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Review

Intrinsic determinants and predictors of superovulatory yields in sheep: Circulating concentrations of reproductive hormones, ovarian status, and antral follicular blood flow

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A B S T R A C T

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Hormonal ovarian superstimulation has contributed to small ruminant reproduction around the world, impacting genetic improvement and zoosanitary programs, contributing to the conservation of endangered species, and supporting other related biotechnologies. Advanced knowledge surrounding the superovulatory treatments in sheep has resulted in enhanced control of influencing factors and improved the protocols currently used. However, in spite of minimization of some adverse factors, superovulatory responses in ewes still remain variable, preventing the more widespread use of superovulation in commercial embryo transfer programs and reproductive research in this species. Recent evidence demonstrates that changes in antral follicular populations and blood supply, and circulating concentrations of certain reproductive hormones determined at the specific time points just before or during the superovulatory treatment are associated with superovulation success in ewes. This review attempts to compile the data from available literature to identify ovarian and hormonal determinants of the superovulatory outcome in ewes, which can be used to substantially improve the existing protocols and to reduce the extra cost and unnecessary stress imposed on poorly responding animals. An overview of most commonly used and some recently developed, FSH-based ovarian stimulation protocols is given at the outset to highlight variation in the frequency and timing of gonadotropin injections, estrus synchronization methods, and follicular wave synchronization and/or ovulation induction techniques during the superovulatory treatments in ewes.

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1. General introduction and overview of superovulatory protocols

Assisted reproductive technologies (ARTs) are widely used in agricultural industry to improve livestock genetics

and boost reproductive efficiency of individual animals [1–4]. Nearly all technologies related to embryo production and manipulation in domestic ruminants have been developed in sheep and subsequently transferred to other livestock species [5,6]. In sheep, hormonal ovarian stimulation is mainly used in multiple ovulation and embryo transfer (MOET) programs [7]. However, considerable variations in superovulatory responses continue to limit the application of superovulation, especially in commercial

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settings [8,9]. The outcomes of superovulatory treatments are highly variable as ovarian responses (Fig. 1) and embryo yields are dependent on several intrinsic and extrinsic factors including, but not limited to, the breed, age, flock management, gonadotropin preparations and doses used, type of insemination, and the interval between successive treatments [10–12]. The superovulatory outcomes are strongly influenced by the reproductive status and history of ewes as well as season and photoperiod/melatonin secretion [13–18]. All these factors can affect embryo yields and quality in breeds maintained in temperate climates; under tropical and subtropical conditions, sheep undergoing ovarian stimulation are somewhat less sensitive to photoperiodic changes [4]. Although the relationship has yet to be fully corroborated, insufficient nutrition may also impinge on embryo output by compromising follicle/oocyte competence [19], luteal function [20], and/or early embryonic development [21–23].

Despite an increased control of extrinsic factors influencing the superovulatory outcome, ovarian responses in hormonally superstimulated sheep remain variable, suggesting that the primary causes of this variability are related mainly to intrinsic factors. One of the main inherent factors linked to variability in superovulatory yields is genotype. Prolific breeds generally show enhanced superovulatory responses, with greater numbers of transferable embryos than less prolific genotypes [24,25]. Sheep with a heterozygous inactivating mutation in the bone

morphogenetic protein 15 (BMP15) gene exhibit significantly greater ovulation rates during either a natural estrous cycle or after the superovulatory treatment [24]. The BMP15 protein is a member of the transforming growth factor β superfamily. It is a paracrine signaling molecule involved in oocyte maturation and follicular development [25]. In more than 75% of ewes actively immunized with a BMP15-keyhole limpet hemocyanin peptide in an oil-based adjuvant, given to completely neutralize BMP15 bioactivity, there was no superovulatory response to exogenous gonadotropins [26]. Premature luteinization of antral follicles during the hormonal ovarian superstimulation appeared to be the main reason for this suppression [26]. Moreover, prolific strains of sheep are more likely to be affected by a possible ovulatory threshold, which has been proposed to influence fertilization rates in superovulated sheep; a study conducted in Lacaune ewes reported a significant decrease in fertilization and transferable embryo rates in animals with more than 30 ovulations [10].

In addition to genetics, the age of animals also affects the superovulatory outcome in sheep [27], with the maximal embryo outputs typically occurring at or around 6 years of age [28,29]. Owing to the diminished follicular sensitivity to gonadotropins, induction of multiple ovulations in prepubertal females is significantly less successful compared with that in sexually mature donor ewes [30]. However, the genetic predisposition and age are not the only intrinsic factors that can modify the superovulatory

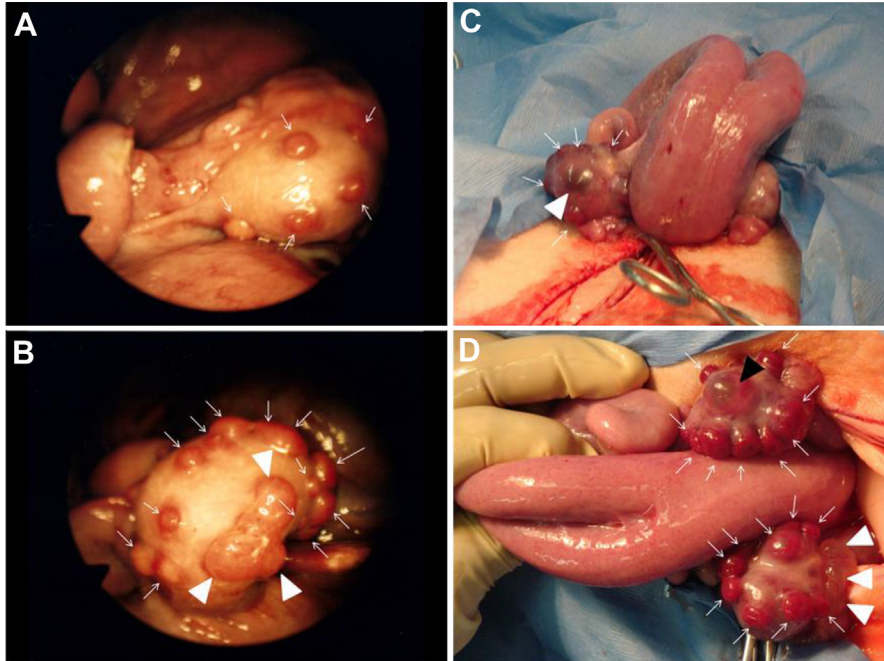


Fig. 1. Pictures of ovaries in superovulated ewes of the Olkuska breed (highly prolific genotype) obtained just before laparoscopic embryo flush (A and B) and in Rideau Arcott sheep (moderately prolific strain) at the time of laparotomy after the superovulatory treatment (C and D). Please note a relatively small size of corpora lutea (white arrows) in prolific Olkuska ewes due to ovulation of smaller antral follicles compared with Rideau Arcott sheep. A and C depict ovaries in poorly responding individuals, whereas (B and D) in well-responding ewes. The ewes were age and weight matched, and multiparous animals superovulated in the 4-day ovine FSH regimen with declining gonadotropin doses (Olkuska breed) or the 3-day porcine FSH protocol (Rideau Arcott). At the time of embryo recovery, unovulated cystic-like follicles could be observed (white arrowheads), some of them partially luteinized (black arrowhead), in animals of both genotypes.

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