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Variations in the plasma levels of gonadotrophin and testosterone and in Leydig and Sertoli cell populations between birth and adulthood in Romanov lambs born in spring or autumn.

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Summary. Plasma gonadotrophin and testosterone levels during the prepuberal period have been compared in spring and autumn-born Romanov lambs ; the somatic and germ cell populations of these lambs have also been compared at birth and at adulthood.

At 1 and 3 months of age, the number of LH pulses per hour and mean plasma LH levels were significantly higher in spring than in autumn lambs. In adults, no such differences were observed. Similarly, at 1 and 3 months of age, the number of testosterone pulses per hour was higher in spring than in autumn animals.

In the prepuberal period, the ratio of the levels of mean plasma testosterone to LH was higher in autumn than in spring lambs. The highest ratio was observed in adults but there was no variation according the season of birth.

At 1 month of age, mean plasma FSH levels were higher in autumn than in spring lambs ; this difference did not persist later on.

Despite these endocrinological differences, testis weight, total Sertoli and Leydig cell numbers per testis, total number of gonocytes per testis at birth and daily production of round spermatids per testis in adult rams were similar in spring and autumn-born animals.

Introduction.

The secretion of plasma LH and testosterone in adult rams varies with the season, being highest in the breeding season (Sanford, Palmer and Howland, 1974 ; Schanbacher and Ford, 1976 ; Wilson and Lapwood, 1979 ; Schanbacher and Ford, 1980 ; Pelletier *et al.*, 1982 ; Sanford, Palmer and Howland, 1982). In growing Ile-de-France male lambs, the season of birth modifies testicular growth and the plasma levels of LH and testosterone : LH levels increase more rapidly in those born in spring than in those born in autumn (Courot *et al.*, 1975 ; Cotta *et*

al., 1975). In Ile-de-France (de Reviers *et al.,* 1980) and Finn Dorset Horn (Hochereau-de Reviers *et al.,* 1984 a) postpuberal lambs born in early winter or summer, the total numbers of Sertoli and Leydig cells differ with the season of birth.

The purpose of this work was to investigate the existence of variations in the mean plasma levels of LH, FSH and testosterone and the frequency of pulses from birth to adulthood in early spring and autumn-born Romanov lambs. The cellular composition of the testis at birth and in adult animals during the sexual season were also compared in spring and autumn-born animals to detect the influence of seasonal hormonal status before puberty on this parameter.

Material and methods.

Group I (spring-born lambs) included 18 Romanov ram lambs born between the 1st of March and the 1st of April and group II (autumn-born lambs) 20 Romanov ram lambs born between the 1st of September and the 1st of October. Of these animals, 7 in group I and 13 in group II were maintained until the sexual season of their second year ; the others were slaughtered around 5 months of age.

Blood was sampled by jugular venipuncture twice weekly during the first 3 months and thereafter twice a month until adulthood. Serial samples were collected every 30 min for 4 h at 1 and 3 months of age and before slaughter in adults during the sexual season.

After centrifugation, the plasma samples were stored at -15 °C until assay. Plasma FSH (Blanc and Poirier, 1979) and LH (Pelletier *et al.,* 1968) were measured by double antibody radioimmunoassay using NIH-P-56-HG-FSH 225 (= 2.6 NIH FSH S3) and LH — CNRS M3 (= 1.8 NIH LH S1), respectively, as standards. Testosterone was radioimmunoassayed directly without extraction according to the method of Cotta *et al.* (1975).

Mean monthly hormonal levels were determined from biweekly samples collected during the first 3 neonatal months. These levels will be referred to as monthly plasma levels. Mean serial plasma levels were calculated from the serial values for each hormone at 1 or 3 months of age. Pulses of LH or testosterone were defined as obvious rises in the hormone concentration, followed by at least two declining values. The number of pulses per hour was calculated for LH and testosterone at each serial sampling period.

In addition, ram lambs born around the 1st of April ($n = 5$) and the 1st of October ($n = 5$) were castrated in the first neonatal days. After castration or slaughter, all the testes were fixed in Bouin Hollande solution and treated for histological study as previously described (Hochereau-de Reviers *et al.,* 1976, 1979). The total numbers of Sertoli and Leydig cells were calculated in new-born and adult animals. The total number of gonocytes was also determined at birth and the daily production of round spermatids was measured in adult animals.

The data were analysed using either the analysis of variance, Student's t-test or the non-parametric U-test.

Results.

A) *Endocrine variations.*

1. *Mean monthly plasma levels.*

a) *LH.* — Plasma LH levels increased significantly ($P < 0.05$) between the first week and the end of the second neonatal month in spring and autumn-born animals (3.0 to 8.2 ng/ml and 0.8 to 7.1 ng/ml, respectively). Following this rise, plasma LH decreased sharply in autumn lambs but was maintained at relatively high levels in spring lambs (fig. 1A). Comparisons of the monthly plasma LH levels for the first 3 neonatal months in the two groups revealed two main facts. First, the autumn-born lambs had lower plasma LH levels than spring-born lambs. Second, the first and third monthly values were nearly identical and the maximum in the two groups occurred during the second neonatal month (table 1).

During the second year of the experiment, plasma LH levels increased again in late spring and summer in both groups and were always higher in spring than in autumn lambs (fig. 1A).

b) *Testosterone.* — Plasma testosterone levels increased significantly ($P < 0.05$) from the first week to the 7th neonatal month (0.4 to 6.0 ng/ml) in both spring and autumn lambs (fig. 1B).

During the first two neonatal months, there was no difference between the two groups of animals, but during the third month, plasma testosterone values were higher in autumn than in spring lambs (table 1). Testosterone increased again sharply during the late summer and autumn of the second year but was not significantly different in the two groups.

c) *FSH.* — Plasma FSH levels increased significantly ($P < 0.05$) from the first neonatal week to the end of the second month when the highest values were observed for both spring and autumn lambs. The FSH level was higher in autumn than in spring lambs during the first three neonatal months (fig. 1 C ; table 1).

TABLE 1

A comparison of the monthly mean plasma levels of LH, testosterone and FSH during the first 3 neonatal months in spring and autumn-born Romanov lambs (ng/ml).

	Hormone								
	LH			Testosterone			FSH		
Months	1	2	3	1	2	3	1	2	3
Spring	4.4 ± 0.5a	7.5 ± 0.8b	5.0 ± 0.5a	2.4 ± 0.3a	3.5 ± 0.3b	4.0 ± 0.3a	2.5 ± 0.1a	3.3 ± 0.2b	2.0 ± 0.2a
Autumn	2.6 ± 0.6c	4.6 ± 0.4a	3.2 ± 0.5ac	2.6 ± 0.4a	4.3 ± 0.9b	11.5 ± 2.5c	3.5 ± 0.2b	4.2 ± 0.2c	3.1 ± 0.3b

For each parameter, the superscripts a, b, c, d, indicate significant differences ($P < 0.05$) in rows and in columns (mean ± SEM).

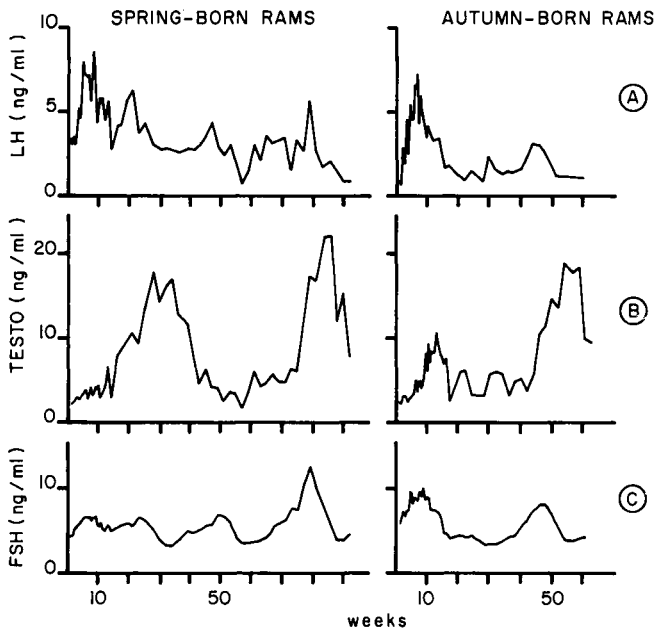

FIG. 1. — *Comparative changes in LH* (1A), *testosterone* (1B) *and FSH* (1C) *levels in spring and autumn-born rams from birth till the second sexual season* (1.5 years in spring-born and 1 year in autumn-born).

Thereafter, these levels decreased slightly and then plateaued in spring lambs, declining around 5 months of age. In autumn animals, the FSH levels decreased sharply after the second neonatal month. During the second year of life, the FSH increased again either at two different periods (spring and early autumn) in spring rams or in a single period (late summer) in autumn rams.

2. *Serial sampling.*

a) *LH.* — At 1 and 3 months of age, the number of LH pulses per hour and the mean plasma LH levels were significantly higher in spring than in autumn lambs ; these levels then fell so they were slightly lower at 3 months than at 1 month of age (table 2). During the sexual season in adult rams, the number of LH pulses per hour was lower in spring than in autumn animals, but the mean plasma LH levels did not differ significantly (table 2).

b) *Testosterone.* — At 1 and 3 months of age, the number of testosterone pulses per hour was higher in spring than in autumn lambs. The mean testosterone levels were only higher in the former than in the latter at 1 month of age (table 2). In adult rams, the number of testosterone pulses per hour and the mean testosterone level did not differ significantly between spring and autumn animals (table 2).

TABLE 2

A comparison of the hormonal parameters during serial sampling at 1 and 3 months of age and at adulthood in spring and autumn-born Romanov lambs and rams (ng/ml).

		Season of birth	
Age	Hormonal parameters	Spring	Autumn
1 month	no. of LH pulses/h	0.48a	0.28b
	mean	5.7 ± 0.6a	1.67 ± 0.23b
	no. of testosterone pulses/h	0.36ab	0.28b
	mean	3.2 ± 0.2a	2.4 ± 0.2b
	mean FSH	2.88 ± 0.12a	4.6 ± 0.35b
3 months	no of LH pulses/h	0.49a	0.28b
	mean	4.32 ± 0.6a	0.85 ± 0.1c
	no. of testosterone pulses/h	0.48a	0.20b
	mean	4.51 ± 0.46c	4.79 ± 0.93c
	mean FSH	2.58 ± 0.16a	1.96 ± 0.23a
Adult	no. of LH pulses/h	0.25b	0.41a
	mean	0.67 ± 0.05c	0.89 ± 0.07c
	no. of testosterone pulses/h	0.32ab	0.46a
	mean	11 ± 3.2d	11.6 ± 1.9d
	FSH	2.26 ± 0.47a	1.77 ± 0.12a

For each parameter, the superscripts a, b, c, d, indicate significant differences ($P < 0.05$) in rows and in columns (m ± SEM).

c) *FSH.* — FSH was not secreted in a pulsatile pattern. At 1 month of age, mean plasma FSH levels were higher in autumn than in spring lambs. These levels were not significantly different between 3-month old and adult rams (table 2).

d) *Ratio of testosterone to LH.* — The ratio of testosterone to the mean number of LH pulses per hour did not differ significantly from 1, except in spring lambs at 1 month of age and in autumn lambs at 3 months of age, when it was lower. This indicates that each LH pulse was followed by a testosterone pulse (table 3). The ratio of the mean levels of plasma testosterone to LH was higher in autumn than in spring lambs at 1 and 3 months of age ; the highest ratio was observed in adult rams during the sexual season and it did not differ significantly between spring and autumn animals.

B) *Testicular variables.*

Testicular weight, the total numbers of Sertoli and Leydig cells per testis, the total number of gonocytes per testis at birth, and the daily production of round spermatids per testis in adult rams were similar for the two groups of animals (table 4).

TABLE 3

The relationship between the different hormonal parameters observed during serial sampling at 1 and 3 months of age and at adulthood in spring and autumn Romanov lambs and rams.

		Spring	Autumn
No. of testosterone pulses/ no. of LH pulses	1 month	0.76	1.00
	2 months	0.98	0.71
	Adult	1.28	1.12
Mean testosterone level/ mean LH level	1 month	0.56	1.44
	3 months	1.04	5.64
	Adult	16.4	13.0

Discussion.

The pattern of mean plasma levels of LH and testosterone that we observed in Romanov lambs born in spring or autumn is similar to that reported in Romanov lambs born in winter (Ricordeau *et al.,* 1979) and in Ile-de-France lambs born in either spring, autumn (Courot *et al.,* 1975) or late winter and then submitted to artificially increasing or decreasing daylength (Alberio, 1976). The increase in LH in the present study was greater than that reported by Walton *et al.* (1980) in cross-bred lambs. A comparison of the monthly mean LH levels and of the mean number of LH pulses per hour at 1 and 3 months of age indicates that, at both seasons of birth, the highest frequency of LH pulses should have occurred around 7 weeks of age in the Romanov breed, as shown previously by Ricordeau *et al.* (1979).

However, in our study, the number of LH pulses as well as the mean plasma LH levels were much higher in spring than in autumn-born Romanov lambs, corroborating the effects found by Courot *et al.* (1975) in the Ile-de-France breed. The decrease in mean LH levels observed just before puberty, around the third neonatal month, ceased in spring animals when the seasonal stimulation of LH pulsatility (Pelletier *et al.,* 1982) was superimposed on the puberal pattern. The increase in plasma testosterone levels that we observed is similar to that found previously (Cotta *et al.,* 1975 ; Garnier *et al.,* 1978 ; Walton *et al.,* 1980). The pulsatile discharge of testosterone increases gradually from birth to puberty (Savoie *et al.,* 1979). However, the autumn lambs in our study entered the non-breeding season at the time of puberty and the testosterone level ceased to rise. On the other hand, in spring lambs a seasonal increase was superimposed on the puberal one. This could explain the variations in the ratio of testosterone to LH.

As seen for LH, the mean FSH levels increased from birth to the second neonatal month ; this increase was greater than that observed by Walton *et al.* (1980). We also found a seasonal variation in FSH, with an increase during the sexual season, as previously reported by Sanford *et al.* (1976). A transitory increase was also observed in adult spring rams in the early spring. There was no

TABLE 4

A comparison of the histological testicular parameters of spring and autumn-born Romanov lambs at birth and at adulthood.

Season of birth		Testis weight (g)	Tot. no. Leydig cells $\times 10^8$	Leydig cell area μm^2	Tot. no. Sertoli cells $\times 10^8$	Sertoli nuclei area μm^2	To. no. gonocytes $\times 10^8$	Daily production round spermatids $\times 10^9$
New-born	Spring n = 5	0.588 ± 0.068	1.12 ± 0.18	48.3 ± 1.3	2.99 ± 0.41	23.7 ± 0.42	0.13 ± 0.03	–
	Autumn n = 5	0.630 ± 0.093	1.22 ± 0.18	52.3 ± 2.9	3.16 ± 0.59	22.2 ± 0.6	0.14 ± 0.02	–
Adult	Spring n = 7	191 ± 13	8.8 ± 0.8	64.5 ± 2.5	19.4 ± 1.1	63.6 ± 2.4	–	2.8 ± 0.2
	Autumn n = 13	185 ± 6	7.5 ± 0.5	65.3 ± 2.2	20.1 ± 1.4	67.7 ± 1.6	–	2.48 ± 0.15

Mean ± sem.

pattern of FSH pulsatility at any age in our Romanov animals. The finding is similar to that of D'Occhio *et al.* (1982) and differs from the episodic pattern of FSH secretion in the Soay ram reported by Lincoln *et al.* (1977).

Testicular testosterone production in response to LH stimulation, expressed as the ratio of testosterone to LH, depends partly on the number of Leydig cells per testis. The total number of Leydig cells per testis did not vary much with the season of birth in either new-born or adult rams. The number of Leydig cells per testis increases gradually during testicular growth (Monet-Kuntz *et al.*, 1984), and the number of LH receptors per testis increases from 2 months of age onwards (Barenton *et al.*, 1983). However, seasonal differences in Leydig cell population have been observed in 6-month old summer and winter lambs (Hochereau-de Reviers *et al.*, 1984 a), indicating the superimposition of seasonal changes on the puberal rise in this population. In adult rams, a seasonal periodicity of testicular LH receptors and steroid content has been found, with the lowest values at the winter solstice and the highest at the summer solstice (Barenton and Pelletier, 1983). In new-born and adult rams, the total numbers of Sertoli and germ cells per testis did not differ with the season of birth despite the wide postnatal hormonal variations observed in our two groups of lambs. Interestingly, in previous studies on Ile-de-France (de Reviers *et al.*, 1980) or cross-bred Finn X Dorset (Hochereau-de Reviers *et al.*, 1984 a et b) lambs born around the winter or summer solstices, we found differences in the total number of Sertoli cells per testis and in spermatid production. This is probably not due to genetic differences since in spring or autumn-born Prealpes du Sud X Romanov X Ile-de-France lambs, which are nearly equivalent to the Finn X Dorset cross-bred from a genetic viewpoint, the total number of Sertoli cells per testis is equivalent at 80 days of age, after mitosis has ceased (Hochereau-de Reviers *et al.*, 1984 b).

In adult rams, testicular FSH receptors are lowest in winter and highest in summer (Barenton and Pelletier, 1983). Seasonal changes in the hormonal receptivity of Sertoli cells could be superimposed on prepuberal variation. As the last Sertoli cell multiplications take place early in life, during the first two neonatal months (Courot, 1962), the number of these cells could vary in lambs born during periods of maximum or minimum sensitivity, while lambs born in-between these periods would not evidence such variations.

In conclusion, we have demonstrated variations in gonadotrophin secretion during the prepuberal period in spring and autumn-born Romanov lambs. This results in the variation of testosterone production, but these differences do not persist into adulthood.

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Résumé. *Variations des teneurs plasmatiques en hormones gonadotropes et en testostérone, des populations de cellules de Leydig et de Sertoli entre la naissance et l'âge adulte chez des béliers Romanov nés au printemps ou à l'automne.*

L'influence de la saison de naissance, printemps ou automne, sur les teneurs plasmatiques en hormones gonadotropes et en testostérone et sur l'histologie testiculaire à la naissance et à l'âge adulte durant la saison sexuelle a été analysée chez des agneaux mâles de race Romanov.

Aux âges de 1 et 3 mois, le nombre de pulses et le niveau plasmatique moyen de LH sont significativement plus élevés chez les agneaux nés au printemps par rapport à ceux nés à l'automne. Parallèlement, le nombre de pulses de testostérone est plus important chez les agneaux nés au printemps.

Cependant, le rapport entre les niveaux plasmatiques moyens de testostérone et ceux de LH augmente avec l'âge et est plus élevé durant la période prépubère chez les agneaux nés à l'automne que chez ceux nés au printemps. Cette différence ne persiste pas à l'âge adulte où ce rapport est maximum.

Les niveaux moyens de FSH diffèrent selon la saison de naissance, et sont plus élevés à l'automne, seulement durant le 1er mois d'âge.

En dépit de ces différences endocriniennes le poids testiculaire, les nombres totaux de cellules de Sertoli et de Leydig, le nombre total de gonocytes à la naissance ou la production quotidienne de spermatides rondes à l'âge adulte par testicule, ne diffèrent pas en fonction de la saison de naissance.

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