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Review

Seasonal changes in ovarian activity: Lessons learnt from the horse

F.X. Donadeu *, E.D. Watson

Easter Bush Veterinary Centre, Royal (Dick) School of Veterinary Studies, University of Edinburgh, Roslin, Midlothian EH25 9RG, UK

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Abstract

The annual reproductive cycle in the horse involves a reduction in ovarian activity during short days. The absence of ovulatory activity during winter has important consequences for an equine industry eager to breed mares early during the year. The anovulatory season results from a reduction in the secretion of pituitary gonadotropin that is in turn triggered by the inhibitory effects of short photoperiod on the hypothalamus–pituitary axis. Recent studies have provided evidence that the response of the ovaries to endocrine stimuli during the anovulatory season is affected not only by circulating concentrations of trophic hormones but also by locally produced growth factors that are putative modulators of follicular responses to gonadotropins. The present review summarises current knowledge on ovarian dynamics during the equine anovulatory season and the regulatory mechanisms involved at both systemic and local levels.

Keywords: Mares; Ovulation; Follicular growth; Seasonal reproduction; Gonadotropins; Growth factors

1. Introduction

Despite the early suggestion by Burkhardt during the 1940s that reproductive activity could be induced during the anovulatory season in mares by altering photoperiod (Burkhardt, 1946) it was not until about 25 years later that the first comprehensive studies on equine reproductive seasonality were undertaken. Studies during the 1970s and 1980s (reviewed in Ginther, 1992) demonstrated that decreasing photoperiod during fall and winter suppresses GnRH secretion, an effect mediated,

* Corresponding author. Tel.: +44 131 651 3910; fax: +44 131 650 6585.
E-mail address: xavier.donadeu@ed.ac.uk (F.X. Donadeu).

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at least partly, by changes in melatonin secretion from the pineal gland. The low GnRH levels result in reduced gonadotropin secretion that in turn leads to reduced follicular growth and anovulation. Increased day length during spring induces a gradual recrudescence of the hypothalamic–pituitary axis which allows the re-initiation of follicular growth and eventually ovulation. The anovulatory season has thus been divided typically into three periods, fall transition, corresponding to the initial period of declining activity of the hypothalamus–pituitary–ovarian axis, deep anoestrus, corresponding to the winter period of lowest axis activity, and spring transition, a period of reproductive recrudescence preceding the onset of ovulatory activity. It has been long known that, in addition to photoperiod, factors such as nutrition, body condition and environmental temperature have an effect on seasonal reproductive activity and, in fact, more recent studies have revealed a complex neuro-endocrine system regulating seasonal changes in hypothalamic and pituitary activity that involves not only melatonin but also neurotransmitters such as opioids and catecholamines (Nagy et al., 2000).

Underlying the interest in understanding the mechanisms controlling seasonal reproduction in mares was, and still is, a commercial need to have foals born early during the year so that they can adjust better to the artificially imposed official birth date for performance horses (first of January). Additional benefits to the horse industry from artificially eliminating the period of spring transition would be expected in relation to the natural tendency for mares to develop one or more large anovulatory follicles and display oestrous behaviour during that period. Enormous waste of time, effort and money results from attempts to produce fertile inseminations from these unproductive follicles.

The search for strategies to advance the onset of the ovulatory season was initially focused on artificial manipulation of day length (Sharp and Ginther, 1975). Exposure to artificial lighting during winter has shown to consistently induce ovulatory activity within a period of 6–12 weeks, depending on the level of ovarian activity at the start of the treatment (Nagy et al., 2000). Alternatively, a variety of hormone-based approaches have been used during the anovulatory season in an attempt to induce a neuro-endocrine milieu that favours the development of ovulatory follicles (reviewed in Nagy et al., 2000). Successful ovulation has been achieved by administration of GnRH alone or in combination with dopamine antagonists, and by administration of pituitary extracts. In addition, progesterone therapy is widely used in an attempt to hasten ovulation at the end of the spring transition, although controversy exists on its actual efficacy. It is important to realise that, as it is the case for light-based treatments, the ovulatory response to hormonal therapy strongly depends on the level of ovarian activity at the start of treatment. For example, the ability of GnRH treatments to induce ovulation is dramatically reduced in mares with low levels of ovarian activity such as during deep anoestrus, with success rates of 26% in mares with small follicles ($\leq$15 mm) at the beginning of treatment versus 70% for mares with medium to large follicles (21–29 mm; Bergfelt and Ginther, 1992). Thus, it is clear that the process of seasonal ovarian recrudescence is not solely controlled by the hypothalamus and pituitary but also by the ovary itself, which dictates the responsiveness of the follicles to trophic stimuli at any given moment and therefore the time of ovulation. In that regard, evidence that local ovarian mechanisms play an important role in the regulation of follicular development during the anovulatory season in mares has been recently obtained (Watson and Al-zi'abi, 2002; Watson et al., 2004a; Acosta et al., 2004a). Yet, research on seasonal reproduction in mares has to this date focused primarily on neuro-endocrine regulatory mechanisms and often has neglected the ovary itself. In addition, because of a commercial interest in advancing the onset of the ovulatory season, considerably more effort has been devoted to studying the period of spring transition than other phases of the anovulatory season, as will later become evident to the reader. This review focuses on the ovarian