

13 *Human birth seasonality*

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Introduction

Seasonal variation in the frequency of births is a nearly universal phenomenon in human populations (Cowgill 1965; Lam & Miron 1991; Bronson 1995). Indeed, the absence of birth seasonality in any particular population can be considered a remarkable observation (Brewis *et al.* 1996; Pascual *et al.* 2000). However, the broad prevalence of human birth seasonality does not imply simple causation. Several mechanisms have been proposed to account for the seasonality of births in different specific cases, and most investigators acknowledge that multiple causes are almost certainly involved. Nevertheless, some of the causes of human birth seasonality are likely to have deeper roots in our biology as hominoid primates than others. It will not be possible to review all the hypotheses that have been put forth or to survey the extensive empirical literature on human birth seasonality in this chapter. Rather, the purpose of this chapter is to discuss some of the major hypothesized causes of human birth seasonality in a way that highlights their relevance to the evolutionary ecology of our species and their relationship to the ecology of other primates.

The major hypotheses regarding human birth seasonality can be grouped under three headings: seasonality due to social factors that influence the frequency of intercourse; seasonality due to climatological factors that directly affect human fecundity; and seasonality due to energetic factors that principally affect female fecundity. The first group of hypotheses does not necessarily posit any change in reproductive physiology underlying human birth seasonality, placing primary emphasis on behavior. The second group of hypotheses posits changes in reproductive physiology tied to climatological variation, but often without implying any clear adaptive significance to the resulting pattern. The third group of hypotheses both posits a physiological basis for birth seasonality and argues for the adaptive significance of the underlying mechanism.

It is important to acknowledge at the outset, however, that these different hypotheses are not mutually exclusive and to reiterate that more than one cause can be operating simultaneously on a given population. Given this fact and the inherently cyclical nature of seasonal phenomena, distinguishing between competing hypotheses can be extremely difficult. It is also important to note that several of the major hypotheses regarding human birth seasonality actually view seasonality in the strict sense as an epiphenomenon and not as a consciously desired or adaptively designed outcome. That is, some hypotheses posit that a given aspect of human reproduction is contingent on an environmental variable for reasons that are independent of any seasonal pattern in that variable. When that particular environmental variable varies in a strongly seasonal pattern, reproductive seasonality may result as an epiphenomenon. For example, a relationship between high ambient temperature and sperm production might produce reproductive seasonality in an environment with seasonally high temperatures. The relationship between temperature and sperm production, however, may have an ultimate explanation that is totally unrelated to environmental seasonality. This differs from mechanisms that are hypothesized to have evolved in order to synchronize reproductive patterns with a seasonally varying environment.

Social factors influencing human birth seasonality

Until relatively recently, the leading hypothesis for human birth seasonality in the demographic literature has been that social factors influencing the probability of intercourse often lead to seasonal clustering of conceptions (Huntington 1938; Udry & Morris 1967). Conception peaks often can be identified with major secular and religious holidays, such as the Christmas–New Year season in the USA and the August vacation period in France (National Center for Health Statistics 1966; Lam & Miron 1994). Differences in conception peaks between different religious groups are sometimes observed to correlate with differences in the occurrence of major religious festivals or other aspects of the religious calendar (Rajan & James 2000).

Socially determined seasonal patterns of conception in developed countries often are viewed as divorced from any important ecological causation. In subsistence societies, however, seasonal cycles of social activity and interaction often are shaped and constrained by the annual subsistence cycle. In many agricultural populations, for example, marriages tend to be clustered either before or after the major season of agricultural labor

(Danubio & Amicone 2001). In migratory populations, including circumstances of seasonal labor migration, that undergo seasonal dispersal and aggregation, marriage and conception peaks often are observed in the season of aggregation (Menken 1979; Condon 1982; Huss-Ashmore 1988). Major cultural and religious festivals also tend to be coordinated with the calendar of annual subsistence activities. It has been argued that the cultural patterning of conceptions in subsistence societies is thus partly a result of ecological constraints, producing the most pronounced birth seasonality in populations where the subsistence regime is itself most seasonally constrained (Condon & Scaglione 1982).

The seasonality of human subsistence activities in non-industrial societies usually correlates with seasonality of weather conditions and with seasonality of food intake and workload. Because of this, there is a certain degree of overlap between hypotheses of human birth seasonality based on social factors and those based on climatological and energetic factors. For instance, both the heat of the summer months and the exhaustion of the agricultural work season have been suggested as causes of reduced frequency of intercourse in agricultural societies, as has anxiety for the coming harvest (Stoekel & Chowdhury 1972; Thompson & Robbins 1973; Malina & Himes 1977; Ayeni 1986). As noted above, it is not necessary that we treat these as mutually exclusive possibilities. Rather, in this context, we can include them as factors related to subsistence ecology that may influence the seasonality of conception.

If we view the social patterning of conception frequency as having a historical basis in the constraints of human subsistence ecology, then we may be able to see some phylogenetic continuity as well. Group size can influence mating opportunity in some ape species, and where group size is influenced by ecological factors, seasonality of mating opportunity can result. The occurrence of large fruiting patches can, for instance, lead to increased mating frequency in chimpanzees (Wrangham 2000; Knott 2001). Orangutans provide a particularly extreme example of the influence of ecological seasonality on mating frequency. Synchronous mastings of major food trees results in increasing density of both female and male orangutans, higher encounter rates between potential mating partners, and higher mating frequencies than during non-mast periods (Knott 1997a, 1999).

Climatological factors influencing human birth seasonality

As noted above, climatological factors sometimes have been invoked as causes of seasonal variation in the frequency of intercourse within human

populations. High ambient temperatures often are cited as having a negative influence, while heavy rainfall sometimes is cited as having a positive influence, on the assumption that it leads to couples spending more leisure time indoors (Thompson & Robbins 1973; Dyson & Crook 1981). More recently, however, increasing attention has been paid to the possibility that climatological factors have a direct influence on human reproductive physiology and thereby on human fecundity, or the biological capacity to conceive and bear offspring. The two factors most often discussed in this context are temperature and photoperiod.

Sperm production in mammals is temperature-sensitive and optimized at temperatures below the core body temperature of many species (Bedford 1991). As a result, testes are located in external scrotal sacs in most mammals, including primates (Bedford 1977). Sperm production in humans similarly has been observed to be temperature-sensitive, even leading to suggestions for contraceptive manipulation (Appell & Evans 1977; Kandeel & Swerdloff 1988).

This well-known temperature sensitivity of sperm production has led to interest in whether high ambient temperatures could compromise male fecundity by affecting sperm quantity or quality. Certain geographical patterns tend to support such a hypothesis. A north-south gradient in the amplitude of birth seasonality in the USA has been noted, with higher amplitude at lower latitude (Lam & Miron 1994, 1996). It has also been suggested that the amplitude of the birth peak in the southern states has declined in recent years with the wider prevalence of air-conditioning (Seiver 1989). Initial studies in the southern USA produced evidence of significant seasonal variation in sperm production among men working outdoors, with suppressed values being found in the hot months of the year. However, subsequent studies found similar seasonal patterns in the indices of sperm production among men who worked in air-conditioned indoor environments and among those who worked outdoors at high ambient temperatures, weakening the case for high ambient temperature exposure as a cause of the pattern (Levine *et al.* 1988; Levine 1994).

The temperature sensitivity of sperm production clearly has been a selective force in mammalian evolution resulting in external testes as a common anatomical characteristic. Given the ancient nature of this adaptation, however, and the evolutionary origin of our species in tropical latitudes, it is difficult to imagine that humans would be less well adapted to ambient temperature effects than other tropical primate species. If temperature effects on male fecundity do occur in modern human populations, then they are likely to result from temperature exposures that would be uncharacteristic of our evolutionary past, as a result of either the

colonization of extreme habitats or the adoption of clothing that inhibits natural scrotal heat loss.

Photoperiod also has been suggested to influence human fecundity (Wehr 2001). The argument in this case stems primarily from the observation of photosensitive secretion of melatonin by the pineal gland. Pineal melatonin secretion is known to be important in the maintenance of both circadian cycles and seasonal patterns of reproduction in many mammals (Karsch *et al.* 1984; Tamarkin *et al.* 1985; Bronson 1989).

Melatonin secretion in humans is photosensitive, occurring primarily at night (Bojkowski *et al.* 1987; Wehr *et al.* 1993). Evidence of seasonal variation in the period or magnitude of melatonin secretion in human populations is equivocal, however (Illnerova *et al.* 1985; Kauppila *et al.* 1987; Matthews *et al.* 1991; Wehr 1991). It is possible that artificial light now buffers natural photoperiodicity in many populations and so attenuates any seasonal effect. However, it is not clear whether variation in melatonin levels or periods of secretion within the normal range has any effect on the human reproductive axis. Most clinical reviews of the subject have concluded that the evidence for such an effect is weak (Brzezinski & Wurtman 1988).

There is no question that the physiological substrate for sensitivity to photoperiod is intact in most mammals, including primates, even if it does not have a direct influence on reproductive physiology. Given the presence of such an endogenous signal of day length, it is easy to imagine selection acting to make use of that information to coordinate reproduction when circumstances render such coordination advantageous. Photoperiod sensitivity has been documented in rhesus monkeys related to patterns of seasonal reproduction observed both in the wild and in captivity (Wilson & Gordon 1989; Chik *et al.* 1992; Wehr 2001). As human populations spread out of the tropics to higher latitudes, they may have become subject to new selective pressures for the coordination of reproduction, with day length as a reliable predictor of environmental conditions. The best use of that information is not intuitively obvious, however. It would depend on there being a single critical period in the human reproductive cycle that could be optimized by seasonal coordination; whether that critical period is conception, gestation, birth, early lactation, or weaning is debatable. Nor is it clear whether the critical feature of the environment is temperature, food availability, or disease prevalence.

Thus, while an effect of photoperiod on human fecundity may be reasonable from a phylogenetic and evolutionary perspective, clear evidence of such an effect in contemporary human populations is lacking. Nor are the specific selective pressures that would have activated a latent capacity to respond to photoperiod understood well.

Energetic factors influencing female fecundity

Reproduction is an energetically demanding process for most organisms. Among placental mammals, females bear a particularly heavy energetic burden due to the metabolic requirements of gestation and lactation. Humans are no exception. At the end of gestation and during early lactation, the metabolic requirements of an offspring can equal as much as a third of its mother's non-pregnant metabolic budget. A large part of the offspring's metabolic demand derives from the requirements of its large and rapidly growing brain, a characteristic that, while shared with other Old World primates, is particularly accentuated in humans.

A number of features of human reproductive biology help to meet the energetic demands of reproduction for females, many of these being shared with other primates (Prentice & Whitehead 1987; Martin 1990; Lee *et al.* 1991). Fetal and infant growth rate tend to be slow relative to maternal mass, and the gestation period is relatively long compared with that of other mammals, resulting in a relatively low daily energy demand. Maternal metabolism favors fat storage early in gestation, when the energetic demands of the pregnancy are low. These energy reserves are then mobilized to help meet the high demands of late gestation and early lactation. Under conditions of constrained energy availability, human females can lower their own basal metabolic rates to free up energy for gestation and lactation, even at a cost to their own wellbeing.

In addition to these general features of energetic management, there is substantial evidence that human ovarian function is directly sensitive to female energetic conditions (Ellison 2001). Three aspects of female energetics need to be distinguished in this context: (i) energy status, or the amount of stored somatic energy that can be mobilized to meet the demands of reproduction, primarily in the form of fat and glycogen; (ii) energy balance, or the net of energy intake over expenditure; and (iii) energy flux, or the total rate of energy turnover. Although often correlated, these aspects of energetics are logically separable and often vary independently. Low energy status, for example, is often associated with a recent history of negative energy balance. But two individuals can have the same energy status (level of stored fat) while being in opposite states of energy balance, one losing weight and fat while the other is gaining weight and fat. Similarly, both high energy flux, as in a trained endurance athlete, and low energy flux, as in a famine victim, can be associated with low energy status and neutral energy balance.

Considerable evidence now exists indicating that human ovarian function is sensitive to energy balance. Even modest changes in weight, in the

range of 2 kg in a month, are associated with significant changes in the production of the principal ovarian hormones, estradiol and progesterone (Pirke *et al.* 1985; Lager & Ellison 1990; Lipson & Ellison 1996). These changes in turn are associated with changes in the probability of conception in a given cycle. In addition, there is evidence that high energy flux is associated with suppressed ovarian function, even when energy balance is neutral and energy status is normal. Moderate recreational exercise, for example, has been associated with lower ovarian steroid levels in women of constant weight (Ellison & Lager 1986). Similarly, heavy agricultural work has been associated with suppressed ovarian steroid profiles, even when energy intake is increased to result in neutral energy balance (Jasienska & Ellison 1998). Evidence for an independent effect of energy status on ovarian function is lacking, however, at least within the normal range of healthy human variation in energy status (Ellison 2001). As noted above, extremes of energy status are difficult to dissociate from the confounded effects of energy balance and energy flux.

Several physiological pathways exist by which energetic variables can affect female ovarian function. Both high and low energy flux have been shown to reduce the pulsatile release of gonadotropin hormones by the pituitary, suggesting an effect on the hypothalamic-pituitary (H-P) axis (Boyar *et al.* 1974; Veldhuis *et al.* 1985; Vigersky *et al.* 1977; Dixon *et al.* 1984). Both endogenous opioids and corticotropin-releasing hormone, which are increased under conditions of energetic stress, may contribute to this suppression of pituitary gonadotropin release (Loucks *et al.* 1989; Loucks 1990; Ferin 1999). Leptin, a protein hormone secreted by adipose tissue, may affect the H-P axis, in this case supporting pituitary gonadotropin release (Flier 1998). Leptin also may affect ovarian function directly (Spicer & Francisco 1997; Brannian *et al.* 1999). Leptin levels are affected not only by the amount of adipose tissue that an individual has but also by energy balance and energy flux (Rosenbaum *et al.* 1997; Warden *et al.* 1998). Leptin production is also influenced strongly by both insulin, a major regulator of energy metabolism, and gonadal steroids (Rosenbaum & Leibel 1999; Carmina *et al.* 1999). Hence, the information carried by leptin levels is a complex signal reflecting energetic variables, gender, and reproductive state. Finally, there is increasing evidence that ovarian function is subject to regulation by major metabolic hormones, including insulin and growth hormone (Poretsky *et al.* 1999; Yoshimura *et al.* 1993). Insulin in particular stimulates the ovarian response to gonadotropins (Willis *et al.* 1996). Insulin levels increase under conditions that favor energy storage and therefore help to promote ovarian function at such times.

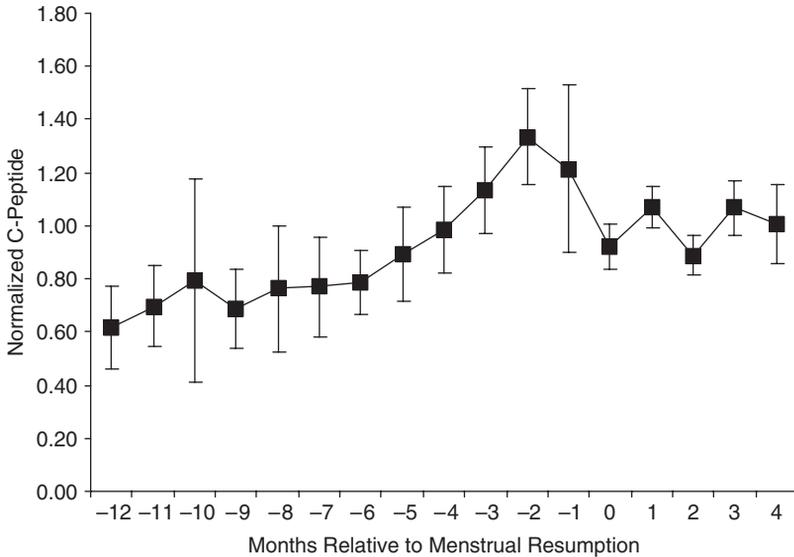


Figure 13.1 C-peptide levels (mean \pm standard error) in relation to the resumption of menstrual cycles postpartum in 70 lactating Toba women from northern Argentina, expressed as a fraction of each individual's average level when menstruating regularly. C-peptide is a marker of insulin production.

The resumption of ovarian function postpartum is also sensitive to energetic variables (Valeggia & Ellison 2001). Intensive lactation represents a particularly high state of energy flux that is usually associated with suppressed ovarian activity (Ellison 1995). It appears that this low level of ovarian activity is more a function of suppressed responsiveness to gonadotropin stimulation than a function of low gonadotropin stimulation itself (McNeilly *et al.* 1994). As the metabolic demand of lactation declines, particularly with the introduction of supplementary foods to the infant's diet, ovarian function resumes. Resumption of ovarian function is correlated closely with a shift in energy balance reflected in rising insulin levels (Valeggia & Ellison 2001; Ellison & Valeggia 2003). The rise in insulin levels is, in turn, implicated in the restoration of ovarian responsiveness to gonadotropin stimulation (Fig. 13.1).

The sensitivity of ovarian function to energetic variables provides a mechanism by which ecological constraints on energy availability for reproduction can affect the probability of conception. It is likely that this sensitivity is adaptive and reflects the action of natural selection (Ellison 2001). Given that reproduction represents a sizable metabolic commitment for a female over and above her own maintenance requirements, success

will be dependent on the ability of the female to divert energy to reproduction. Positive energy balance is the single best predictor of such excess energy availability, and negative energy balance is a strong predictor of constraint. High and low energy flux ordinarily also indicate a situation of constrained energy availability for humans, the former representing high workloads and the latter inadequate intakes (Jasienska 2001). Energy status, perhaps counterintuitively, is often a poor indicator of current energetic constraints, being more reflective of past history than of current conditions. The sensitivity of ovarian function to these signals of energetic constraint may well have evolved because energetic constraints have such an immediate impact on the ability of a female to meet the metabolic demands of reproduction.

When ecological constraints on energy availability vary seasonally, they can result in a seasonal pattern of conceptions and births. This pathway has been traced in detail for the Lese, a group of slash-and-burn horticulturalists living in the Ituri Forest of the Democratic Republic of the Congo (Ellison *et al.* 1989; Bailey *et al.* 1992). The subsistence ecology, reproductive ecology, and demography of the Lese were studied for over a decade, from the early 1980s to the early 1990s. Long-term data revealed a typical "hunger" season between January and June, when food stores from the previous year's harvest become progressively depleted. During the hunger season, most individuals in the population lose weight, indicating negative energy balance. Indices of ovarian function, including levels of estradiol and progesterone, frequency of ovulation, and duration of menstruation all decline in parallel with weight during this period, while the average intermenstrual interval increases. With the onset of the new harvest season in June, body weights begin to increase and the indices of ovarian function improve. As one would predict from this pattern of ovarian function, the distribution of births and backdated conceptions over the decade of observation indicates a dearth of conceptions during the hunger season and a peak in conceptions during the period of positive energy balance following the new harvests. Variation in the severity of the hunger season between years was also correlated with variation in the degree of conception clustering.

Birth seasonality in the western Toba community of Vaca Perdida

Other agricultural populations show similar patterns of birth seasonality correlated with harvests and either observed or imputed variation in energy balance. Foraging populations are often but not always, buffered

from extreme seasonality by their ability to shift between food resources, (Hurtado & Hill 1990). One example of birth seasonality associated with a foraging subsistence ecology is presented by our current work with the indigenous populations of northern Argentina.

The Toba, who belong to the Guaycuruan linguistic family, are one of the many indigenous peoples inhabiting the Gran Chaco of South America (Miller 1999). Historically, these populations have been semi-nomadic, hunter-gatherers. Nowadays, Chacoan Indians can be found in sedentary villages with different degrees of acculturation, from rural communities relying on the forest and river for most of their subsistence to urban communities with cash economy.

Vaca Perdida is a Toba village of approximately 250 people located in western Formosa, northern Argentina. The western region of the Gran Chaco is characterized by low xeric vegetation, patches of thorny bushes, bromeliads, and cacti. Seasonal changes in temperature and resources are pronounced. The first rains of September mark the beginning of the rainy and "bountiful" season. During the summer, western Toba have abundant food from the forest, such as game, fruits, and honey. The highlight of the season is the collection of algarroba (*Prosopis alba*) fruits, which reaches its peak in December (Mendoza 1999). Riverine communities enjoy a second bountiful season during the winter (June–July), as this is when fish in the Pilcomayo River are most abundant (Mendoza 1999).

The western Toba have been experiencing a profound ecological and cultural transition, which started in the 1930s with the arrival of the Anglican church missionaries (Gordillo 1994). One of the most important changes in their lifestyle has been the sedentarization of their communities, including Vaca Perdida. However, until the late 1980s, most villagers were still relying heavily on hunting, fishing, and gathering for their subsistence. During the late 1980s and early 1990s, the subsistence economy changed from mostly hunting/gathering to a newly acquired cash economy. However, during the last half of the 1990s, many men lost their cash-paid jobs (Gordillo 2002). For the past five years, at the time of writing, many families in Vaca Perdida have relied on a combination of foraging and temporary jobs.

We analyzed a total of 256 births from 105 women, corresponding to all births occurring in Vaca Perdida between 1980 and 2001, to determine whether the changes in subsistence ecology were associated with changes in birth seasonality. We divided the sample into three groups: births occurring before the transition to market economy (1980–86, $n = 78$), births occurring during the increase in male waged labor (1987–1993, $n = 78$), and births occurring after the transition (1994–2001, $n = 100$). There was a marked

seasonal variation in food availability and reduced the seasonal energy expenditure associated with foraging (Gordillo 1994). Although not as seasonal as the 1980–86 period, conceptions occurring during the socioeconomically unstable mid and late 1990s are less frequent during the winter (Fig. 13.2c). Informal interviews with Vaca Perdida villagers indicated that the winter is a “bad time for *changas* [temporary jobs]” and that younger men “have forgotten” how to fish and have developed a preference for store-bought food. Therefore, they say, the winter has become their hunger season.

These data are preliminary and should be taken with caution due to the small sample size. However, they do suggest that changes in the subsistence ecology of the Vaca Perdida community are associated with changes in the degree of birth seasonality that they experience. We are currently collecting reproductive histories and hormonal data on seven other villages in the area, which should help to further test the relationship between food availability and fecundity in this region.

Energetics and birth seasonality in other great apes

Although it has been known for some time that apes do not exhibit restricted birth seasons, seasonal distributions in the frequency of births have become evident as a result of long-term field studies. Early reports suggested the possibility of birth peaks for mountain gorillas (Lancaster & Lee 1965), gibbons (Lindburgh 1987), and chimpanzees (Goodall 1986), but small sample sizes and long interbirth intervals made it difficult to observe and document reproductive seasonality for apes in the wild. Over the past decade or so, a clearer picture has emerged with respect to chimpanzees as data continue to accumulate from long-term field studies in a diverse set of habitats and locations.

Chimpanzee communities are being studied in semideciduous woodlands at Gombe, Tanzania, in lakeshore forest at Mahale, Tanzania, in mid-altitude rainforest at Kibale, Uganda, in lowland rainforest at Taï, Ivory Coast, and in highland rainfall/secondary forest at Bossou, Guinea. Reports from Gombe (Wallis 1995, 1997), Mahale (Nishida 1990), Taï (Boesch & Boesch-Achermann 2000), and Kibale (Sherry 2002) indicate that seasonal birth peaks are a typical feature of chimpanzee reproduction in the wild. Like natural fertility populations of humans, births for chimpanzees generally take place throughout the year, but with notable peaks or clusters in certain seasons. For chimpanzees, the pattern of reproductive seasonality appears to be related to seasonal rainfall and changes in food supply (Wallis 1995; Nishida 1990; Boesch & Boesch-Achermann 2000).

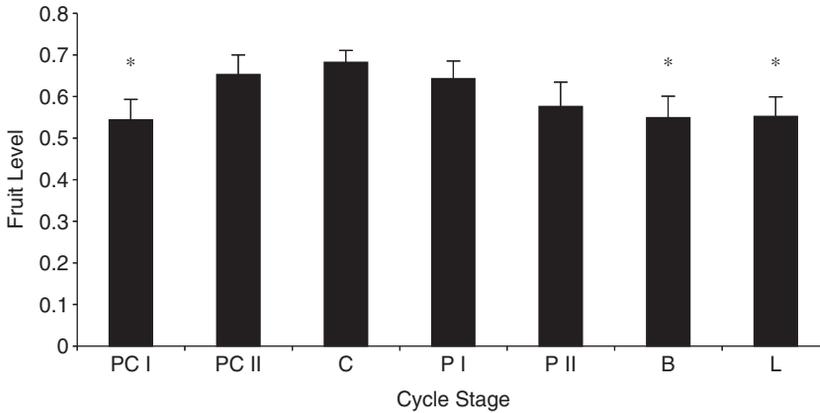


Figure 13.3 The fraction of observed feeding episodes (mean \pm standard error) per month that involved ripe fruit among reproductive female chimpanzees in Kibale, Uganda, by stage of the reproductive cycle. PCI, 3–4 months preconception; PCII, 1–2 months preconception; C, month of conception; PI, months 2–4 of pregnancy; PII months 5–7 of pregnancy; B, month of birth; L, first three months of lactation.

*Significantly different from C at the $P < 0.05$ level.

Recently, research at Kibale has focused on a more detailed, functional explanation of chimpanzee reproductive seasonality and has found that conceptions tend to occur during periods of increased food supply. Based on long-term feeding records and phenological data, Sherry (2002) has evaluated food availability and dietary quality across the various stages of the chimpanzee reproductive cycle. The most favorable feeding conditions were associated with the conception period rather than with birth or lactation. Conceptions occurred in association with periods in which high-quality food in the diet (ripe fruit and preferred succulent fruits) was both more abundant in the environment and recorded more frequently in feeding observations compared with both preceding and subsequent stages of the reproductive cycle (Fig. 13.3). The least favorable feeding conditions were associated with the birth window and early lactation phase of the reproductive cycle, both of which contained significantly lower proportions of ripe and succulent fruits in feeding observations compared with the conception period (analysis of variance [ANOVA], $P < 0.05$). The early lactation phase also showed the highest proportion of figs in feeding observations. Figs are considered a less preferred fallback food for chimpanzees at Kibale (Wrangham *et al.* 1993).

Additional evidence of an effect of energetics on the reproductive ecology of wild apes comes from orangutans in Borneo. Knott (1997b, 1998,

1999) (see also Chapter 10) has described the marked variation in food availability and diet quality experienced by orangutans at Gunung Palung, Borneo, as a result of the dramatic mast fruiting episodes that alternate with periods of pronounced scarcity of preferred fruits. Patterns of ketone excretion in urine samples indicate that the periods of fruit scarcity are associated with the catabolism of fat reserves. Steroid profiles measured from urine samples indicate that female ovarian function is suppressed during these periods, while higher steroid levels indicative of higher fecundity occur during the mast periods. Conceptions also are more likely during the periods of dramatic food abundance.

Adaptive significance of the connection between energetics and female fecundity

Ovarian function in human females appears to be sensitive to the availability of metabolic energy to support reproduction, with a result that conception probability is increased when energy balance is positive and decreased when energy balance is negative. Both high and low energy flux appear to suppress ovarian function. However, high and low energy flux represent conditions under which energy availability for reproduction is constrained, either by high energy expenditure on other functions or by low energy intake. In either case, the potential for allocating additional energy to reproduction is reduced. Hence, positive energy balance and moderate energy flux are conditions that favor a female's ability to allocate energy to reproduction. Energy status is not a particularly good marker of this ability, since it is more reflective of history than current state.

The ability to allocate energy to reproduction is particularly important in early pregnancy when fat is stored to offset the high energy demands of later pregnancy and early lactation. Pre-pregnancy weight and early gestational weight gain are both important predictors of birth weight, which is in turn a powerful predictor of infant survivorship (Villar *et al.* 1992). Other periods in the human reproductive cycle are more demanding of energy, however, than the period immediately after conception. Would it not be more adaptive to have a mechanism that would synchronize one of these other stages with periods of high energy availability?

The fact that humans share the pattern of increased conception probability during periods of high energy availability with other apes suggests that the adaptive significance of this pattern may lie in shared aspects of our ecology. One important factor may be the degree to which periods of high energy availability are predictable in advance. Preferred chimpanzee

food resources are notoriously patchy in space and time, and the masting episodes that characterize the Bornean rainforest are particularly irregular. It may well be that food resources in formative human environments were similarly unpredictable. Other features of our biology, such as our highly developed subcutaneous adipose deposits, suggest adaptation to unpredictable resources. In an unpredictable environment, optimizing energetic conditions at conception may have had a more positive effect on fitness than strategies dependent on predicting conditions in the future.

A second biological characteristic shared by humans and other apes is our relatively slow life history, with long periods of gestation and lactation periods that are both longer and lower in demand at their peaks than those of other mammals of comparable body size (Martin 1990; Oftedal 1984; Lee *et al.* 1991). This low but prolonged arc of energetic investment during reproduction effectively eliminates the pronounced peaks of energetic investment seen in most other mammals. For female apes, a low level of sustained energetic investment may have allowed a shift away from coordinating any one particular stage of the reproductive cycle with seasonal food availability and may have placed emphasis instead on female condition going into a reproductive bout.

These hypothesized scenarios for the selective advantage derived from coordinating conception with favorable energetic conditions are not mutually exclusive. It has been argued elsewhere (Ellison 2001) that unpredictable high-amplitude variation in energy availability in the environment may have been a particular feature of early hominid evolution, selecting for increased ability to sequester energy reserves as fat primarily in the service of survival rather than reproduction. Later in human evolution, this same ability may have been co-opted to support the development of an increasingly large-brained fetus. An enhanced sensitivity of female reproductive function to environmental energy constraints may have been a result. Nevertheless, it is likely that the general pattern of female reproduction being sensitive to environmental energy availability is much more ancient and typical of mammalian species with slow life histories and/or unpredictable environments. There is increasing evidence that this pattern is shared with other great apes at the very least.

Summary

The pattern of birth seasonality displayed by human populations around the world probably derives from multiple causes, with the most important factors varying between populations and through time. Three groups of

factors have been suggested most often as playing important roles: social factors affecting the frequency of intercourse; climatological factors affecting male and female fecundity; and energetic factors principally affecting female ovarian function. Continuity with broader primate patterns can be seen in all three. However, evidence is particularly compelling for phylogenetic continuity in the importance of energetic factors on female fecundity leading to a coordination of conception with periods of enhanced energy availability. The adaptive significance of a link between energetics and female fecundity may lie in optimizing female reproductive effort under conditions of unpredictable resources and/or under a prolonged pattern of heavily reproductive investment.

References

- Appell, R. A. & Evans, P. R. (1977). The effect of temperature on sperm motility and viability. *Fertility and Sterility*, **28**, 1329–32.
- Ayeni, O. (1986). Seasonal variation in births in rural southwestern Nigeria. *International Journal of Epidemiology*, **15**, 91–4.
- Bailey, R. C., Jenike, M. R., Ellison, P. T., *et al.* (1992). The ecology of birth seasonality among agriculturalists in central Africa. *Journal of Biosocial Science*, **24**, 393–412.
- Bedford, J. M. (1977). Evolution of the scrotum: the epididymis as prime mover? In *Reproduction and Evolution*, ed. J. H. Calaby & P. Tynsdale-Biscoe. Canberra: Australian Academy of Science, pp. 171–82.
- (1991). Effects of elevated temperature on the epididymis and the testis: experimental studies. In *Advances in Experimental Biology and Medicine: Temperature and Environmental Effects on the Testis*, ed. A. W. Zorngiotti. New York: Plenum, pp. 19–32.
- Boesch, C. & Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest: Behavioral Ecology and Evolution*. Oxford: Oxford University Press.
- Bojkowski, C. J., Aldhous, M. E., English, J., *et al.* (1987). Suppression of nocturnal plasma melatonin and 6-sulphatoxy melatonin by bright and dim light in man. *Hormone and Metabolic Research*, **19**, 437–40.
- Boyar, R. M., Katz, J., Finkelstein, J. W., *et al.* (1974). Anorexia nervosa: immaturity of the 24-hour luteinizing hormone secretory pattern. *New England Journal of Medicine*, **297**, 861–65.
- Brannian, J. D., Zhao, Y., & McElroy, M. (1999). Leptin inhibits gonadotrophin-stimulated granulosa cell progesterone production by antagonizing insulin action. *Human Reproduction*, **14**, 1445–8.
- Brewis, A., Laylock, J., & Huntsman, J. (1996). Birth non-seasonality on the Pacific equator. *Current Anthropology*, **87**, 842–51.
- Bronson, F. H. (1989). *Mammalian Reproductive Biology*. Chicago: University of Chicago Press.

- Bronson, F. H. (1995). Seasonal variation in human reproduction: environmental factors. *Quarterly Review of Biology*, **70**, 141–64.
- Brzezinski, A. & Wurtman, R. J. (1988). The pineal gland: its possible roles in human reproduction. *Obstetric and Gynecological Survey*, **43**, 197–207.
- Carmina, E., Ferin, M., Gonzalea, F., & Lobo, R. (1999). Evidence that insulin and androgens may participate in the regulation of serum leptin levels in women. *Fertility and Sterility*, **72**, 926–31.
- Chik, C. L., Almeida, O. F. X., Libre, E. A., *et al.* (1992). Photoperiod-driven changes in reproductive function in male rhesus monkeys. *Journal of Clinical Endocrinology and Metabolism*, **74**, 1068–74.
- Condon, R. G. (1982). Inuit natality rhythms in the central Canadian arctic. *Journal of Biosocial Science*, **14**, 167–77.
- Condon, R. G. & Scaglione, R. (1982). The ecology of human birth seasonality. *Human Ecology*, **10**, 495–510.
- Cowgill, U. M. (1965). Season of birth in man, contemporary situation with special reference to Europe and the Southern Hemisphere. *Ecology*, **47**, 614–23.
- Danubio, M. E. & Amicone, E. (2001). Biodemographic study of a central Apennine area (Italy) in the 19th and 20th centuries: marriage seasonality and reproductive isolation. *Journal of Biosocial Science*, **33**, 427–49.
- Dixon, G., Eurman, P., Stern, B. E., Schwartz, B., & Rebar, R. W. (1984). Hypothalamic function in amenorrheic runners. *Fertility and Sterility*, **42**, 377–83.
- Dyson, T. & Crook, N. (1981). Seasonal patterns of births and deaths. In *Seasonal Dimensions to Rural Poverty*, ed. R. Chambers, R. Longhurst, & A. Pacey. London: Pinter, pp. 135–62.
- Ellison, P. T. (1995). Breastfeeding, fertility, and maternal condition. In *Breastfeeding: Biocultural Perspectives*, ed. K. A. Dettwyler & P. Stuart-Macadam. Hawthorne, NY: Aldine de Gruyter, pp. 305–45.
- (2001). *On Fertile Ground*. Cambridge, MA: Harvard University Press.
- Ellison, P. T. & Lager, C. (1986). Moderate recreational running is associated with lowered salivary progesterone profiles in women. *American Journal of Obstetrics and Gynecology*, **154**, 1000–1003.
- Ellison, P. T. & Vaggia, C. R. (2003). C-peptide levels and the duration of lactational amenorrhea. *Fertility and Sterility*, **80**, 1279–80.
- Ellison, P. T., Peacock, N. R., & Lager, C. (1989). Ecology and ovarian function among Lese females of the Ituri Forest, Zaire. *American Journal of Physical Anthropology*, **78**, 519–26.
- Ferin, M. (1999). Stress and the reproductive cycle. *Journal of Clinical Endocrinology and Metabolism*, **84**, 1768–74.
- Flier, J. S. (1998). What's in a name? In search of leptin's physiologic role. *Journal of Clinical Endocrinology and Metabolism*, **83**, 1407–13.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.
- Gordillo, G. (1994). La presión de los más pobres: reciprocidad, diferenciación social y conflicto entre los Tobas del oeste de Formosa. *Cuadernos del Instituto Nacional de Antropología y Pensamiento Latinoamericano*, **15**, 53–82.

- (2002). Locations of hegemony: the making of places in the Toba's struggle for *La Comuna*, 1989–99. *American Anthropologist*, **104**, 262–77.
- Huntington, E. (1938). *Season of Birth*. New York: John Wiley & Sons.
- Hurtado, A. M. & Hill, K. R. (1990). Seasonality in a foraging society: variation in diet, work effort, fertility, and sexual division of labor among the Hiwi of Venezuela. *Journal of Anthropological Research*, **46**, 293–346.
- Huss-Ashmore R. (1988). Seasonal patterns of birth and conception in rural highland Lethoto. *Human Biology* **60**, 493–506.
- Illnerova, H., Zvolsky, P., & Vanecek, J. (1985). The circadian rhythm in plasma melatonin concentration of the urbanized man: the effect of summer and winter time. *Brain Research*, **328**, 186–9.
- Jasienska, G. (2001). Why energy expenditure causes reproductive suppression in women: an evolutionary and bioenergetic perspective. In *Reproductive Ecology and Human Evolution*, ed. P. T. Ellison. New York: Aldine de Gruyter, pp. 59–84.
- Jasienska, G. & Ellison, P. T. (1998). Physical work causes suppression of ovarian function in women. *Proceedings of the Royal Society of London B*, **265**, 1847–51.
- Kandeel, F. R. & Swerdloff, R. S. (1988). Role of temperature in regulation of spermatogenesis and the use of heating as a method for contraception. *Fertility and Sterility*, **49**, 1–23.
- Karsch, F. J., Bittman, E. L., Foster, D. L., *et al.* (1984). Neuroendocrine basis of seasonal reproduction. *Recent Progress in Hormonal Research*, **40**, 185–232.
- Kauppila, A., Kivelä, A., Pakarinen, A., & Vakkuri, O. (1987). Inverse seasonal relationship between melatonin and ovarian activity in humans in a region with a strong seasonal contrast in luminosity. *Journal of Clinical Endocrinology and Metabolism*, **65**, 823–8.
- Knott, C. D. (1997a). Interactions between energy balance, hormonal patterns and mating behavior in wild Bornean orangutans (*Pongo pygmaeus*). *American Journal of Physical Anthropology*, **24**, 145.
- (1997b). Interactions between energy balance, hormonal patterns and mating behavior in wild Bornean orangutans (*Pongo pygmaeus*). *American Journal of Primatology*, **42**, 124.
- (1998). Changes in orangutan diet, caloric intake and ketones in response to fluctuating fruit availability. *International Journal of Primatology*, **19**, 1061–79.
- (1999). Reproductive, physiological, and behavioral responses of orangutans in Borneo to fluctuations in food availability. Ph.D. thesis, Harvard University.
- (2001). Female reproductive ecology of the apes: implications for human evolution. In *Reproductive Ecology and Human Evolution*, ed. P. T. Ellison. New York: Aldine de Gruyter, pp. 429–64.
- Lager, C. & Ellison, P. T. (1990). Effect of moderate weight loss on ovarian function assessed by salivary progesterone measurements. *American Journal of Human Biology*, **2**, 303–12.
- Lam, D. & Miron, J. (1991). Seasonality of births in human populations. *Social Biology*, **38**, 51–78.

- (1994). Global patterns of seasonal variation in human fertility. *Annals of the New York Academy of Sciences*, **709**, 9–28.
- (1996). The effect of temperature on human fertility. *Demography*, **33**, 291–305.
- Lancaster, J. B. & Lee, R. B. (1965). The annual reproductive cycle in monkeys and apes. In *Primate Behavior: Field Studies of Monkeys and Apes*, ed. I. DeVore. New York: Holt, Rinehart, & Winston, pp. 486–513.
- Lee, P. C., Majluf, P., & Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of Zoology*, **225**, 99–114.
- Levine, R. J. (1994). Male factors contributing to seasonality of human reproduction. *Annals of the New York Academy of Sciences*, **709**, 29–45.
- Levine, R. J., Bordson, B. L., Mathew, R. M., *et al.* (1988). Deterioration of semen quality during summer in New Orleans. *Fertility and Sterility*, **49**, 900–907.
- Lindburgh, W. G. (1987). Seasonality of reproduction in primates. In *Comparative Primate Biology*, Vol. 2B. Behavior, Cognition, and Motivation, ed. W. R. Dukelow & J. Erwin. New York: Alan R. Liss, pp. 167–218.
- Lipson, S. F. & Ellison, P. T. (1996). Comparison of salivary steroid profiles in naturally occurring conception and non-conception cycles. *Human Reproduction*, **11**, 2090–96.
- Loucks, A. B. (1990). Effects of exercise training on the menstrual cycle: existence and mechanisms. *Medicine and Science in Sports and Exercise*, **22**, 275–80.
- Loucks, A. B., Mortola, J., Girton, L., & Yen, S. (1989). Alterations in the hypothalamic-pituitary-ovarian and hypothalamic-pituitary-adrenal axes in athletic women. *Journal of Clinical Endocrinology and Metabolism*, **68**, 402–11.
- Malina, R. M. & Himes, J. H. (1977). Seasonality of births in a rural Zapotec Municipio, 1945–1970. *Human Biology*, **49**, 125–37.
- Martin, R. D. (1990). Primate reproductive biology. In *Primate Origins and Evolution: A Phylogenetic Reconstruction*, ed. R. D. Martin. Princeton: Princeton University Press, pp. 427–75.
- Matthews, C. D., Guerin, M. V., & Wang, X. (1991). Human plasma melatonin and urinary 6-sulphatoxy melatonin: studies in natural annual photoperiod and extended darkness. *Clinical Endocrinology*, **35**, 21–7.
- McNeilly, A. S., Tay, C. C. K., & Glasier, A. (1994). Physiological mechanisms underlying lactational amenorrhoea. *Annals of the New York Academy of Sciences*, **709**, 145–55.
- Mendoza, M. (1999). The western Toba: family life and subsistence of a former hunter-gatherer society. In *Peoples of the Gran Chaco*, ed. E. S. Miller. Westport, CT: Bergin & Garvey, pp. 81–108.
- Menken, J. (1979). Seasonal migration and seasonal variation in fecundability: effects on birth rates and birth intervals. *Demography*, **16**, 103–19.
- Miller, E. (1999). Peoples of the Gran Chaco. *Native Peoples of the Americas*. Westport, CT: Bergin & Garvey.
- National Center for Health Statistics. (1966). *Seasonal variation of births: United States, 1933–1963. Series 21, no. 9*. Washington, DC: US Government Printing Office.

- Nishida, T. (1990). Demography and reproductive profiles. In *The Chimpanzees of the Mahale Mountains*, ed. T. Nishida. Tokyo: University of Tokyo Press, pp. 63–97.
- Oftedal, O. T. (1984). Milk composition, milk yield and energy output at peak lactation: a comparative review. *Symposia of the Zoological Society of London*, **51**, 33–85.
- Pascual, J., Gardia-Moro, C., & Hernandez, M. (2000). Non-seasonality of births in Tierra del Fuego (Chile). *Annals of Human Biology*, **27**, 517–24.
- Pirke, K. M., Schweiger, U., Lemmel, W., Krieg, J. C., & Berger, M. (1985). The influence of dieting on the menstrual cycle of healthy young women. *Journal of Clinical Endocrinology and Metabolism*, **60**, 1174–9.
- Poretsky, L., Cataldo, N. A., Rosenwaks, Z., & Giudice, L. C. (1999). The insulin-related ovarian regulatory system in health and disease. *Endocrine Reviews*, **20**, 535–82.
- Prentice, A. M. & Whitehead, R. G. (1987). The energetics of human reproduction. *Proceedings of the Royal Society of London*, **57**, 275–304.
- Rajan, S. I. & James, K. S. (2000). The interdependence of vital events: twentieth-century Indian Kerala. *Journal of Interdisciplinary History*, **31**, 21–41.
- Rosenbaum, M. & Leibel, R. L. (1999). Role of gonadal steroids in the sexual dimorphisms in body composition and circulating concentrations of leptin. *Journal of Clinical Endocrinology and Metabolism*, **84**, 1784–9.
- Rosenbaum, M., Nicolson, M., Hirsch, J., *et al.* (1997). Effects of weight change on plasma leptin concentrations and energy expenditure. *Journal of Clinical Endocrinology and Metabolism*, **82**, 3647–54.
- Seiver, D. A. (1989). Seasonality of fertility: new evidence. *Population and Environment*, **10**, 245–57.
- Sherry, D. S. (2002). Reproductive seasonality in chimpanzees and humans: ultimate and proximate factors. Ph. D. thesis, Harvard University.
- Spicer, J. L. & Francisco, C. C. (1997). The adipose gene product, leptin: evidence of a direct inhibitory role in ovarian function. *Endocrinology*, **138**, 3374–9.
- Stoeckel, J. & Chowdhury, A. (1972). Seasonal variation in births in rural East Pakistan. *Journal of Biosocial Science*, **4**, 107–16.
- Tamarkin, L., Baird, C. J., & Almeida, O. F. X. (1985). Melatonin: a coordinating signal for mammalian reproduction? *Science*, **263**, 1118–21.
- Thompson, R. W. & Robbins, M. S. (1973). Seasonal variation in conception in rural Uganda and Mexico. *American Anthropologist*, **75**, 676–81.
- Udry, J. R. & Morris, N. M. (1967). Seasonality of coitus and seasonality of birth. *Demography*, **4**, 673–81.
- Valeggia, C. R. & Ellison, P. T. (2001). Lactation, energetics, and postpartum fecundity. In *Reproductive Ecology and Human Evolution*, ed. P. T. Ellison. New York: Aldine de Gruyter, pp. 85–105.
- Veldhuis, J. D., Evans, W. S., Demers, L. M., *et al.* (1985). Altered neuroendocrine regulation of gonadotropin secretion in women distance runners. *Journal of Clinical Endocrinology and Metabolism*, **60**, 557–63.
- Vigersky, R. A., Anderson, A. E., Thompson, R. H., & Loriaux, D. L. (1977). Hypothalamic dysfunction in secondary amenorrhea associated with simple weight loss. *New England Journal of Medicine*, **297**, 1141–5.

- Villar, J., Cagwell, M., Kestler, E., *et al.* (1992). Effect of fat and fat-free mass deposition during pregnancy on birth weight. *American Journal of Obstetrics and Gynecology*, **167**, 1344–52.
- Wallis, J. (1995). Seasonal influence on reproduction in chimpanzees of Gombe National Park. *International Journal of Primatology*, **16**, 533–49.
- (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. *Journal of Reproduction and Fertility*, **109**, 297–307.
- Warden, T. A., Considine, R. V., Foster, G. D., *et al.* (1998). Short- and long-term changes in serum leptin in dieting and obese women: effects of caloric restriction and weight loss. *Journal of Clinical Endocrinology and Metabolism*, **83**, 214–18.
- Wehr, T. A. (1991). The durations of human melatonin secretion and sleep respond to changes in daylength (photoperiod). *Journal of Clinical Endocrinology and Metabolism*, **73**, 1276–80.
- (2001). Photoperiodism in humans and other primates: evidence and implications. *Journal of Biological Rhythms*, **16**, 348–64.
- Wehr, T. A., Moul, D. E., Barbato, G., *et al.* (1993). Conservation of photoperiod-responsive mechanisms in humans. *American Journal of Physiology*, **265**, R846–57.
- Willis, D., Mason, H., Gilling-Smith, C., & Franks, S. (1996). Modulation by insulin of follicle-stimulating hormone and luteinizing hormone actions in human granulosa cells of normal and polycystic ovaries. *Journal of Clinical Endocrinology and Metabolism*, **81**, 302–9.
- Wilson, M. E. & Gordon, T. P. (1989). Short-day melatonin pattern advances puberty in seasonally breeding rhesus monkeys (*Macaca mulatta*). *Journal of Reproduction and Fertility*, **86**, 435–44.
- Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In *Great Ape Societies*, ed. P. Kappeler. Cambridge: Cambridge University Press, pp. 248–58.
- Wrangham, R. W., Conklin, N. L., Etot, G., *et al.* (1993). The value of figs to chimpanzees. *International Journal of Primatology*, **14**, 243–56.
- Yoshimura, Y., Makamura, Y., Koyama, N., *et al.* (1993). Effects of growth hormone on follicle growth, oocyte maturation, and ovarian steroidogenesis. *Fertility and Sterility*, **59**, 917–23.

