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Circannual changes in progesterone secretion in intact ewes, luteinizing hormone secretion in ovariectomized estradiol-implanted ewes, and prolactin secretion in three sheep breeds anticipated to differ in seasonality of reproduction

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ABSTRACT

Changes in progesterone secretion in intact ewes (7 or 9 per breed) and luteinizing hormone secretion in ovariectomized, estradiol-implanted ewes (9 or 10 per breed) were monitored for 12 mo in Suffolk, tropically adapted St. Croix, and OOS ewes. The OOS line is a composite population of 50% Dorset, 25% Rambouillet, and 25% Finnish Landrace breeding that was selected for 10 yr for ability to lamb in October and early November. Ewes were isolated from rams, and blood samples were collected twice weekly. Circulating prolactin concentrations were also determined from blood samples collected near the summer and winter solstice and vernal and autumnal equinox. Intact OOS ewes entered anestrus later, began the subsequent breeding season sooner, and had a shorter seasonal anestrus than Suffolk and St. Croix ewes ($P \leq 0.005$). St. Croix ewes did not differ from Suffolk ewes in date of onset or cessation of breeding or duration of anestrus ($P \geq 0.06$). Breed differences in duration of luteinizing hormone inhibition in ovariectomized ewes were essentially identical to those observed for duration of anestrous. Prolactin concentrations varied during the year: annual changes were larger in relatively seasonal Suffolk ewes than in tropically-derived St. Croix ewes ($P < 0.01$), and OOS ewes were intermediate to, and tended to differ from ($P < 0.10$), the other two breeds. We conclude that OOS ewes developed by selection for fertility in spring matings had an abbreviated seasonal anestrus that is one of the shortest ever reported for temperate breeds, and that tropical St. Croix sheep did not have a shorter seasonal anestrus than Suffolk sheep under temperate conditions and ram isolation.

1. Introduction

In temperate regions, the breeding season of the domestic ewe normally begins at some point following the summer solstice, and the period of anestrus normally begins in late winter or early spring (Hafez, 1952). However, breeds have been shown to differ in timing and

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duration of the seasonal anestrus (Dzakuma and Harris, 1989). Breeds of Mediterranean origin generally had longer breeding seasons than British breeds (Thomas et al., 1988). Tropical sheep breeds such as the St. Croix and Barbados Blackbelly have been described as "aseasonal" (Parker et al., 1991) and reported to lamb "year-round" (Wildeus, 1997), but Barbados Blackbelly ewes in France exhibited seasonal variation in estrous activity (Chemineau et al., 2004).

Seasonal reproduction in sheep has been shown to involve entrainment of an endogenous circannual rhythm to prevailing changes in photoperiod (Robinson and Karsch, 1988). Differences among breeds in timing of the endogenous rhythm and sensitivity to photoperiod allowed expression of differences in timing of anestrus. The mechanism driving these reproductive transitions has been attributed to seasonal changes in negative feedback effects of estradiol on pulsatile secretion of luteinizing hormone (LH) (Karsch et al., 1980). Seasonal changes in capacity of estradiol to inhibit LH secretion were demonstrated in ovariectomized (OVX), estradiol-implanted ewes (Legan et al., 1977) such that circulating LH was elevated and displayed a typical pattern of pulsatile release during the breeding season but was generally undetectable during the typical anestrous period. Use of the OVX, estradiol-implanted ewe as an experimental model thus permits assessment of photoperiodic effects on circulating LH independent of naturally-occurring variation in circulating levels of ovarian steroids (Karsch, 1984).

Circulating prolactin has been shown to display strong seasonal effects in sheep (e.g., Webster and Haresign, 1983). However, under natural photoperiods, a causal role for prolactin in explaining seasonal variation in estrous behavior has not been demonstrated (Gomez-Brunet et al., 2008). Seasonal differences among populations in circulating prolactin thus may be under genetic control but may or may not be associated with differences in seasonal reproductive patterns (Curlewis, 1992; Notter and Chemineau, 2001).

Genetic variation in ewe fertility in spring was documented in the Virginia Tech "OOS" (out-of-season breeding) line, a population of 50% Dorset, 25% Rambouillet, and 25% Finnish Landrace breeding selected for ability to lamb following natural matings in May and June (Al-Shorepy and Notter, 1997). The frequency of autumn lambing by adult OOS ewes increased from approximately 60% to approximately 85% after 10 yr of selection (Notter and Cockett, 2005). OOS ewes had a longer breeding season than control ewes when continuously exposed to vasectomized rams (Vincent et al., 2000), and the incidence of ovulation and estrus was not affected by continuous long days (Notter et al., 2011).

This study was designed to compare annual changes in ovulatory behavior in intact ewes, circulating LH in OVX ewes, and circulating prolactin in three sheep breeds (OOS, St. Croix, and Suffolk) anticipated to differ in seasonal breeding patterns. Ewes were isolated from males, thereby allowing ewe behavior in previous studies involving ram exposure to be validated in the absence of males.

2. Materials and methods

2.1. Animals

This study was conducted at the Virginia Tech Copenhaver Sheep Center (37° N latitude) using OOS, Suffolk, and St. Croix ewes. Ewes were at least 214 d postpartum at commencement of the observation period, and were 3–9 yr old with a mean age of 6.2 yr. All procedures were approved and carried out in accordance with Institutional Animal Care and Use Committee of Virginia Tech.

A group of 20 St. Croix, 19 Suffolk, and 20 OOS ewes were identified in August and isolated from rams. Eleven St. Croix, 10 OOS, and 11 Suffolk ewes were randomly chosen and ovariectomized between 28 September and 30 October, and the remaining nine St. Croix, 10 OOS, and eight Suffolk ewes were left intact. One OVX ewe from each breed was designated as a control, and remaining OVX ewes received a subcutaneous implant containing estradiol on 21 November.

Blood samples were collected twice per week for 52 wk beginning on 21 November to monitor circulating concentrations of progesterone in intact ewes and LH in OVX ewes. Three blood samples were also taken from all ewes at hourly intervals beginning at 0900 on or near the annual solstices and equinoxes (i.e., on 18 December, 5 April, 21 June, and 18 September) to determine concentrations of circulating prolactin. Intact and OVX ewes of each breed were kept together. However, ewes of the three breeds were kept in separate pastures after 25 January (i.e., during the anticipated time of anestrus) and had no fence-line contact with other sheep for the duration of the study. Ewes were fed to maintain body condition and consumed pasture grass from May to November and hay for the remainder of the year. One intact Suffolk ewe and two OVX ewes (one OOS and one Suffolk) died before completion of the study, and their records were removed from the data. In addition, one intact OOS ewe appeared to be permanently acyclic based on progesterone profiles, and her records were likewise removed from the data.

2.2. Ovariectomy procedure

A paravertebral nerve block was performed using a 1% lidocaine solution on the left side at the level of the last thoracic and first two lumbar vertebrae to achieve anesthesia of the left paralumbar fossa. The approach to the ovaries was performed by a vertical incision through the skin and external oblique muscles midway between the last rib and tuber coxae. Internal oblique and transverse abdominal muscles were separated using blunt scissors to expose the peritoneum, which was then transected with a scalpel. A LigaSure hemostat was then inserted and sequentially clamped across each oviduct, mesovarium, and ovarian artery and vein. Heat pulses though the LigaSure unit cauterized the oviduct and related blood vessels, resulting in separation of the ovary from the rest of the reproductive tract. Ovaries were removed through the incision site and visually inspected to confirm removal of all ovarian tissue. Ceftiofur (1 mg/kg) was administered subcutaneously, and flunixin megulamine (0.5 mg/kg) was