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Effects of nutritional restriction on metabolic, endocrine, and ovarian function in llamas (*Lama glama*)

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ABSTRACT

The objectives of the study were to determine the effects of nutritional restriction on ovarian function in llamas. Mature female llamas were assigned randomly to a Control group, fed 100% of maintenance energy requirements (MER) ($n=8$), or a Restricted group ($n=8$) fed from 70% to 40% of MER until a body condition score of 2.5 was attained. Blood samples were taken every-other-day to determine plasma concentrations of LH, estradiol, leptin and metabolic markers, and follicular dynamics were monitored daily by ultrasonography for 30 days (Experiment 1). Llamas were then treated with GnRH to compare the ovulatory response and corpus luteus (CL) development between groups (Experiment 2). Blood samples were taken to measure LH, leptin, progesterone and metabolic markers and ovarian structures were assessed as in Experiment 1. Llamas in the Restricted group had lower body mass and body condition scores than those in the Control group ($P<0.001$). Plasma concentrations of cholesterol, non-esterified fatty acids, triglycerides, and urea were higher in the Restricted group ($P<0.05$) than in the Control group. The day-to-day diameter profiles of the dominant follicles were smaller ($P<0.05$) in the Restricted group than in the Control group but plasma estradiol concentration did not differ. The ovulation rate and LH secretion in response to GnRH did not differ. Day-to-day profiles of CL diameter, plasma progesterone and leptin concentrations were smaller ($P<0.01$) in the Restricted group. In conclusion, nutritional restriction in llamas was associated with suppressed follicle and CL development, and lower plasma concentrations of progesterone and leptin.

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1. Introduction

Food intake and body energy reserves are key determinants of reproductive success in mammals. The effect of negative energy balance and body condition on reproductive efficiency has been well documented in cattle (Bean and Butler, 1997; Buckley et al., 2003; Diskin et al., 2003; Roche et al., 2007). Subfertility associated with negative energy balance has been attributed to a lower conception rate, prolonged post-partum anestrus, ovarian dysfunction, abnormal estrous behavior, increased

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embryonic mortality, and delayed uterine involution (Webb et al., 2004).

Body condition at calving is a major determinant in the interval from calving to estrus and pregnancy rate during the following breeding season in beef cattle (Richards et al., 1986; Selk et al., 1988; Short and Adams, 1988). Feeding nutritionally stressed beef cows resulted in the resumption of estrous cycles, but only after body condition scores (BCS) increased to a level greater than at which cycles ceased (Richards et al., 1989).

The physiological mechanisms that control energy balance are reciprocally linked to those related to reproduction. Hence, reproduction is susceptible to changes in fuel availability through a complex interaction of hormones, metabolites and neuropeptides such as leptin, IGF-1, insulin, glucagon, growth hormone, glucose, and neuropeptide Y (Armstrong et al., 2003; Schneider, 2004; Webb et al., 2004; Wettemann et al., 2003).

Leptin, a 16 kDa product of the adipose obese (*ob*) gene, plays an important role in the regulation of energy metabolism, feeding behavior and reproduction in both monogastric and polygastric species (Barb and Kraeling, 2004; Barb et al., 2005; Chilliard et al., 2000; Williams et al., 2002). Leptin is produced in adipose tissue and its receptors in the reproductive system have been identified in the hypothalamus, hypophysis, ovary (oocytes, follicles, corpus luteum), embryos, endometrium and placenta of different species (Karlsson et al., 1997; Koshiba et al., 2001; Sarkar et al., 2010). Several in vitro studies have described an effect of leptin on GnRH and gonadotrophin secretion (Quennell et al., 2009; Watanove, 2002; Yu et al., 1997), and on steroidogenesis (Gregoraszcuk et al., 2004; Ruiz-Cortés et al., 2003; Spicer and Francisco, 1998). Although the pathway by which leptin affects the hypothalamic-hypophyseal-ovarian axis is not well understood, leptin treatment reversed the negative effect of fasting on LH secretion in sheep and rats (Henry et al., 2001; Nagatani et al., 1998).

Few controlled studies have been reported on the effect of long-term energy restriction on ovarian function and reproductive efficiency (Diskin et al., 2003); none were found pertaining to South American camelids. Reproductive efficiency in alpacas and llamas inhabiting the high Andes is affected by high rates of embryo mortality (Bravo et al., 1987, 2010; Fernández-Baca et al., 1970). In alpacas, embryonic losses of 50–80% by Day 30 and 80 of gestation, respectively, have been reported (Bravo et al., 1987; Fernández-Baca et al., 1970). We have recently documented an embryo loss rate of 45% (49/108) during the first 35 days after mating (Ratto et al., 2011), similar to the rates reported in earlier studies (50–58%; Bravo and Sumar, 1985; Fernández-Baca et al., 1970). Ovulatory follicle location (left vs right) and stage of preovulatory follicle development at the time of mating did not influence embryo survival rate in alpacas (Ratto et al., 2011), but the role of restricted food intake and poor body condition on ovarian function and embryo mortality in these species has not been examined.

The objectives of this study were to determine the effects of nutritional restriction on ovarian follicular dynamics (Experiment 1) and the ovulatory

response and CL development (Experiment 2) in llamas.

2. Material and methods

2.1. Animals and nutritional management

The study was conducted from April to September at the Universidad Austral de Chile, Valdivia, Chile (39° 38'S – 73° 5'W and 19 m above sea level). All procedures were reviewed and approved by the Universidad Austral de Chile Bioethics Committee and were performed in accordance with the animal care protocols established by the Universidad Austral de Chile. Mature non-lactating, non-pregnant, female llamas ($n=16$) were assigned randomly to a nutritionally Restricted group or a Control group ($n=8$ per group). Llamas in the Control group were fed *Ballica sp* hay ad libitum (4.42% crude protein [CP], 1.8 Mcal/kg metabolic energy [ME], 5.7% total ash [TA]) on a dry matter basis) and 300 g of commercial concentrate (16.0% CP, 5.4% TA, and 3.0 Mcal/kg ME; Cosetán, Iansagro S.A., Osorno, Chile) per day for the duration of the study. Llamas in the Restricted group were fed the same diet but the amount of food was progressively reduced from 70% to 40% of maintenance energy requirements (MER) over 87 days, until the llamas reached a body condition score of 2.5 (BCS; 1 = thin, 5 = obese; Van Saun, 2009). In succession, a 70% MER diet was given for 1 month, 60% for 1 week, 50% for 1 week, and 40% for 6 weeks. To maintain a BCS of 2.5, the Restricted group was maintained on a 40% MER diet, on average, until the end of the experimental period (i.e., the following 81 days). The MER for each llama in the Restricted group was determined using the equation $61.2 \times \text{initial body mass}^{0.75}$, as previously described (Lopez and Raggi, 1992). Llamas in both groups were provided water and mineral salt mixture (Usablock, Sweetlix, Mankato, Minnesota, USA) ad libitum. Every three weeks, llamas were given vitamins A, D, and E (5 ml, i.m.; Vitamina ADE, Drag PharmaInvetec S.A., Santiago, Chile), vitamin-B complex and methionine-iron (1.5 ml, i.m.; Drag PharmaInvetec S.A., Santiago, Chile).

2.2. Experiment 1

After the target BCS of 2.5 was attained in the Restricted group, transvaginal ultrasound-guided ablation of all ovarian follicles ≥ 5 mm was done in llamas in both groups (7 llamas per group), using a 17-gauge needle attached to a 5 MHz convex-array transducer, to synchronize follicular wave emergence, as described previously (Ratto et al., 2003). After follicle ablation, llamas were examined by transrectal ultrasonography daily for 30 days using a 7.5 MHz linear-array transducer (Aloka, SSD500, International Clinics, Santiago, Chile). Follicles ≥ 3 mm were monitored serially during this period and sketches were made noting the number, diameter and relative position of follicles within the both ovaries (Adams et al., 1990). Follicular dynamics were characterized using the diameter profile of the dominant follicle, the day on which the new dominant follicle reached a diameter of ≥ 7 mm (i.e., capable of ovulating), the number of follicles ≥ 4 mm in diameter at the time of follicular wave emergence and the

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