Physiology of puberty in females: A review

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Abstract
Age at puberty is one of the significant traits that influence production of the animal and thereby profitability to the farmer. Pubertal onset with initiation of normal estrous cycles involves maturation of the hypothalamic-pituitary-ovarian axis. This was dependent on the adequate body weight/metabolic status besides the required age. Various physiological factors like Nutrition, environment, photoperiod and endocrine factors like GH, IGF-1, leptin, NPY are important in the induction of puberty. The role of each of these factors was discussed.

Keywords: Puberty, estrous cycle, hypothalamic-pituitary-ovarian axis, photoperiod, leptin

Introduction
Puberty is the age in postnatal life when gonads produce gametes and sex hormones in sufficient quantities to enable an animal to reproduce. It is not a sudden event, but a gradual process of maturation of the endocrine and reproductive systems enabling the animal for successful reproduction (1). Hypothalamus plays a very important role in regulation of onset of puberty. The onset of puberty was dependent on many factors like age, species, genotype, body weight and growth rate (1) and energy status (2). The role of growth hormone and insulin-like growth factor 1, in the modification of GnRH synthesis and subsequent action on the pituitary gonadotropes was proposed (3).

Neuroendocrine mechanisms underlying puberty
The series of hypophysial and gonadal endocrine events that take place during pubertal onset were dependent on the release from hypothalamic negative feedback mechanism (1). This could be explained by the concept of “gonadostat hypothesis” which states that prior to puberty, the small amount of oestrogens produced from the growing follicles inhibits the surge center of hypothalamus (1). The tonic secretion of LH prior to puberty was not sufficient for the maturation of follicles (4). However as the puberty was advanced, the increased LH pulses augments the follicular development with a subsequent increase in production of 17β-estradiol (1,5). This was associated with a decreased sensitivity of the tonic center of hypothalamus (ventral) due to fall in oestrogen receptors (1) with a simultaneous increased sensitivity of the surge centre (anterior). This depicts the positive feedback effect of increasing levels of oestrogens produced by the growing follicles on the hypothalamus at the pubertal onset (1,4). Stimulation of surge centre releases LH in a surge fashion triggering follicular maturation (6,7). Ovulation can be made in pre-pubertal animals occur by inducing LH surge, but animals return to anestrus without continuation of the normal cycling activity (8). It is recognized that nutritional-status, age, bodyweight, genotype as well species of the animal are important factors that regulate the pubertal onset (9). The factors involved in the regulation of the endocrine maturation are obligatory for the normal cycling activity (10). This was dependent on the sufficient somatic growth of the animal and the pubertal age (1,4).
Physiological Factors affecting puberty

1. Nutrition: Nutrients particularly energy and protein are essential to optimize reproduction. Pubertal age in heifers is determined by the nutritional status during early sexual maturity period [11]. Malnourished females lack ovarian activity owing to the suppression of luteinizing hormone in a pulsatile fashion [12]. LH pulse generating system in the hypothalamus and its pre pubertal rise is influenced by the plane of nutrition [13]. Nutrition effects synthesis and release of GnRH, FSH, LH and GH due to its action on hypothalamus and anterior pituitary respectively. The Ovarian follicular growth and steroid synthesis are influenced by nutrition. Acute /chronic dietary restriction results in a gradual reduction of growth rate of dominant follicle. The effects of nutrition on the follicular development mediated by the actions of various growth factors and their receptors proposed was given below in Fig.2. [14].

Fig 1: Neuroendocrine events in the initiation of Puberty

Fig 2: Mechanism of effect of nutrition on follicular development via various growth factors (14).
2. Environment: Pubertal onset in beef heifers was dependent on the birth time. Heifers born in autumn attain puberty earlier compared to spring-born heifers. Autumn and winter environments during first six months of life accelerate the pubertal onset while the same conditions after six months delay it [13]. Interaction among season and other environmental factors affecting breed, nutrition, milk production, suckling by offspring and reproduction was proposed. [15]

3. Age & body weight: The effect of age and weight on the pubertal on set differs among various breeds [10]. The bodyweight of heifers at puberty was 55% to 60% of adult [10]. The role of body weight and growth rate on the pubertal onset was suggested [16]. Improved growth during 4-7 months of age is seems enough stimulus to induce the onset. Better growth rates decrease the negative feedback of estradiol on LH secretion and thus stimulate the follicular growth.

4. Photoperiod: It is the duration of daily light exposure. There are two common time divisions of photoperiod namely long-day photoperiod (16 hours of light and 8 hours of dark) and short-day photoperiod (8 hours of light and 16 hours of dark). Heifers born in autumn attain puberty at younger ages than do spring-born heifers. The role of melatonin in transduction of light stimuli into neuro endocrine signals influencing LH secretion was proposed [13]. It was concluded that supplemental lighting after 22 or 24 wk of age reduced age at first ovulation and first estrus in heifers born from February to July. These effects were accompanied by changes in ovarian development [17]. The outcome of long day photoperiod on feed efficiency followed by early breeding activity was suggested [18].

Endocrine factors affecting puberty
1. Leptin: It is produced primarily by the adipose tissue with other sites being stomach, skeletal muscle, fetal cartilage, pituitary, mammary tissue and placenta [19]. It signals nutritional status of the organism to the central reproductive axis. An increase in the circulating leptin at the pubertal onset was reported in rodents and heifers [20] and its permissive role was supported by studies in different species of animals but not in ruminants [19]. Its role in the activation of GnRH neurons via hypothalamic proopiomelanocortin system was proposed by Amstalden et al., 2014.

2. Growth hormone: Delayed puberty due to declined LH pulses was attributed for the nutrient restriction. This was correlated with changes in mean concentration and amplitude of GH pulses just before puberty [21]. Puberal onset was positively associated with circulatory IGF-I independent of growth rate, leptin concentrations, and body fat [22]. This was reinforced by the modulation of IGF-1 levels and/or bloodborne metabolites in Rahmani ewe lambs during pubertal onset [23].

3. Insulin: The role of Insulin in setting pace for the pubertal onset by monitoring the nutritional status was proposed [22]. However, its role through IGF-I by an increased LH release regardless the steroidal milieu was proposed [23]. This was correlated with a fastened puberty in calves whose metabolic status was favorable with increased leptin and decreased NPY levels [23].

4. NPY: The role of NPY in the inhibition of GnRH and subsequent LH release regardless the steroidal milieu was proposed [23]. This was correlated with a fastened puberty in calves whose metabolic status was favorable with increased leptin and decreased NPY levels [23].

5. Pineal gland: It secretes the hormone melatonin. Its activity is dependent on the photoperiod. There were few studies depicting its direct role in pubertal development. Its vital role in the developmental changes in the gonads of puppies was proposed [20].

Discussion
Maturation of the hypothalamo-pituitary-ovarian axis was dependent on the adequate body weight and age. Nutrition, environment, species, genetics, endocrine and paracrine factors affect the age at puberty. The role of Leptin as a permissive factor in the pubertal onset was established in rodents [21] but not in ruminants [29]. Integrated efforts of modulation of GnRH and NPY levels on the body weight and earlier pubertal onset through feed across different species was reported [30, 31, 27]. The significant role of feed in the hastening of puberty was reported [22, 53]. Similarly the role for GH in the pubertal onset earlier was reported in heifers [34, 35, 36].

Conclusion
Age at which the pubertal onset occurs is the most important factor that influences the reproductive as well productive life of an animal. The physical factors body weight of approximately 60% of the adult along with age is the most important factors that determine the puberty. Therefore a well balanced feed from weaning period to puberty should be given to ensure proper growth and maturity. There are a number of endocrine and paracrine factors at the hypothalamic level that essentially influence puberty. But then No single factor alone can essentially influence the onset of puberty. The concerted effects of feed/nutrition mediated via various hormones discussed had to be tested across different species involving trials on a large scale. This may give a fine understanding of the phenomenon underlying the pubertal onset and utilized for the benefit of the mankind.

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