental function that would prevent this (Higgins, 1954; Ellison, 2001a). However, on the contrary, low energy availability is associated with shorter gestational duration (Kline et al., 1989). This fact probably reflects constraints on an undernourished mother's ability to meet the metabolic demands of a fetus in late gestation. Glucose flux across the placenta is the primary form of maternal energy allocation to the fetus. The vascular anatomy of the human hemochorial placenta leads to particularly high maximal rates of glucose flux (Ellison, 2001a), but fetal glucose levels are still highly dependent on maternal glucose levels (Morriss and Boyd, 1988). As energy flux across the placenta starts to fall short of meeting fetal energy requirements, which grow exponentially near term due to the growth of the fetal brain, a fetus begins to mobilize its own fat reserves as a supplemental source of energy. The mechanisms that are initiated to serve fetal energy mobilization, including increases in cortisol production by the fetal adrenal gland, the positive feedback of fetal cortisol on corticotrophin-releasing hormone production in the placenta, and arachidonic acid mobilization and prostaglandin production in the placenta, also contribute to the initiation of parturition (Strickland et al., 1982; Soloff, 1989; Majzoub et al., 1999; McClean and Smith, 2001; Smith et al., 2002). Labor appears to be initiated when the fetus starts to starve, avoiding the fetal wasting that can occur as a consequence of prolonged gestation (Ellison, 2001a).

MODULATION OF THE DURATION OF LACTATIONAL AMENORRHEA

After birth the energetic requirements of a newborn continue to increase along with

continued brain and somatic growth and with new metabolic demands related to digestion, respiration, thermoregulation, and other functions that must now be carried out independently. Initially, the mother's metabolism continues to meet her infant's energetic needs through the production of breast milk. But progressively this product of maternal metabolism is supplemented and then replaced by other foods. While the mother's metabolism is fully meeting the energetic demands of a newborn, which exceed even those of a full-term fetus, her ability to generate enough residual metabolic energy to meet the requirements of a new pregnancy is highly constrained. Indeed, resting metabolic rate is often reduced in early lactation in order to meet the metabolic demands of unsupplemented breast-feeding, much as it is in early gestation, indicating that allocation of energy to maternal maintenance functions is often sacrificed in order to sustain the reproductive effort represented by milk production (Prentice and Whitehead, 1987). The energetic content of breast milk also appears to be buffered by maternal metabolism in order to meet minimal infant requirements even under conditions of severely restricted maternal energy intake (Prentice et al., 1983; Prentice and Prentice, 1990).

During unsupplemented lactation the high metabolic investment in a nursing offspring represents a significant constraint on the availability of metabolic energy to support a new pregnancy. The cost of milk production during this period is ordinarily around 700 kcal/day (Dewey, 1997; Prentice and Whitehead, 1987), which can represent as much as a third of a woman's entire energy flux. This high metabolic load is usually accompanied by ovarian suppression and amenorrhea, precluding any risk of a new conception. As the metabolic burden of supporting the infant is shifted away from milk production, the potential for meeting the energetic cost of a new pregnancy is restored and ovarian function resumes (Valeggia and Ellison, 2001; Ellison and Valeggia, 2002). The timing of the resumption of ovarian function depends both on the demand for milk by the infant and on the mother's ability to meet that demand.

The course of lactation is typically characterized by decreasing frequency and duration of nursing. Longitudinal studies have shown that resumption of ovarian activity

is closely correlated with declines in these parameters of nursing behavior, which are in turn closely correlated with the introduction of supplementary foods (Howie and McNeilly, 1982; Ellison, 1995). An additional correlate of declining nursing intensity is a decline in prolactin levels and in the prolactin response to individual nursing episodes. Prolactin was once thought to play a direct role in suppressing ovarian function (Ellison, 1995). Although it is no longer thought to play that role, it does reflect the degree to which metabolic energy is directed toward milk production. Other things being equal, women who nurse more frequently and for longer duration with lesser use of supplementary foods tend to have higher prolactin levels and lower indices of ovarian function. Those who sustain such a pattern of nursing longer tend to have longer periods of amenorrhea.

Nursing intensity alone, however, is not the only determinant of the duration of postpartum amenorrhea. The availability of metabolic energy to meet the demands of milk production can also vary between women. For a well-nourished woman the same level of milk production may represent a smaller proportion of available metabolic energy than for a poorly nourished woman. This can be reflected in the prolactin levels associated with sustaining a given level of milk production. For example, when rural Gambian women received energy supplements during lactation, neither the volume of breast milk produced nor the energy content of the milk changed (Prentice et al., 1983). However, prolactin levels declined and ovarian function resumed more rapidly (Lunn et al., 1980, 1984).

While prolactin levels may reflect the proportional allocation of metabolic energy to milk production, baseline insulin levels may reflect residual energy availability. Insulin promotes both energy storage and ovarian function. The influence of insulin on ovarian function is primarily through its effects on steroidogenesis, where it acts both independently and in synergy with gonadotropins. In vitro experiments, for example, have demonstrated marked increases in steroid production by cultured granulosa cells incubated with either insulin alone or insulin plus follicle-stimulating hormone (Willis et al., 1996). Similar experiments have demonstrated comparable effects of insulin on androgen production by theca cells (Nahum

et al., 1995). It has also been shown that these effects are directly mediated by insulin receptors on follicular cells, not by cross-talk with other receptors systems (such as insulin-like growth factors) (Willis and Franks, 1995).

The resumption of menses postpartum shows a clear relationship to changes in metabolic energy availability as reflected in changing baseline insulin production. In nursing Toba women in Argentina, for example, C-peptide levels (a molecule split off from the proinsulin molecule in the process of producing active insulin) rise from an average of 60% of normal after birth to an average of 140% of normal in the months immediately before the resumption of menses, after which they rapidly return to 100% of normal. This pattern of change reflects the increasing availability of metabolic energy net of milk production, also reflected in postpartum changes in body weight. The overshoot of normal levels prior to menstrual resumption may help to stimulate the resumption of ovarian steroidogenesis. Increasing estrogen levels in turn may help to restore peripheral responsiveness to insulin and normal levels of baseline insulin production (Ellison and Valeggia, 2002).

The postpartum resumption of ovarian function thus appears to be determined by the availability of metabolic energy to support the allocation of effort to a new pregnancy. That availability of energy is in turn determined both by the level of allocation to milk production and by the energetic condition of the mother.

MODULATION OF MALE MATING EFFORT

In men, as in males of most mammalian species, gamete production entails very little energetic investment. This, together with the fact that the energetic costs of pregnancy and lactation fall on females, means that direct metabolic effort in offspring production by males is quite low. Given this fact, it is not surprising that direct indices of male fecundity, such as sperm count and viability, show very little association with energetic conditions that are not life-threatening (Abbas and Basalamah, 1986). Even very high levels of energy expenditure, for example, have no clear impact on sperm production (Bagatell and Bremner, 1990;

Lucia et al., 1996; Hall et al., 1999; Arce and De Souza, 1993).

Males may direct considerable energy to reproduction, however, in the form of mating effort. While mating effort may be thought of as falling in the domain of behavior, it has important physiological correlates. The production and maintenance of muscle mass, for example, can be viewed as a form of somatic reproductive effort in males (Ellison, 2001a). This somatic effort, in turn, shows evidence of clear modulation by testosterone. Sexual dimorphism in muscle mass and strength arises in humans after puberty as a consequence of differential testosterone production (Round et al., 1999). Clinical studies of testosterone suppression and replacement have shown unambiguous effects on muscle anabolism and strength (Bhasin et al., 2001a,b).

Muscle mass contributes to competitive ability in males of many mammalian species. But muscle is also metabolically expensive tissue to maintain. Modulation of muscle mass provides an important mechanism for the modulation of overall metabolic requirements. Bribiescas (1996, 2001) has argued that energetic constraints on males may lead to suppression of testosterone levels in order to reduce somatic reproductive effort in the form of muscle mass. It is interesting in this regard to note that population differences in testosterone levels are greatest among young adult males and that these differences are much less apparent with increasing age (Ellison et al., 2001). This suggests that there is a general, age-specific pattern to the physiological regulation of male somatic reproductive effort that is common to most human populations, with the investment greatest in young adulthood and diminishing thereafter. Population differences in energetic conditions manifest themselves primarily as differences in the physiological support for somatic investment during young adulthood.

In addition to contributing to the regulation of somatic reproductive effort, testosterone may help regulate behavioral mating effort in human males as well. Efforts to develop effective hormonal contraception for males have underscored the importance of testosterone in supporting male libido (Bagatell et al., 1993). The role of testosterone in modulating human male aggressive and competitive behavior has also been a renewed subject of research, particularly

given the development of techniques for measuring salivary testosterone levels (Dabbs, 1993). In male subjects, short-term testosterone responses to competitive situations have been observed in many different contexts, with "winners" usually demonstrating higher levels relative to their own average levels than "losers" (Elias, 1981; Rabow, 1987; Booth et al., 1989). These changes are comparable to the changes in testosterone profiles that have been observed in captive and wild primates associated with the outcome of dominance interactions (Rose et al., 1971; Muller and Wrangham, 2001). Such observations have led to speculation that testosterone plays an important role in modulating confidence and assertiveness in social situations, qualities that are assumed to support male mating effort (Mazur and Booth, 1998; Muller and Wrangham, 2001).

MODULATION OF MALE PARENTING EFFORT

Although females may bear the primary physiological burden of offspring production, human males in many societies do contribute to direct parental care after birth (Hewlett, 1992). In species with significant levels of male parental care a trade-off between mating effort and parenting effort can often be observed, both in terms of patterns of behavior and in the hormonal correlates of behavior. Wingfield and Moore (1987) have argued that testosterone plays an important role in modulating that trade-off, with high testosterone levels supporting male mating effort and low levels facilitating parenting effort. In bird species with high levels of male parental care, for example, individual males alternate between high and low testosterone states as they progress through the cycle of courtship, incubation, and feeding of nestlings, in many species more than once per breeding season.

Given that male parental care is common in many human societies, there has been speculation regarding the role of testosterone in modulating a trade-off in behaviors typical of mating effort and parenting effort. At least one preliminary report suggests that this may indeed be the case. After correcting for age, Boston men with children under age 4 years were found to have lower salivary testosterone levels at the end of the day than men without children (Gray et al., 2002).

In another preliminary study, men were observed to have lower salivary testosterone levels on days when they cared for their infant children than on days when they did not (Pham, 2000).

The study of male parental care and its hormonal correlates in humans has not yet progressed to the point of considering possible effects of variation in energetic conditions. However, if the energetic demands of parenting effort and mating effort are different, it would be reasonable to hypothesize that differences in energy availability might affect the trade-off implicit between them. Perhaps male reproductive effort is subject to a transition between investment in a current offspring and investment in the next mating opportunity that is in some way analogous to the transition in females between investment in lactation and investment in the next pregnancy. If so, it would be interesting to examine the effect of differences in energetic conditions on that transition.

SUMMARY

As is true of all living organisms, humans invest considerable metabolic energy in the production of offspring. This investment always involves trade-offs with potential alternative categories of investment, including categories that contribute to survival. Natural selection favors mechanisms that contribute to the optimal allocation of reproductive effort, including those that modulate reproductive effort in response to energy availability. In human females, such mechanisms appear to modulate the probability of conception, the length of gestation, and the length of postpartum amenorrhea. In human males there is some evidence for mechanisms that modulate male mating effort, particularly somatic effort, but perhaps also behavioral effort. There is also reason to suspect that physiological mechanisms may play a role in modulating male parental effort.

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