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Dynamics and regulation of goat reproduction

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A B S T R A C T

Goats are the most important and beneficial animal for common rural people of India for their nutritious milk, delicious meat and leather and thus regarded as “Poor Man’s Cow” in India. Despite of being such an economically beneficial animal, the management of goat reproduction was mostly neglected by veterinarians for a long period of time. Further, goats are the ruminant short day breeders and seasonality in terms of reproduction is prevalent in this animal under different environmental and experimental conditions. But, till date reports are limited considering the reproduction in this animal model. Neurohormone melatonin is universally regarded as pro-inflammatory and anti-stress hormone but the role of melatonin in modulation of reproduction is species specific. In some species it is anti-gonadotrophic in nature and some species it is pro-gonadotrophic. Melatonin modulation of reproduction can be explained by affecting hypothalamo-pituitary-gonadal (HPG) Axis. In case of goats, reproduction is performed under the positive influence of melatonin. The present review article elaborates the key features of dynamicity of goat reproduction, the different experimental conditions (e.g. hormonal treatment, exposure to photoperiod) which may affect the goat reproduction with a special focus on energy requirement as reproduction is one of the most energy demanding processes.

Introduction

Goats are cosmopolitan and found across all agro-ecological environments and nearly in all livestock production systems. The goat is known as a poor man’s cow all over the world. In Switzerland, the milk goat is said to be the “Swiss baby’s foster mother”. The goat is an animal that adapts itself readily to almost any climate. India is bestowed with

17% of total world’s goat population comprised of 21 recognized and many non-descript local breeds (Mir *et al.*, 2013). The goat is the principal meat producing animal in India and its flesh is preferred over other animals’ meat. Goats’ flesh also provides better price than mutton and beef in most of the urban markets. Mohair from Angora

goats and Pashmina from Kashmiri goats are greatly valued for the manufacture of superior dress fabrics and shawls. The intestines of goats are used to make cat-gut. The average milk production of a (Indigenous/local) doe in India is 55 kilograms per lactation term. Goats along with sheep have an important role in income generation, capital storage, employment generation and improving household nutrition. The manures of goats are used as herbal fertilizers by the rural Indians (Halder and Ghosh, 2014). Further, goats are ruminant short day breeder (Kaushalendra and Halder, 2012) and their reproductive processes and behavior are regulated by different environment cues (like photoperiod, availability of food etc.). Despite of being such economically important animal the regulation of goat reproduction is still less explored except for some partial reports (Zarazaga *et al.*, 2009, 2012). Thus, the present review elaborates the key features of dynamicity of goat reproduction, the different experimental conditions (e.g. hormonal treatment, exposure to photoperiod) which may affect the goat reproduction with a special focus on energy requirement as reproduction is one of the most energy demanding processes.

Reproduction in goats

Estrous cycle in goats

During the course of the breeding season, females can undergo several estrous cycles successively and the number of successive cycles is dependent on the length of the breeding season and the breed of goat. The length of estrous cycle is defined by the interval between two successive expressions of estrus or two successive ovulations. While the average duration of the goat estrous cycle is of 21 days, its length is highly variable. A study with Alpine goats

during the breeding season recorded 77% cycles of normal in duration (17–25 days), 14% were short cycles (8 days in average) and 9% were long cycles (39 days in average; Baril *et al.*, 1993). The relative high frequency of short cycles is characteristic of goats and increases when ovulation is induced either just before or during breeding season. This proportion can be modulated by environmental factors such as photoperiod and nutrition.

Ovarian cycle and endocrine regulation

During the estrous cycle, ovaries undergo a number of morphological (follicular recruitment and growth), biochemical (follicle maturation) and physiological (endocrine regulations) changes leading to the ovulation. These cyclical changes in the gonads are referred to as the ovarian cycle. Follicular growth evolves in a wave-like manner throughout the cycle. A follicular wave is characterized by the sequence of three gonadotropin-dependent events in follicular growth: recruitment, selection and dominance (Driancourt, 2001). The follicle development is under influence of follicular waves (generally 2-6 in number) amongst them 3-4 waves are most prevalent. The last wave provides the ovulatory follicle. When double ovulations occur they are usually of follicles derived from the same wave, but in a few cases they derive from two consecutive follicle waves (Ginther and Kot, 1994). The ovarian cycle is classically divided in two phases: the follicular phase and the luteal phase. The follicular phase corresponds to the wave of follicle development providing the ovulatory follicle and involves maturation of gonadotropin-dependant follicles until ovulation (terminal growth). During the follicular phase, FSH secreted by the pituitary gland stimulates follicular growth. A cohort of gonadotropin-dependant antral follicles of 2–3mm of

diameter is recruited and follicles enter their terminal growth. Only 2–3 of these follicles reach 4mm diameter and are selected to enter the dominance phase. Under the influence of LH, they reach the pre-ovulatory stage (6–9 mm), while subordinate follicles degenerate (follicular atresia). The increase in peripheral concentrations of 17β -oestradiol, secreted by bigger follicles, induces estrous behavior and acts as a positive retro-control on the gonadotropic axis. The consequent increase in GnRH secretion induces the pre-ovulatory LH surge which induces ovulation 20–26 h later and subsequently luteinization of follicular cells.

The beginning of the follicular phase, before overt estrous behavior is observed, is also referred to as the proestrus. The estrous phase includes events from overt estrous behavior to ovulation. The luteal phase starts from the time of ovulation. About 5 days after the onset of estrus, cells of the ovulating follicle turn into luteal cells and form the corpus luteum (CL). They secrete progesterone causing its concentrations to increase and remain at a high level (>1 ng/ml) during 16 days. During this luteal phase, gonadotropin-dependant follicular growth continues in a wave-like manner but progesterone inhibits ovulation. At the end of the luteal phase, 16–18 days after estrus, prostaglandin $F2\alpha$ secreted by the non-gravid uterus induces the CL regression – called luteolysis – and the decrease of progesterone secretion. The decrease of plasma concentrations of progesterone gradually removes the inhibition of gonadotropic hormones secretion and a new follicular phase then commences (Baril *et al.*, 1993). The luteal phase is also called the post-estrous period, which can be divided in met-estrus, when peripheral concentrations of progesterone begin to rise, and di-estrus, when peripheral concentrations of

progesterone are high up to the start of luteolysis.

Cyclical changes in the cytology and secretions in the genital tract

During the estrous cycle, changes occur in the genital tract in order to facilitate sperm transport and fertilization and then to prepare for embryo implantation. Vaginal, cervical and uterine mucosa congest and become oedematous at the time of estrus due to high estrogen levels (Hamilton and Harrison, 1951). In addition, uterine, cervical and vaginal glands secrete important quantities of aqueous mucus, clear at the beginning of estrus then becoming more viscous and compact as the period of estrus continues.

The cervical mucus plays a central role in cervical function by controlling and directing sperm migration. Estrogens stimulate the secretion of sialomucin by mucus cells located at the bottom of the large cervical folds within the cervix. Sulfomucins are also secreted in smaller quantities by mucus cells on the upper parts of the cervical folds (Heydon and Adams, 1979). At estrus, the cervical mucus becomes more watery and penetrable to sperm, allowing their migration through the cervix. Cervical secretion is inhibited by the post-ovulation rise in peripheral progesterone. Different studies have recorded cytological changes in the genital tract of the female goat during the estrous cycle. The relationships between vaginal exfoliated cells and ovarian steroids secretion cycle have been well established in goats. This pattern of exfoliation of vaginal cells could be used to determine the estrous cycle status. In this respect, superficial cells appear to be associated with the pro-estrus, estrus and early met-estrus (Hulet and Shelton, 1980). Intermediate and parabasal

cells are observed in larger quantities during the progesterone dominated luteal phase. Exfoliated cells in the vaginal lumen are the result of rising peripheral estrogen which causes the vaginal wall to thicken. As the outermost layer moves further from the vascular supply, the cells keratinise and detach from the wall (Pérez-Martinez *et al.*, 1999).

Distribution of mast cells also varies depending on physiological changes during the estrous cycle in the goat reproductive tract and ovarian tissues. The numbers of mast cells in the ovary, uterus, uterine cervix and uterine tubes are highest on pro-estrus and lowest on met-estrus (Karaca *et al.*, 2008). Mastocytes are derived from haematopoietic precursors and represent critical effector-cells in allergic diseases. It is assumed that these cells might operate as sentinel cells to help mediate the uterine host defense systems and might have a role in the uterus with regard to the embryo implantation.

Estrous behavior in goats

Estrous behavior includes two phases: proceptivity and receptivity. Proceptivity consists in seeking out and stimulating the male partner. Receptivity consists in the expression of the immobilization reflex in response to male nudges, inducing serial mounting and copulation. At the beginning of estrus, proceptivity always precede receptivity, then both behavior components are expressed simultaneously the duration of estrous behavior is about 36 h but varies from 24 h to 48 h depending on age, individuals and breeds, season and the presence of a male. Angora goats and Mossi goats are known to have a short estrus lasting only 22 h and 20 h, respectively (Shelton, 1978; Tamboura *et al.*, 1998). Creole goats exhibit 27 h of estrous behavior and French Alpine goats are reported to

experience a 31 h estrus (Baril *et al.*, 1993). In Boer goats, the mean duration of estrous period is about 37 h (Greyling, 2000) and it is of about 58 h in Matou goats in Central China (Moaen-ud- Din *et al.*, 2008). Continuous presence of a male and service during the estrous period may reduce the duration of estrus although it did not affect ovulation times or ovulation rates in Nubian dairy goats (Romano and Fernandez Abella, 1997).

Recognizing heat periods in goats

If a buck is in an adjoining pen, it is usually easy to recognize heat period in the doe, as she will attempt to get in with the buck. If there is no buck in the adjoining pen, then it is more difficult to recognize the signs of heat. However, experienced goat men will recognize heat periods because the does tend to decrease in milk yield, their appetite is less and they show a characteristic nervousness and frequent bleating. There will be much wagging of the tail from side to side; the external genital organs (vulva) will be swollen and red. If heat recurs in 18 to 21 days, the doe did not conceive and mating should be repeated. The normal period of gestation in goats varies from 145 to 152 days.

The application of laws of animal health and reproduction genetics has contributed towards increase in milk and meat productivity. The increase in egg production brought about the Silver revolution in the area of animal husbandry. The methods being widely used are artificial insemination and embryo transplant.

Breeding and gestation in goats

Copulation occurs during estrus, therefore usually before ovulation. Hence, sperm progressing through the female genital tract may be present in the oviduct by the time of

ovulation. Meanwhile, other sperm is retained in the cervix where preservation conditions are good (up to 3 days) and released continuously in the uterus where survival is limited to about 30 h (Hulet and Shelton, 1980). The primary mode of sperm transport is by contractility of the female reproductive tract, though sperm motility might be important in the cervix for migration through the cervical mucus (Cox *et al.*, 2006). Ova may remain viable for 10–25 h. Fertilization occurs in the ampullae of the oviduct a few hours after ovulation. The fertilized ovum migrates down the oviduct while undergoing successive divisions. The embryo reaches the uterus 4–5 days after estrus at an early morula stage. Migration of the ovum is the result of combined movements of ciliated epithelial cells in the oviduct, peristaltic activity of muscular layers and a liquid current from the infundibulum to the uterus. Implantation of the embryo is observed 18–22 days after the onset of estrus. In goats, the presence of a functional corpus luteum is indispensable throughout gestation. The placental production of progesterone in goats is unable to maintain pregnancy after ovariectomy or lutectomy (Sheldrick *et al.*, 1981). Parturition in goats is preceded by a drastic decline in progesterone 12–24 h before the beginning of labor. Gestation length averages about 149 days but it may vary a little between breeds. Breed of dam, litter weight, breeding season and parity effects on gestation length have been observed by Mellado *et al.* (2000). The number of kids born and gender of kids were not a significant source of variation affecting this trait. Granadina goats had the shortest gestation (149.0 ± 0.31 days), whereas Toggenburg (151.7 ± 0.28 days) and Alpine (151.4 ± 0.46 days) had the longest. Boer goats also have a short gestation period of 148.2 ± 3.7 days (Greyling, 2000). Gestation of goats bred in summer was 1 day longer

than those mated in autumn and there was a progressive reduction of gestation length as parity increased.

Seasonality in sexual behavior

Reproduction in goats is commonly described as seasonal with differences in seasonality between breeds and locations. The onset and length of the breeding season in goats is dependent on a number of factors: latitude and climate, breed, physiological stage, presence of a male, breeding system but mainly photoperiod. The main environmental factor affecting seasonal breeding in small ruminants is the annual change in day length. Photoperiodic control of reproductive patterns is mediated through circadian rhythmic secretions of melatonin by the pineal gland during darkness, which influences the gonadotropin-releasing hormone pulse generation and the hypothalamic–pituitary–gonadal feedback loop. Animals bred in tropical and equatorial regions subjected to less change in photoperiod and temperature, display a longer breeding season than those bred in temperate and Polar Regions which exhibit more distinct seasonal effects.

Seasonality at higher latitudes

The sexual activity in female goats can be assessed by their spontaneous ovulatory activity and demonstration of sexual behavior. Two distinct periods are observed throughout the year in temperate latitudes: a period of deep anoestrus, when neither estrous behavior nor ovulations are noted, and the breeding period, with both estrous behavior and cyclic ovarian activity observed. During the transition periods, anovulatory estrus or silent ovulations (ovulation not accompanied by estrous behavior) can also be observed. Seasonal breeding is observed in most breeds of goats

originating from high latitudes ($>35^{\circ}$) and in some local breeds from subtropical latitudes ($25-35^{\circ}$). In temperate regions the breeding period is observed in the fall and winter. In France (45° North Latitude), the breeding season starts in September, when day length is declining, and persists until March (Bodin *et al.*, 2007). In Australia ($10-39^{\circ}$ South Latitude), goats have a brief period of spontaneous ovulatory activity, from April to August, centered on the winter solstice with a peak in June (Restall, 1992). In the Alpine and local goats bred in subtropical Mexico, the breeding season begins in the early autumn and ends in the late winter (Delgadillo *et al.*, 1997, 2004). With increasing latitude, for example in Swedish Landrace goat, the breeding season tends to be restricted to the autumn months and most kids are born in spring.

Seasonality in lower latitudes

In equatorial, tropical and subtropical regions, changes in day length are less pronounced. Seasonality in reproduction is therefore less marked and most local goats in the tropics have the ability to breed all year-round and have a relatively short post-partum anoestrus. However, environmental factors (forage availability and temperature changes) have a strong influence which often does not allow these potentials to be fully expressed. In particular insufficient nutrition is often responsible for the appearance of prolonged anoestrous and anovulatory periods, a reduction in fertility and prolificacy and also causes an elevated spring mortality rate (Delgadillo *et al.*, 1997, 2004). The most suitable times for mating and kidding are determined by climatic or management factors. For example, in some regions estrus is thought to be induced by monsoon rains so as to delay kidding until after the monsoon is over (Lassoued and Rekik, 2005; Moaen-ud- Din *et al.*, 2008).

Year-round kidding potential has been observed in tropical goats, like Creole goats bred in Guadeloupe, though not homogeneously distributed throughout the year: a peak period still occurs in spring with few kidding recorded in autumn.

Control of sexual activity

Role of hormonal treatment

Hormonal regimens based on progestagens, eCG (equine chorionic gonadotropin) and/or prostaglandins have been established for over four decades allowing estrous and ovulation synchronization during both the breeding and non-breeding seasons. In France, the treatment consists of the deposition of a vaginal sponge impregnated with a progestagen (20–45mg fluorogestone acetate) for 11 days. An intramuscular injection of a PGF 2α analogue (50 μ g cloprostenol) and 250–600 IU of eCG (dosage is dependent on parity, season and milk production level) is made 48 h before sponge removal.

Artificial insemination is carried out 43–45 h after sponge removal. For out-of-season AI with frozen-thawed semen, this treatment allows a conception rate of about 60–65% (Leboeuf *et al.*, 2000). It is currently used on 95% of inseminated dairy goats in France, but is also used to facilitate natural mating (in combination with photoperiodic treatment when used out of the breeding season). This treatment can be used at any time of the year, independently of the strength of seasonality. Other progestagens and other progestagen dispensers have been used in different countries including vaginal sponge impregnated with 60mg medroxyprogesterone acetate, subcutaneous implants containing 3–6mg Norgestomet and controlled internal drug releasing device (CIDR) containing 330mg progesterone.

Photoperiodic treatment

Seasonality of reproduction in goats is strongly dependant on photoperiod. In temperate and subtropical regions, out-of-breeding season breeding can be achieved using strategies based on manipulation of the photoperiod (Chemineau *et al.*, 2006; Delgadillo *et al.*, 1997). Following extended exposure to decreasing day length, animals become photo-refractory to the short day stimulus and will cease cyclic activity, unless a period of long day photostimulation is supplied. Photoperiod treatments are based on alternation of long and short days. First, the animals are subjected to long days (provided by artificial lighting in winter or by natural days in spring and summer) in order to prepare them to respond to the stimulatory effects of subsequently administered short days (Chemineau *et al.*, 2004, 2008). Under field conditions, short day effects are easily provided by melatonin implants. These photoperiodic treatments can induce sexual activity in males and females similarly to hormonal treatment in females (Chemineau *et al.*, 1999). Photoperiod treatments can induce ovulation over several weeks but cannot synchronize ovulation sufficiently to facilitate AI. Photo-periodic treatments are generally combined with hormonal treatments or the buck effect for synchronizing ovulations.

Melatonin treatment

The control of seasonal reproductive activity in sheep and goats in open sheds, needs extra-light (E) during the photosensitive phase (equivalent to long days, LD), followed by treatment with melatonin (equivalent to short days, SD). Melatonin, synthesized by the pineal gland, is the chemical messenger which allows seasonally reproductive animals to perceive day length changes. In the ewe, the neural

message, transformed into a hormonal one, triggers pulsatile activity of the LHRH neurons. About 40 days are necessary for melatonin to centrally stimulate the pulsatile LHRH activity. Its sites and mode of action are not yet known completely, but a precise hypothalamic zone has been defined in which radioactive melatonin binds specifically and where cold melatonin delivered locally stimulates LHRH activity. In the veterinary clinic, the most frequent mode of distribution is a sub-cutaneous implant, which induces an advancement of the cyclical ovulatory activity of ewes and goats. The date of fertilization is advanced and fecundity of females is improved. It can be used alone, or in association with other hormonal treatments, or after an artificial photoperiodic treatment.

Under these conditions, it allows a quantitative and qualitative increase in out-of-season sperm production in rams and billy-goats. Such an implant is registered and marketed in France, the UK, Greece, Australia and New Zealand (Chemineau *et al.*, 2004). In autumn-born Ile-de-France or Lacaune ram lambs, 2 months of E followed by decreasing day length for 90 days, advanced onset of the first breeding season by allowing males to reach their maximum testis volume and sperm production earlier than for untreated ram lambs. Substitution of decreasing day length with melatonin implants allowed a transient increase in testis volume. Adult Ile-de-France rams maintained under short light rhythms with 2 month-period, demonstrated, during at least 2 consecutive years, a testis volume equivalent to that observed during the normal breeding season. These light-treated rams produced, during non-breeding season, spermatozoa in the same quantity and quality as during the normal breeding season. In anovulatory out-of-season dairy goats, E treatment was demonstrated to be necessary before melatonin treatment and

melatonin to be necessary after E treatment to stimulate estrous and ovulatory activities. Stimulation of the anovulatory females by the introduction of treated males ("male effect") appeared to be necessary to obtain maximum stimulation of the treated females. Two months of E, followed by melatonin treatment (daily injection or drenching or subcutaneous implants) allowed cycles with ovulation to be maintained for more than 2 months. Although effective for control of out-of-season reproductive activity, melatonin slightly decreased milk production when applied soon after kidding. So, total control of reproduction in sheep and goats by manipulation of photoperiod in open sheds and melatonin treatments appears feasible in both sexes (Cheminieu *et al.*, 2006).

Buck Effect

The "Ram effect" or "Ram effect" is when non-cycling (anestrous) ewes are stimulated to ovulate by the sudden introduction of a ram or "teaser" ram. Rams produce a chemical substance called a pheromone, the smell of which stimulates the onset of estrus. When ewes and rams are in constant contact (sight or smell), the pheromones are much less effective at inducing estrus. Likewise, does and bucks are sensitive to their social environment, which can be used to manage their reproductive cycle. The so-called male effect is a technique to stimulate the sexual activity in seasonally anovulatory goats (Pellicer-Rubio *et al.*, 2007). Most female goats have a short ovarian cycle of 5–7 day-length following the introduction of bucks, followed by a second ovulation associated with estrous behavior and a normal luteal phase (Cheminieu *et al.*, 2006). One of the major factors affecting the efficacy of response to the male effect depends on the strength of seasonality of the female and male goats. In this respect, the response to

the male effect varies within breeds through the seasonal anoestrous period, and among breeds from different latitude origins (Walkden-Brown *et al.*, 1999). For example, in breeds exhibiting moderate seasonality, such as the Creole goats of Guadeloupe Island, introduction of the male may induce highly fertile ovarian activity in anovulatory goats throughout the year. In contrast, when used alone in highly seasonal breeds, the male effect can only advance the onset of the breeding season by a few weeks; it does not satisfactorily induce full sexual activity in the middle of the anoestrous period (Walkden-Brown *et al.*, 1999). Depending on breed and/or on anoestrous period, the pre-treatment of females and/or males with photoperiod may be necessary to optimize the response to the male effect (Flores *et al.*, 2000). For instance, in Alpine and Saanen breeds in France, the treatment of males and females with artificial photoperiod is necessary to improve the response to the male effect. Under these conditions, most does exposed to males ovulated (99%) and 81% kidded (Pellicer-Rubio *et al.*, 2007).

Adapted nutrition

Most characteristics of the reproductive cycle can be modulated through adapted nutrition. Nutritional strategies have recently been developed based on knowledge of precise nutritional needs for each stage of the reproductive process and interaction between metabolic status and reproductive performance. Both in sheep and goats, a long-term increase in body weight as well as a timed supplementation are known to affect folliculogenesis (Blache and Martin, 2009). Targeted nutrition can thus increase potential litter size by optimizing ovulation rate. The total number of offspring produced per doe can also be increased with planned nutrition to advance puberty. This was observed in Savannah Brown goats and

seemed independent of their body weight (Fasanya *et al.*, 1992). During pregnancy, nutrition can also affect both embryo survival and foetal programming of adult performance. Nevertheless, these tools can only increase reproductive performance within biological limits and should be adjusted to the considered breed and environment.

Reproduction and energy budget

Food availability and energetic requirement fluctuate in most of the habitats. Living cells require a continuous supply of fuels for the biosynthesis and metabolism, and hence in odd condition, cessation of eating is a primary response and organisms engage in other behaviors involved in perpetuation of species. In such condition when there is no food available, the organism depends on fuels and nutrients from internal and external source they have (body fat and food storage, respectively). Evolution always favored animals that are able to store a significant quantity of energy inside the body (Nelson *et al.*, 1995). This is necessary to inhibit ingestive behaviors so that animals may engage in activities that improves reproductive success. Some species increase energy intake during a period of intense parental care, whereas others increase both energy intake and storage in anticipation of the birth of offspring. In mammals, the biological processes like lactation in female, parental care and thermoregulation in both sexes are one of the most costly processes. In some mammalian species, females over eat and store the excess fuel during the gestation as lipids that are used in lactation later on. In other mammalian species, fooding is at the basal rate during the gestation but store a lot to be eaten during the energetically demanding period of lactation. Thus, Energy budget management and reproduction are integrated with those

which control reproduction (Bronson and Heideman, 1994; Wade and Schneider, 1992). When food is plentiful and energy requirements are low, energy is available for all of the processes necessary for immediate survival. Metabolic signals, hormonal mediators and modulators and neuropeptides give expression to these priorities in at least two interrelated ways. First, they are permissive for the neuroendocrine events that control spermatogenesis, ovulatory cycles and fertility. Second, in many species, the same metabolic signals and chemical messengers that increase the motivation to engage in reproductive behaviors also attenuate the motivation to engage in foraging, hoarding and eating (Schneider *et al.*, 2002).

On the other hand, when energy is narrow, the energy routes towards the biological processes that confers the survival of the individual rather than promoting growth, longevity and reproduction. The physiological processes like foraging, storage of food and ingestion become the topmost priorities over reproduction because reproductive processes are energetically expensive and can be carried later on (Bronson, 1985). During low food availability when the thermoregulatory demands are high, generally gonadal regression occurs and species undergoes sexual rest. Even in species that breed year round, reproductive processes are curtailed under low food availability (Bronson, 1998). Further, in case of goats the sources of energy are very much uncommon and striking in nature. They can store energy in forms of glycogen and fat. But, under favorable and unfavorable conditions of foraging they are able to get energy from glucose and protein. In almost all of the animals glucose is most important ready source of energy. But, for protein the explanation is different. Under malnutrition

(which may be caused due to scarcity of food, heavy competition and obviously due to huge parasitic load) proteins are used by them. But, under favorable and well nourished condition goats generally consume protein and use it for the maintenance of basal metabolism. Explanation may come from the evolution of goats from wild ones to domesticated animal. Under wild conditions they are thrived to migrate from one portion of grazing land to another one. At that time fat may be used as direct source of energy or by producing glucose (by gluconeogenesis). This is the only reason that under restricted conditions (food and water deprivation for prolonged time) they are never under “deprived stress” (Machen, 1981).

During the period of energetic challenges, ingestive behavior is favored over other activities. The ingestive process is triggered by a variety of metabolic sensory stimuli i.e. low glucose in blood and its metabolites, low level of peripheral hormone like insulin and leptin along with central feeding-stimulatory circuits involving neuropeptide Y (NPY) and agoutirelated protein (AgRP). These processed are of highly adaptive to the survival, bringing metabolic fuels, nutrients, water, salt and minerals for the maintenance of cell structure and function as survival of the organism is the utmost for species perpetuation.

This is the reason the neuropeptides that stimulate ingestion during energetic challenges, inhibit the hypothalamic–pituitary–gonadal (HPG) system. When food becomes available *ad libitum* creating low energy demands, eating becomes minor and reproduction becomes the topper. Natural selection always favors the population whose individuals give priority to reproduction over feeding (Schneider *et al.*, 2000).

The mechanisms that integrate the energy to reproduction might be important in clinical as well as agricultural aspects. Human female having the body weight at both extremes and also the one who is diabetic have more chances of reproductive abnormalities (Loucks *et al.*, 1994). These abnormalities are mainly due to low circulating levels of ovarian steroids especially estrogens those causes osteoporosis and other impaired cognitive function (Misra, 2008). In addition to its clinical relevance, this area of research is now focused to improve breeding and lactation performance in dairy and meat animals. More over this beautiful adaptive strategy has made this group of ruminants a successful survivor under harsh conditions, environmental stresses and has made this animal a short day breeder when immune modulation and reproduction are occurring simultaneously under cold stress.

Energetic effects on the HPG system

There are many chemical messengers and metabolic processes that influence the reproduction acting through HPG system. Gonadotrophin releasing hormone (GnRH) being the master control of HPG and whose cell bodies are located in the area spanning from the preoptic area (POA) to the arcuate nucleus (Arc) of the hypothalamus. The neurohormone, GnRH has two modes of secretion. The pulse mode occurs during the follicular phase, when low concentration of estradiol causes hyposecretion of GnRH and LH. It means that in pulse mode the estradiol exerts negative feedback and limits the secretion of GnRH and LH. The other mode of GnRH secretion is surge mode which occurs during the periovulatory phase when high concentrations of estradiol exert positive feedback effects on GnRH. The GnRH pulse generator is a little-understood oscillating neural circuit that results in the

pulsatile secretion of GnRH from terminals in the median eminence into the pituitary portal system. Each pulse of GnRH leads to the release of a pulse of LH from leuteotrophs in the anterior pituitary (Qarke and Cummins, 1982) along with FSH. These LH and FSH pulses are critical for follicle development and steroid secretion. The rising levels of estradiol have positive feedback on GnRH and LH, and these actions of estradiol are required for the LH surge, which triggers ovulation.

Metabolic challenges, such as food deprivation, inhibit the HPG system at many levels. The primary target is the GnRH pulse generator, and these effects are similar in males and females (Bronson, 1985). Pulsatile LH secretion, follicle development and ovulation can be reinstated by pulsatile treatment with GnRH in food-deprived rats, sheep, pigs, cows, monkeys and women (Armstrong and Britt, 1985; Bronson, 1985; Cameron, 2004; Cameron and Nosbisch, 1991). In addition, metabolic challenges alter the GnRH, LH and FSH surge, independent of their effects on pulsatile LH secretion (Crump *et al.*, 1982; Medina *et al.*, 1998). In sheep, metabolic challenges, such as food deprivation, inhibit GnRH secretion into the pituitary portal circulation (Foster and Bucholtz, 1995; Ansar-Ahmed *et al.*, 1985). GnRH gene expression, immune reactivity or content are either unchanged or increased by energetic challenges, perhaps reflecting inhibited GnRH release from neurons (Ebling *et al.*, 1995; McShane *et al.*, 1992). Inhibition of GnRH secretion leads to a cascade of inhibitory effects, including decreased gonadotrophin secretion, retarded follicle development, inhibited synthesis of gonadal steroids and, in rodents and nonhuman primates, decreases in steroid-induced reproductive behaviors. GnRH transcription or translation might be important in those mammals that are

induced ovulators. In musk shrews, the inhibitory effects of food restriction on reproduction are rapidly reversed by refeeding (Gill and Rissman, 1997; Temple and Rissman, 2000). These results emphasize a role for direct effects of metabolic challenges on GnRH neurons.

Energetic effects on motivation vs performance of ingestive and reproductive behavior

The metabolic signals, hormones and neuropeptides optimize reproductive success by prioritizing behavioral options, i.e., by changing the motivation to engage in either reproductive or ingestive behaviors. For example, in rats, food restriction increases the tendency to eat and decreases the tendency to engage in sex behavior. It is important to note that this process does not always include laboratory measures of behavioral performance, such as the amount of food eaten in a restricted time period. Brain mechanisms that control sex behavior and eating behavior do so by altering motivational aspects of the behavior as well as performance, and the neuroendocrine mechanisms that govern motivation are only partially representative of those that determine performance. For example, in some species, metabolic signals, peripheral hormones and central neuropeptides influence food procurement behaviors without necessarily influencing the amount of food ingested (Schneider *et al.*, 2002). In Syrian hamsters, a period of food deprivation fails to influence subsequent food intake. In fact, hamsters rarely change meal size and frequency in response to a variety of stimuli that influence these parameters in rats (Buckley and Schneider, 2003; Schneider *et al.*, 2000), and yet, these same metabolic stimuli increase hunger motivation, as measured by the tendency to eat an unpalatable substance (DiBattista and

Bedard, 1987., Schneider *et al.*, 1988). In nature, Syrian hamsters live in burrows where they are known to hoard large quantities of food. In the laboratory, when their nest boxes are connected to artificial burrows leading to an external food source, Syrian hamsters exhibit hoarding behavior. After a period of food deprivation, Syrian hamsters show significant increases in the amount of food hoarded, and treatment with leptin during food deprivation significantly attenuates the food-deprivation-induced increase in hoarding (Buckley and Schneider, 2003). Similarly, in Siberian hamsters, hoarding behavior is increased by food deprivation (Bartness and Clein, 1994) and by central treatment with AgRP (Day *et al.*, 2005), NPY or NPY agonists, and hoarding is decreased by treatment with NPY antagonists (Schneider *et al.*, 2002). It would be interesting to examine whether the reverse is true; that is, when food is plentiful and energy demands are low, does the increased availability of energy, elevated concentrations of plasma leptin, and decreased central NPY secretion decrease the motivation to engage in hoarding and increase the motivation to engage in sex? These results emphasize that effects of leptin or other hormones and neuropeptides and metabolic sensory stimuli on the motivational aspects of sex behavior should be examined separately from the performance of the behaviors. Leptin treatment increases performance; that is, lordosis duration in OVX, steroid-primed hamsters fed ad libitum (Wade *et al.*, 1997) and food deprivation-induced decreases in lordosis duration are prevented with NPY antagonists (Keen-Rhinehart and Bartness, 2007). It would be interesting to examine the motivational aspects of sex behavior, such as courtship and solicitation. It is plausible that neuropeptides, hormones and metabolic signals do not universally influence the ingestion of food or the performance of sex,

but rather, they influence the motivation to engage in species-specific behaviors that ensure survival and reproductive success. So far, it appears that in hamsters, these factors influence food hoarding, which allows hamsters to ingest the food at a constant rate in the relative safety and more temperate environment of their burrow, and might also modulate fertility, sexual motivation and performance.

Hormones inform the brain about the energetic status and reproductive state of the animal, and thereby enhance the occurrence of behavioral and metabolic adjustments that are appropriate for the environmental, reproductive and energetic conditions. For example, leptin secretion is related to adipocyte number and the flux of oxidizable metabolic fuels into adipocytes (Levy *et al.*, 2000; Wang *et al.*, 2007). In most cases, the animal has the option to ignore the hormonal information if more urgent energetic needs arise related to survival and reproduction. Hormones can alter or modulate the metabolic stimulus. For example, some hormones alter the availability of oxidizable fuels (the primary metabolic sensory stimulus), and thus, have indirect effects on the central effector systems. For example, leptin increases energy expenditure, thermogenesis and fuel oxidation, and thus, has the capacity to influence food intake and reproduction indirectly by making more fuels available for oxidation, thereby changing the primary sensory metabolic stimulus (Bai *et al.*, 1996). In food-restricted ewes, pulsatile LH secretion was reinstated within an hour of refeeding and restored to the pulse frequency of fed ewes by 9 days of refeeding, despite the fact that adipose tissue and plasma leptin concentrations did not increase significantly above the levels of the food-restricted groups (Szymanski *et al.*, 2007). Together, these results show the GnRH pulse generator and sex behavior are

influenced by the minute-to-minute availability of oxidizable metabolic fuels.

According to the metabolic hypothesis, body fat content, caloric intake and energy expenditure control reproductive function by acting through a common sensory stimulus, the general availability of oxidizable metabolic fuels. Body fat can buffer against food deprivation by virtue of the fuels that can be hydrolyzed and mobilized from lipids. Factors that increase energy expenditure, such as cold exposure, can inhibit estrous cyclicity, but only when the increase in energy expenditure is not offset by utilization of oxidizable fuels mobilized from adipose tissue or by increased food intake. For example, prolonged housing at cold ambient temperatures inhibits estrous cycles in Syrian hamsters only when the increased energy expenditure is not offset by increased intake (Schneider and Wade, 1990).

Conclusion

In summary, there is evidence that metabolic challenges inhibit reproduction at many levels, including the GnRH pulse generator, the GnRH, LH and FSH surges, and finally, by direct effects of metabolic fuel availability on the brain mechanisms that prioritize courtship, mating and ingestive behavior. This review will summarize evidence that metabolic and hormonal signals are detected in the caudal brain stem and periphery. Peripheral neural signals from the vagus nerve are relayed in the nucleus of the solitary tract (NTS), and metabolic signals are detected in the area postrema (AP) or medial NTS and relayed to hypothalamic areas, such as the paraventricular nucleus (PVN), or to the POA via the parabrachial nucleus. From the PVN, neuronal projections are purported to influence GnRH secretion via contact with

GnRH axons in the Arc. GnRH neurons also receive input from the anteroventral nucleus. Other hormones and neuropeptides might act more directly in the hypothalamus to influence GnRH neurons in the Arc or POA.

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