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Reproduction is energetically expensive. While the physiological cost is primarily born by the mother, males of many species use considerable energy both to mate and to aggressively prevent other males from mating. As an adaptation to these high energy costs, mating of many species is restricted to a specific season. The timing of when mating occurs ensures that females have a maximal food supply during the energetically expensive periods of late pregnancy and lactation. For example, wild sheep living in Northern latitudes breed in the fall and lambs are born in the spring. For males, a specific breeding season restricts the biological and behavioral costs of breeding to the time of year when females are fertile. The onset of the breeding season has specific physiological underpinnings and is associated with activation of the hypothalamic-pituitary-testis axis. Thus, the synchronization of this axis to specific environmental cues is important to the reproduction of males of many species.

While men are not seasonal breeders, there is evidence that season and other environmental cues affect human male reproduction. Herein we summarize data on the effects of season, time of day, temperature, and nutrition on sperm numbers, morphology, or function and on serum levels of testosterone (T) and Luteinizing Hormone (LH).

The effects of season and time of day on male reproduction.

Even though modern societies buffer most of their inhabitants from changes in the seasons, these changes nonetheless affect reproduction. Conceptions vary seasonally in many countries in the Northern hemisphere, with peaks occurring in late spring. However, seasonal effects were substantially greater in the past when communities and homes lacked electric lighting, when homes and workplaces were

not efficiently heated or cooled, and when the ability to obtain, store and distribute nutritious food was limited.

Current data indicate that seasonality in conceptions is associated with changes in numbers of sperm in the ejaculate. Independent studies of healthy men from Boston and from Denmark reported that sperm counts are highest in spring, lowest in summer and intermediate in fall and winter. A study of men from San Antonio, Texas, compared sperm counts in summer and winter. Consistent with the data from Boston and Denmark, Texans had lower sperm counts in the summer.

Numerous studies have tested the hypothesis that a man's serum T levels vary with the season. Results from many but not all studies support this hypothesis, and most of those studies identify peak serum T levels as occurring in late spring. However, others report that T levels peak in late fall or early winter. Discrepancies between different studies may be due to differences in their designs. Some studies have relied on the measurement of testosterone in single serum samples collected from thousands of men at different months and at unrecorded times of day. Differences between individuals and effect of time of day cannot be accounted for during the statistical analysis of those studies

One study of men living in the State of Washington was particularly well-designed. That study used a repeated measures design, where serum hormone levels were measured each month in sixteen healthy men, 19-42 years of age. Importantly each serum sample was collected from a given man at the same time of day. Results demonstrated a significant effect of season on serum T concentrations, with levels of this hormone peaking in May and June.

In many experimental and domestic male animals, serum T levels not only change with season but also with the time-of-day. Diurnal changes in levels of this hormone have also been reported to occur in men, with T levels peaking in early morning and falling to their nadir by early evening.

In summary, even though artificial lighting and central heat and air conditioning buffer most individuals in highly developed countries from seasonal and diurnal cues, there is evidence that these cues still affect a man's reproductive function. Human conceptions, sperm counts and serum testosterone levels peak in the spring. The time of day is also important for serum T levels are highest in early morning.

Physiological mechanisms underpinning seasonal and diurnal changes in a man's serum T levels.

The mechanisms regulating seasonal and diurnal cycles of serum T levels in men are poorly understood. However, data support the conclusion that LH is an important proximal regulator. The previously noted study of men from Washington State demonstrated not only that serum T levels were elevated in May and June, so, too were their serum LH levels. Changes in serum T and LH levels throughout the day are also significantly correlated. Multiple studies of testosterone and LH levels in serum collected every 10-20 minutes from healthy men have revealed a significant relationship between spikes in serum LH levels and spikes in serum T levels; a spike in LH is followed within one to two hours by a spike in testosterone.

What remain to be identified are the molecules and mechanisms regulating diurnal and seasonal changes in serum LH levels of men. In species that are strict seasonal breeders, the pineal gland, and its hormonal product, melatonin, play a significant role in the regulation of LH secretion by gonadotropes. In all seasonal breeders that have been studied, melatonin levels are higher at night than in the day and melatonin secretion decreases as days grow longer and increases as days grow shorter. Depending on whether a species breeds during the summer or winter, a decrease in serum melatonin increases or decreases secretion of LH, respectively. For example, when male arctic foxes, who breed in the winter, were implanted with melatonin pellets during the arctic summer, the initiation of the winter rise in serum T levels was advanced by two months and the testicular regression that normally occurred with the end of the breeding season was blocked. In contrast, melatonin inhibits the ability of long (summer-like) days to stimulate spermatogenesis in Djungarian hamsters. While mechanisms of action of melatonin are not completely defined, in some species, melatonin increases GnRH secretion. In other species, melatonin suppresses LH secretion, or suppresses gonadotropin-stimulated steroidogenesis. However, a role for melatonin in seasonal changes in human male reproduction has not been established. While numerous human studies have reported that serum melatonin levels peak in the night, changes in day length do not consistently alter this hormone's levels. Furthermore, there is no convincing evidence that a sustained increase in serum melatonin levels affects serum LH or T levels in men. Thus, it remains an open question as to whether melatonin plays an important role in human male reproduction.

The effects of heat on male reproduction.

While there is no definitive evidence that changes in day length drive seasonal changes in a man's serum LH levels or sperm counts, there is evidence that very high summer temperatures can affect sperm. A study of the effects of ambient air temperature on sperm in an ejaculate demonstrated that excessive heat and, interestingly, extreme cold, significantly reduce sperm count, concentration, and motility. Effects of high heat are also observed in men who take sauna baths. A single, 15-20 minutes sauna session (80° to 100°C dry heat) was reported to cause swelling of the plasma membranes of sperm in the ejaculate, and to-disorganization of the arrangement of their mitochondria. Repeated sauna sessions (2 sessions per week for 3 months) reduced sperm counts, concentration and progressive motility by 50%. A return to normal did not occur until 3 and 6 months after the last sauna bath. It is worth noting, however, that there are no reports that saunas reduce a man's serum testosterone levels.

Nutrition and male reproduction.

Food, like light and temperature is an important component of our environment. Many individuals in highly developed countries have access to adequate nutrition year-round. But some individuals are malnourished because they live in a food desert or suffer from an eating disorder. Thus, it is noteworthy that there is growing evidence that nutrition has a significant impact on male reproduction, even in apparently healthy men. For example, when non-obese men with low sperm counts ate a well characterized, healthy Nordic diet for one week, there was a significant increase in the numbers of motile sperm in their ejaculates. Greek men who strictly adhered to a Mediterranean diet (fresh vegetables and fruit, fish, and whole grains) are reported to have higher sperm counts and motility than Greek men who infrequently eat such a diet.

Effects of malnourishment on male fertility are evident in obese men, who often do not consume a healthy, balanced diet. In a metanalysis of 30 publications, Campbell and colleagues concluded that obese men are more likely to be infertile, to have higher percentage of morphologically abnormal sperm and to have a reduced rate of live births per IVF cycle. Furthermore, clinical studies demonstrate that obese men tend to have lower sperm counts and serum testosterone levels.

In summary, access and consumption of healthy diet has a significant effect on a man's fertility.

Conclusion

While most males in developed countries are less affected by environmental cues than their ancestors, there is evidence that cues from their environment still affect the number and motility of ejaculated sperm as well as serum LH and testosterone levels. The changes in the seasons, the progression of the day, excessive heat and availability and consumption of nutritious food can all impact a man's reproductive function. It follows that changes in the geographic locations of a man's home, when and where he works, and his access to a balanced, nutritious diet may affect his reproductive potential.

Suggested reading

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