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Original article

Sperm production, testicular size, serum gonadotropins and testosterone levels in Merino and Corriedale breeds

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Abstract — The relationships between testis size, hormone secretion and sperm production were studied during the spring (December) and autumn (May) in rams of two breeds with different breeding seasons and body weights (Corriedale and Australian Merino) maintained on native pastures and under natural photoperiods in Uruguay. Blood samples were collected at 20-min intervals during a 260–360-min period in 13 rams (four Corriedale, nine Australian Merino) during the late spring and autumn. Rams were weighed and testis size was estimated by orchimetry at each time period. Sperm production was estimated during a 2-week period, 2 months before blood collection and during each week following every blood collection. There was no relationship between testicular size and sperm production measured at the same time, nor between live weight and sperm production. In contrast, testicular volume during the late spring was correlated with sperm production in the autumn (r = 0.65; $P = 0.02$). The autumn serum LH was higher in Corriedale than in Merino rams. LH pulsatility was unaffected by season, but LH pulse frequency tended to be higher in Corriedale than in Merino rams, particularly in the late spring (2.37 versus 1.56 pulses/6 h; $P = 0.08$). Serum testosterone concentration was similar in both breeds and seasons. FSH levels were higher in the late spring than in the autumn in both breeds (Corriedale: 2.83 ± 0.48 versus 2.17 ± 0.24 ng·mL^{-1}; Merino: 2.23 ± 0.24 versus 1.88 ± 0.17 ng·mL^{-1}). FSH and testosterone concentrations during the late spring were positively correlated with autumn sperm production ($P = 0.07$ and $P = 0.03$, respectively). In conclusion, the present experiment suggests that LH secretion is not a good parameter for the prediction of sperm production. In contrast, in our conditions (breeds and native pastures) testicular size and testosterone

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or FSH concentrations from the late spring may be used to predict sperm production in the autumn.

sperm production / testicular size / gonadotropins / testosterone / rams

Résumé — Production spermatique, taille testiculaire et niveau d'hormones gonadotropes et de testostérone chez des béliers de deux races (Mérinos et Corriedale). Les relations entre la taille testiculaire, les niveaux hormonaux et la production spermatique ont été étudiées à deux saisons, décembre et mai chez des béliers de deux races qui présentent des différences de poids vif et de période de saison sexuelle (Corriedale et Mérinos Australien) au pâturage naturel et soumis à la photopériode naturelle de l'Uruguay. Des prélèvements sanguins à raison d'une fois toutes les 20 min pendant 4–6 h ont été réalisés sur treize béliers (quatre Corriedale et neuf Mérinos Australien) au printemps et en automne. Les béliers ont été pesés et la taille testiculaire a été estimée par orchimetrie pendant chaque période. La production spermatique a été estimée durant deux semaines, 2 mois avant et pendant chaque semaine suivant les prélèvements sanguins. Il n'existe aucune relation entre la taille testiculaire et la production spermatique mesurées au même moment, ni entre le poids vif et la production spermatique. En revanche, la taille testiculaire pendant le printemps est corrélée avec la production spermatique en automne (r = 0,65 ; p = 0,02). En automne les béliers Corriedale présentent une concentration plasmatique de LH supérieure à celle des Mérinos. La pulsatilité de LH n'est pas dépendante de la saison, mais la fréquence de pulses de LH est largement plus élevée chez les Corriedale que chez les Mérinos, particulièrement au printemps (2,37 versus 1,56 pulses/6 h ; p = 0,08). La concentration plasmatique de testostérone est similaire chez les deux races et indépendante de la saison. Les niveaux de FSH sont supérieurs au printemps par rapport à l'automne pour les deux races (Corriedale : 2,83 ± 0,48 versus 2,17 ± 0,24 ng·mL^{-1} ; Mérinos : 2,23 ± 0,24 versus 1,88 ± 0,17 ng·mL^{-1}). Les concentrations de FSH et de testostérone pendant le printemps sont positivement corrélées avec la production spermatique en automne (p = 0,07 and p = 0,03 respectivement). En conclusion, cette expérience suggère que la sécrétion de LH n'est pas un bon paramètre prédicteur de la production spermatique. En revanche, sous nos conditions (race et pâturage naturel) la taille testiculaire et les concentrations de testostérone ou de FSH au printemps peuvent être utilisées comme prédicteur de la production spermatique en automne.

production spermatique / taille testiculaire / gonadotrophines / testostérone / béliers

1. INTRODUCTION

In the ram, artificial or natural variations of photoperiod induce changes in hormone secretion and libido [8, 9, 23, 27]. Levels of gonadotropins, testosterone, prolactin and inhibin vary with season [8, 13, 17, 24, 25, 28]. Testicular size is linearly related to the mean level of LH and testosterone in the blood [6] and is also influenced by photoperiod [1, 4, 5, 8, 15, 17]. Spermatogenesis is sensitive to variations in the levels of circulating hormones. There is a positive correlation between the number of renewing spermatogonia and LH peripheral levels [6]. Furthermore, spermatogenesis has been shown to change with photoperiod [7, 10, 15]. Seasonal variations in daily sperm production [7] and semen characteristics have also been observed, the best semen generally being obtained in the winter [2, 14]. It has been shown that photoperiod has an important effect on production of ejaculated sperm and fertility in rams [3]. In addition, feeding and environmental temperature (according to latitude) may modulate photoperiod effects [10, 19–21]. Finally, seasonal effects have been shown to differ among breeds [7, 17, 24, 27].

The objective of the present work was to identify, amongst a range of parameters (testis size and LH, FSH and testosterone serum concentrations) the most efficient predictors of sperm production during the sexual season, on a farm in adult Uruguayan Corriedale and Australian Merino rams which are the principal breeds in Uruguay: 68 and 12 % of the sheep population, respectively.

2. MATERIALS AND METHODS

2.1. Animals

Thirteen rams aged 5 years old were used: four Corriedale rams (1/2 Merino ancestry) and nine Australian Merino rams. The rams were fed on native pastures under natural lighting (latitude 31.25°S).

In our conditions, the Merino breed has a larger breeding season (starting in December) than Corriedale (starting in February) [11]. Furthermore, in the summer and autumn the sperm output is higher in Merino rams (12–15 %) [9, 10].

2.2. Measurements

In the late spring (13 December: 14 h 30 min daylight per 24 h) and in the autumn (9 May: 11 h 13 min) blood samples were collected at intervals of 20 min during a 360-min period in the spring (8.45 am–14.45 pm) and a 260-min period in the autumn (8.20 am–12.40 pm). On each occasion blood samples were collected by venipuncture from the jugular vein and sera were separated at 3 000 *g* for 20 min. Sera were frozen and stored at –20 °C in duplicate vials prior to the hormone assays. Each day, before blood collection, the rams were weighed and testicular volume (orchimetry) was estimated with the animal in a standing position.

Sperm output (production and the losses by the urogenital tract) was determined by semen collection during a 2-week period (2 × 2: 2 ejaculations/day, twice a week) 2 months before blood collection and the week after every blood collection. Semen samples were collected using an artificial vagina (40 °C). Spermatozoa concentration was determined by means of a spectrophotometer according to a standard calibration ($r^2 = 0.95$).

2.3. Hormone assays

Serum samples were measured in duplicate for LH and FSH with RIA kits provided by NIDDK. The results were expressed in terms of oLH-25 (for biological studies) and oFSH-RP1. Cross-reactivities with oGH, Vasopressin, hACTH, oPRL and oLH in the case of the FSH antiserum, and with oFSH, oGH, bTSH and PRL in the case of the LH antiserum, were always three orders of magnitude lower according to the kits. Intra- and inter-assay coefficients of variation were 7.2 and 12.8 %, respectively, for a concentration of 2.0 $ng \cdot mL^{-1}$ of LH and 8.0 and 13.2 % for a concentration of 1.8 $ng \cdot mL^{-1}$ of FSH. Minimal sensitivities of these assays were 0.2 and 0.39 $ng \cdot mL^{-1}$ for LH and FSH, respectively.

Testosterone was measured by RIA using an anti-T-3-O-carboxymethyloxime-bovine serum albumin antiserum with a previous ether extraction of experimental sera, as described previously [29]. Intra- and inter-assay coefficients of variation were 6.3 and 9.8 %, respectively, for a concentration of 1.6 $ng \cdot mL^{-1}$. Sensitivity of the assay was 200 $pg \cdot mL^{-1}$.

2.4. Statistical analyses

Pulse analysis (LH and testosterone) from individual rams at each sampling period was performed using the computer program described by Martin et al. [18]. Pulse frequency was expressed as the number of pulses occurring during a 6-h sampling period. Mean concentrations of LH and testosterone were calculated for each ram as average values of 14 or 19 individual sera. LH data were also transformed logarithmically for statistical analysis.

Mean FSH concentration was analysed for each ram using blood samples taken after 0, 120, 240 and 360 min of the sampling period.

Two-way analysis of variance was used to determine the respective effects of breed and season, followed by a Scheffé test for individual comparisons between means if the F value of the interaction was significant, or, between groups of means if the interaction was not found to be significant. Correlation analysis and residual Pearson correlations were performed using the SAS statistical package (Statistical Analysis System Institute, Windows Version 6.08, 1995).

3. RESULTS

Within-breed live weight was studied throughout time (autumn and late spring). Corriedale rams were heavier than Australian Merino rams during both seasons (*table I*).

Testicular volume was similar in both breeds and at both time periods. There was a non-significant tendency for higher values for both groups in the autumn ($P > 0.10$). Correlations between live weight and testicular volume were not observed, except in Corriedales during the autumn ($r = 0.92$; $P = 0.08$).

In the late spring, a lower sperm output was observed in Corriedale in comparison to Merino rams (6.10 versus 8.64 millions per day, respectively; $P = 0.05$). There was no difference between breeds in the autumn (*table I*). No differences in sperm production or concentration were found within breeds between late spring and autumn.

When measured during the same season, there was no correlation between testicular size and sperm output, nor between live weight and sperm output. In contrast, testicular volume in the late spring, correlated positively with sperm production in the autumn in both groups ($r = 0.65$; $P = 0.02$).

In the late spring, average LH levels were not significantly different between breeds (*figure 1*); however, after logarithmic transformation of LH, there were significant ($P = 0.04$) breed differences. Corriedale rams had higher LH levels than Merino

Table I. Testis volume, sperm production and hormone concentrations (LH, FSH, testosterone) in the late spring and autumn in Corriedale versus Merino breeds.

	Corriedale (mean ± SD)	Merino (mean ± SD)	*P* (signification) (%)
Late spring			
Live weight (kg)	75.3 (6.0)	65.5 (2.33)	4.35
Testis volume (cc)	256.3 (47.3)	267.0 (36.6)	NS
Daily sperm output (10^6)	6.10 (1.38)	8.64 (2.10)	5.09
Sperm output 2 months before (10^6)	6.43 (1.91)	8.05 (2.11)	NS
LH ($ng \cdot mL^{-1}$)	3.13 (0.42)	2.20 (1.24)	NS
LH (Log $ng \cdot mL^{-1}$)	0.49 (0.05)	0.29 (0.24)	3.59
LH (pulses/6 h)	2.37 (0.48)	1.56 (1.01)	7.98
Testosterone ($ng \cdot mL^{-1}$)	1.26 (0.71)	2.03 (0.12)	NS
(pulses/6 h)	2.13 (0.63)	1.50 (0.66)	NS
FSH ($ng \cdot mL^{-1}$)	2.83 (0.48)	2.23 (0.24)	NS
Autumn			
Live weight (kg)	80.3 (8.4)	72.5 (6.25)	8.86
Testis volume (cc)	317.5 (66.9)	296.7 (67.4)	NS
Daily sperm output (10^6)	7.1 (0.97)	8.42 (1.57)	NS
Sperm output 2 months before (10^6)	5.71 (0.94)	6.35 (1.33)	NS
LH ($ng \cdot mL^{-1}$)	3.18 (0.62)	2.09 (0.58)	1.04
LH (Log $ng \cdot mL^{-1}$)	0.50 (0.09)	0.30 (0.11)	1.67
LH (pulses/6 h)	2.60 (1.18)	1.69 (0.71)	NS
Testosterone ($ng \cdot mL^{-1}$)	1.40 (0.65)	1.57 (0.80)	NS
(pulses/6 h)	2.26 (0.66)	1.77 (0.61)	NS
FSH ($ng \cdot mL^{-1}$)	2.17 (0.24)	1.88 (0.17)	NS

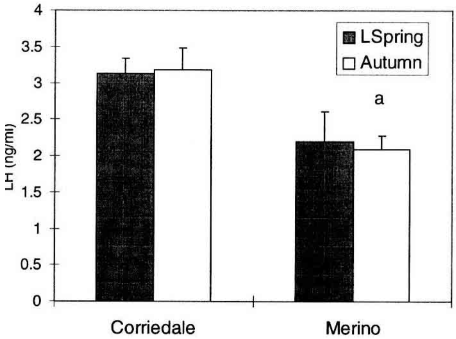

Figure 1. Mean LH levels (± SEM) in Corriedale and Merino rams during the late spring and autumn. a: $P < 0.05$ versus Corriedale in the same season.

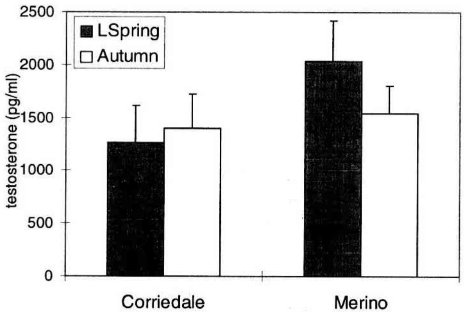

Figure 2. Mean testosterone levels (± SEM) in Corriedale and Merino rams during the late spring and autumn.

rams. This was more obvious in the autumn ($P < 0.02$). LH pulse frequency was unaffected by period and Corriedale had a higher frequency than Merino rams, during both seasons. This difference almost reached significance in the late spring ($P = 0.08$). When LH concentrations (determined throughout the experiment) were examined, differences were more commonly found in the first hours of blood sampling.

Mean testosterone levels (*figure 2*) did not differ between seasons, in either breeds, owing to large individual variations. Mean number of testosterone pulses was unaffected by season and breed. There was, however, a non-significant trend for Corriedale rams to have higher pulse frequencies than Merino rams (*table 1*). The correlation linking LH and testosterone pulse frequency pulses was high in the late spring and similar in both breeds ($r = 0.85$; $P = 0.03$; $r = 0.84$; $P = 0.04$). In the autumn, this correlation was non-significant ($r \leq 0.17$; NS).

The FSH concentrations were higher in the late spring than in the autumn but were similar between breeds (Corriedale: $P = 0.05$; Merino: $P = 0.004$) (*figure 3*). In the late spring there was a positive correlation approaching significance between testosterone (pulsatility and mean concentration) and testicular size ($r = 0.51$, $P = 0.07$; $r = 0.56$, $P = 0.05$). Moreover, FSH levels and testosterone concentrations were correlated with an autumn sperm production ($r = 0.51$, $P = 0.07$ and $r = 0.61$, $P = 0.03$, respectively).

In the autumn, mean LH levels were negatively associated with testosterone levels and sperm production ($r = -0.53$, $P = 0.06$; $r = -0.52$, $P = 0.06$ for Merino and Corriedale, respectively). In contrast, testosterone levels were positively correlated with sperm production ($r = 0.74$; $P = 0.01$). During this season the association between LH or testosterone pulses and sperm production or testicular volume were non-significant.

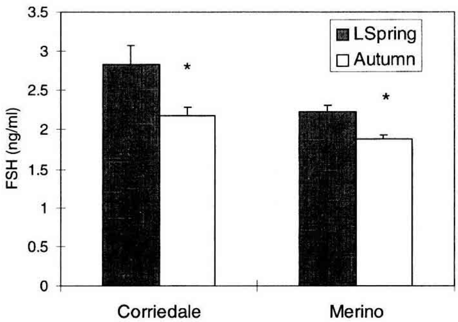

Figure 3. Mean FSH levels (± SEM) in Corriedale and Merino rams during the late spring and autumn. * $P < 0.05$ versus late spring within breed.

The best multiple correlation which allows the prediction of about 40 % of the variation in sperm production in the autumn, was obtained when testicular size and testosterone levels in the late spring were taken into account ($r = 0.66$; $P < 0.01$).

4. DISCUSSION

The present study confirms previous reports which indicated that Corriedale rams are heavier than Merino rams (76.7–83.3 versus 66.4–68.5 kg, respectively [9, 10]). In the late spring, Corriedale rams present lower sperm output than Merino rams owing to a lower number of spermatic cells per volume of testicular tissue (23.1 versus 30.4×10^6 per cc). In this breed testicular volume has been previously reported as a good predictor of future sperm production [9, 10]. In the present study a positive correlation between testicular size in the late spring (December) and sperm production in the autumn (March–May) was detected. This could be related to the length of the spermatogenetic process (56 days). Therefore, these results show that it is possible to identify rams with a greater sperm production a few months before mating. The low correlation between testicular size during the spring and the autumn obtained in the present experiment ($r = 0.50$) indicates that ram selection according to testicular size at the time of service is of limited value.

The relationships between testis size, serum gonadotropins or testosterone levels with sperm production were also evaluated. Previous reports studied the relationship between testicular size and gonadotropins or testosterone secretion [8, 13, 17, 25, 30]. Other studies compared sperm production with hormonal secretion [15, 27] in different breeds.

Corriedale rams presented higher pulsatility of LH than Merino rams. In contrast, pulsatility of LH was unaffected by season. Xu et al. [30] also observed higher LH secretion (pulsatility and mean concentration) in Romney (with a small testicular size in the spring) than in Poll Dorset rams, in the spring and late summer. These results as a whole may indicate that the low sperm production related to an inefficient testicle (Corriedale breed) or to small testicular size (Romney; [30]) determines an increase in LH secretion, partly as a result of a reduced testosterone negative feedback, according to Rhim et al. [26] and Hileman et al. [12].

Ortavant et al. [22] observed maximum LH and testosterone pulse frequency 3–4 h after dawn. In the present experiment in Corriedale rams, this tendency was confirmed because LH levels were greater in the first hours of the sampling period. Lincoln and Short [16] showed that the onset of the breeding season is dependent on increasing gonadotrophin secretion. Some studies [17] indicate a primary role of FSH in dictating the seasonal cycle of testicular size variation, and a genetic effect on the date of the seasonal maximum in FSH concentrations. In the present study, Merino and Corriedale rams presented higher FSH levels in the late spring. Late spring FSH levels were positively correlated with testicular size in the autumn. Testosterone response to LH pulsatility was more efficient in the spring, as shown by greater correlation coefficients. Furthermore, LH and FSH secretion in the late spring affects sperm production collected in the autumn. Therefore, these results show a long-term relationship between hormonal secretions and ejaculated sperm, related to the length of the spermatogenetic process. Thus, Martin et al. [20] suggest that a mechanism independent of gonadotropin secretion determines testicular growth. In this way, in the autumn these relations disappear or shift to negative associations (for example LH versus sperm production). Therefore, in our conditions improvement of sperm production in the winter (with an increasing testicular size) when sexual activity is lower would induce beneficial results in sperm output during the late spring.

LH and testosterone pulses did not correlate positively with sperm production and testicular size, because pulse frequency and mean concentration of hormones are two parameters which are not completely dependent on each other. It has, however, been described that testosterone plasma concentrations present a close correlation with ejaculated sperm [15, 27], and that rams with higher testosterone concentrations have greater testicular sizes [8].

In conclusion, the present experiment suggests that LH secretion is not a good parameter to predict sperm production. Late spring FSH concentration is associated with autumn sperm production. And finally, in our conditions (breeds and native pastures), testicular size and testosterone concentration in the late spring may be used to predict sperm production in the autumn.

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REFERENCES

[1] Amann R.P., Schanbacher B.D., Physiology of male reproduction, J. Anim. Sci. (Suppl. 2) 57 (1983) 380–403.

[2] Colas G., Seasonal variations of sperm quality in adult Ile-de-France rams. II. Fertilizing ability and its relation to qualitative criteria in vitro, Reprod. Nutr. Dev. 21 (1981) 399–407.

[3] Colas G., Guérin Y., Clanet V., Solari A., Influence of the photoperiod on the production and fecundity of spermatozoa in the adult Ile-de-France ram, Reprod. Nutr. Dev. 25 (1985) 101–111.

[4] Colas G., Guérin Y., Lermaire Y., Montassier Y., Despierres J., Seasonal variation in the testis diameter and sperm morphology in the Vendean and Texel ram, Reprod. Nutr. Dev. 26 (1986) 863–875.

[5] Colas G., Lefebre J., Guérin Y., Father-male offspring transmission of seasonal variations in testicular diameter and percentage of abnormal sperm in the Ile-de-France ram. I. Male offspring born in February, Reprod. Nutr. Dev. 30 (1990) 389–603.

[6] Courot M., Ortavant R., Endocrine control of spermatogenesis in the ram, J. Reprod. Fert. 30 (1981) 47–60.

[7] Dacheux J.L., Pisselet C., Blanc M.R., Hochereau de Reviers M.T., Courot M., Seasonal variations in rete testis fluid secretion and sperm production in different breeds of ram, J. Reprod. Fert. 61 (1981) 363–371.

[8] Dufour J.J., Fahmy M.H., Minvielle F., Seasonal changes in breeding activity, testicular size, testosterone concentration and seminal characteristics in rams with long or short breeding season, J. Anim. Sci. 58 (1984) 416–422.

[9] Fernández Abella D., Villegas N., Klappenbach A., Machado A., Efecto de la edad y la raza en la producción de semen y actividad sexual, Bol. Tec. Cienc. Biol. 2 (1992) 37–49.

[10] Fernández Abella D., Villegas N., Echeverría D., Robaina J., Evaluación de las variaciones estacionales en la producción espermática de cuatro razas ovinas, Bol. Tec. Cienc. Biol. 3 (1993) 23–34.

[11] Fernández Abella D., Saldanha S., Surraco L., Villegas N., Hernández Russo Z., Rodríguez Palma, Evaluación de la variación estacional de la actividad sexual y crecimiento de lana en cuatro razas ovinas, Bol. Tec. Cienc. Biol. 4 (1994) 19–44.

[12] Hileman S.M., Lubbers L.S., Kuehl D.E., Schaeffer D.J., Rhodes L., Jackson G.L., Effect of inhibiting 5 alpha-reductase activity on the ability of testosterone to inhibit luteinizing hormone release in male sheep, Biol. Reprod. 50 (1994) 1244–1250.

[13] Howles C.M., Webster G.M., Haynes N.B., The effect of rearing under a long or short photoperiod on testis growth, plasma testosterone and prolactin concentrations, and the development of sexual behaviour in rams, J. Reprod. Fert. 60 (1980) 437–447.

[14] Ibrahim S.A., Seasonal variations in semen quality of local and crossbred rams raised in the United Arab Emirates, Anim. Reprod. Sci. 49 (1997) 161–167.

[15] Islam A.B.M., Land R.B, Seasonal variation in testis diameter and sperm output of rams of breeds of different prolificacy, Anim. Prod. 25 (1977) 311–317.

[16] Lincoln G.A., Short R.V., Seasonal breeding: Nature's contraceptive, Recent Prog. Horm. Res. 36 (1980) 1–51.

[17] Lincoln G.A., Lincoln C.E., McNeilly A.S., Seasonal cycles in the blood plasma concentration of FSH inhibin and testosterone, and testicular size in rams of wild, feral and domesticated breeds of sheep, J. Reprod. Fert. 88 (1990) 623–633.

[18] Martin G.B., Taylor P.L., McNeilly A.S., Effect of small doses of bovine follicular fluid on the tonic secretion of gonadotrophins in the ewe, J. Endocr. 114 (1987) 73–79.

[19] Martin G.B., Ford J.R., Purvis I.W., Environmental and genetic factors affecting reproductive activity in the Merino ram, in: Oldham C.M., Martin G.B., Purvis I.W. (Eds.), Reproductive Physiology of Merino Sheep – Concepts and Consequences, University of Western Australia, Perth, 1990, pp. 111–129.

[20] Martin G.B., Tjondronegoro S., Blackberry M.A., Effects of nutrition on testicular size and the concentrations of gonadotrophins, testosterone and inhibin in plasma of mature male sheep, J. Reprod. Fert. 101 (1994) 121–128.

[21] Masters D.G., Fels H.E., Seasonal changes in the testicular size of grazing rams, Proc. Aust. Soc. Anim. Prod. 15 (1984) 444–447.

[22] Ortavant R., Daveau A., Garnier D.H., Pelletier J., de Reviers M.M., Terqui M., Diurnal variation in release of LH and testosterone in the ram, J. Reprod. Fert. 64 (1982) 347–353.

[23] Ortavant R., Bocquier F., Pelletier J., Ravault J.P., Thimonier J., Volland-Nail P., Seasonally of reproduction in sheep and its control by photoperiod, Aust. J. Biol. Sci. 41 (1988) 69–85.

[24] Pelletier J., Garnier D.H., de Reviers M.M., Terqui M., Ortavant R., Seasonal variation in LH and testosterone release in rams of two breeds, J. Reprod. Fert. 64 (1982) 341–346.

[25] Rhim T.J., Kuehl D., Jackson G.L., Seasonal changes in the relationships between secretion of gonadotrophin-releasing hormone, luteinizing hormone, and testosterone in the ram, Biol. Reprod. 48 (1993) 197–204.

[26] Rhim T.J., Schaeffer D.J., Jackson G.L., Comparison of the effects of pulsatile and constant testosterone on the secretion of gonadotropins in the ram, Endocrinology 132 (1993) 2399–2406.

[27] Sanford L.M., Palmer W.M., Howland B.E., Changes in the profiles of serum LH, FSH and testosterone, and in mating performance and ejaculate in the ram during the ovine breeding season, J. Anim. Sci. 45 (1977) 1382–1391.

[28] Sanford L.M., Voglmayr J.K., Vale W.W., Robaire B., Photoperiod-mediated increases in serum concentrations of inhibin, follicle-stimulating hormone, and luteinizing hormone are accentuated in adult shortened-scrotum rams without corresponding decreases in testosterone and estradiol, Biol. Reprod. 49 (1993) 365–373.

[29] Tesone M., Biella de Souza Valle L., Foglia V.G., Charreau E.H., Endocrine function of the testis in streptozotocin diabetic rats, Acta Physiol. Latinoam. 28 (1976) 387–393.

[30] Xu Z.Z., McDonald M.F., McCutcheon S.N., Blair H.T, Seasonal variation in testis size, gonadotropin secretion and pituitary responsiveness to GnRH in rams of two breeds differing in time of onset of the breeding season, Anim. Reprod. Sci. 26 (1991) 281–292.