Aust. J. Biol. Sci., 1978, **31**, 257–66

Testicular and Epididymal Sperm Numbers and Related Parameters in the Developing Awassi Ram

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Abstract

Testicular parameters, parenchymal spermatid concentration, and epididymal sperm reserves were measured in tracts obtained from 16 Awassi rams classified into three age groups (1, 1·5 and 2·5 years old). Between 1 and 2·5 years of age the paired testis weight increased from 164·9 to 315·2 g, the testicular spermatid number ($\times 10^9$) increased from 15·9 to 55·8, and the total epididymal sperm reserves ($\times 10^9$) increased from 11·1 to 98·8.

Significant correlations were found between the paired testis parenchyma weight and all testicular dimensions and size. Testicular spermatid numbers and concentration were correlated with paired testis weight (r = 0·91 and 0·63), paired testis volume (r = 0·92 and 0·64) and all testicular measurements, particularly paired length × depth (r = 0·92 and 0·66).

Regression coefficients between all parameters were essentially linear and highly significant, allowing accurate predictions of testis weight, volume and spermatid numbers to be made. The total epididymal sperm reserves and the sperm content of each of the caput, corpus and cauda of the epididymis were correlated with the paired weights of the epididymis (r = 0·73, 0·75, 0·73 and 0·70), the testis (r = 0·76, 0·83, 0·91 and 0·72), the total spermatid numbers in testicular homogenates (r = 0·70, 0·85, 0·91 and 0·64), and spermatid concentration (r = 0·56, 0·75, 0·72 and 0·49). The storage capacity of the cauda epididymides appeared to develop more slowly than the rate of sperm production because at 2·5 years of age it was about 1·5 and 2·8 times that in rams aged 1·5 and 1 year respectively.

Introduction

In Iraq the fat-tailed Awassi is one of the major and most popular breeds of sheep. Information on the reproductive performance of this breed and particularly of the rams is very limited (Juma and Dessouky 1969; Injidi 1974). The aim of the present work was to quantify the sperm producing potential and epididymal sperm reserves of Awassi rams in relation to age, to establish their correlation with testis size and weight, and to find out how far the variations in epididymal sperm reserves relate to testicular sperm production.

Materials and Methods

Sixteen Awassi rams (six 1 year old, group *A*; five 1·5 years old, group *B*; five 2·5 years old, group *C*) were slaughtered during October and November 1975. Within 4 h of slaughter the testes were removed and freed from extraneous tissues. The length, width, depth, and circumference of each testis when held vertically with tissue forceps were measured to the nearest 0·1 cm. The organs were placed in separate Petri dishes on filter papers premoistened with 0·85% (w/v) NaCl (physiological saline) in order to minimize dehydration. The epididymis was carefully dissected and sectioned into three major segments corresponding to the caput, corpus and cauda based on gross anatomical structure and tubular size. The 'empirical' testis volume was determined by displacement in physiological saline. The testes and various epididymal segments were weighed and the tunica albuginea carefully peeled off the testis. The weight of testicular parenchyma was then recorded. Each tissue was separately diced and soaked for about 1 h in physiological saline. The macerated tissue was then transferred into a Waring blender and homogenized at 6000 rev/min in 500 ml physiological saline for the testicular parenchyma, 350 ml for the caput and cauda and 150 ml for the corpus epididymides. The saline also contained 1000 i.u. penicillin/ml and 1 mg streptomycin/ml to minimize bacterial growth in the homogenates.

Estimations of the sperm concentration in tissue suspensions were made after 24 h storage at 5°C as indicated by Amann and Almquist (1961*a*). Immediately before counting, each sperm suspension was vigorously shaken for 1 min and a sample of the homogenate withdrawn and further diluted 1:4 (v/v) with 0·2% eosin–saline. Accordingly, the final dilutions were 1:2500 for testicular parenchyma, 1:1500 for the caputa and caudae and 1:750 for the corpora epididymides. These dilutions were selected to allow at least 100 sperm per 80 small squares of the counting chamber of the improved Neubauer haemocytometer. Sperm concentrations in each sample were determined in duplicates prepared from different subsamples of the entire suspension.

The 'theoretical' testis volume was calculated from the ellipsoid formula: $\frac{4}{3}\times\frac{1}{2}$ length $\times\frac{1}{2}$ width $\times\frac{1}{2}$ depth $\times 3\cdot 143$.

Analyses of variance (*F* test) were performed on the various testicular and epididymal parameters after appropriate transformation into their corresponding log values. Whenever variation differed significantly among age groups, a supplementary analysis using the Hartley's variant of the Q method (Snedecor and Cochran 1967) was completed to determine the significance of difference between age groups. Zero-order correlations and linear regression coefficients and equations were calculated as outlined by Snedecor and Cochran (1967).

Table 1. Testicular characteristics in Awassi rams of various ages

Values expressed are means ± s.e. For each parameter, means with different superscripts are significantly different ($P<0\cdot05$)

Parameter	Age group (years)		
	A (1)	*B* (1·5)	*C* (2·5)
Average length (cm)	$7\cdot0\pm0\cdot2^a$	$7\cdot5\pm0\cdot2^a$	$8\cdot7\pm0\cdot3^b$
Average width (cm)	$4\cdot3\pm0\cdot1^a$	$4\cdot4\pm0\cdot1^a$	$5\cdot3\pm0\cdot1^b$
Average depth (cm)	$4\cdot7\pm0\cdot1^a$	$5\cdot1\pm0\cdot1^a$	$6\cdot0\pm0\cdot1^b$
Average circumference (cm)	$15\cdot0\pm0\cdot2^a$	$15\cdot8\pm0\cdot2^a$	$18\cdot1\pm0\cdot2^b$
Paired testis volume (cm^3)	$160\cdot3\pm10\cdot1^a$	$203\cdot4\pm6\cdot9^a$	$315\cdot9\pm22\cdot9^b$
Theoretical volume (cm^3)	$150\cdot1\pm10\cdot3^a$	$171\cdot1\pm9\cdot7^a$	$292\cdot2\pm24\cdot9^b$
Paired testis weight (g)	$164\cdot9\pm10\cdot9^a$	$208\cdot8\pm6\cdot8^a$	$315\cdot2\pm22\cdot0^b$
Paired testicular parenchyma weight (g)	$154\cdot2\pm10\cdot9^a$	$194\cdot0\pm6\cdot9^a$	$301\cdot5\pm22\cdot1^b$
Tunica albuginea (% of testes weight)	6·5	7·1	4·3

Results

There were significant differences ($P<0\cdot01$) among ages in all testicular measurements. Results for the right and left testes did not vary significantly. A rapid increase in testicular dimensions and size occurred between 1·5 and 2·5 years of age (Table 1). The 'theoretical' testes volume was always lower than the 'empirical' volume determined by displacement. The weight of tunica albuginea was 6·5, 7·1 and 4·3% of the testis weight in groups *A*, *B* and *C* respectively. The gonadal spermatid numbers (Table 2) increased significantly ($P<0\cdot01$) with age from an average of $15\cdot9\times10^9$ in group *A*, to $22\cdot1\times10^9$ in group *B* and $55\cdot8\times10^9$ in group *C*. The spermatid concentration ($\times10^6$) averaged 102·8, 113·9 and 185·0 for groups *A*, *B* and *C* respectively. Testicular spermatid numbers and concentration varied widely between rams within groups. Two of the six rams in group A had spermatid concentrations higher than the values found in four animals in group B.

Table 2. Total number of spermatids, number per gram of testicular parenchyma, and estimated daily sperm production in Awassi rams

C, Constant factor for conversion of gonadal spermatid number into daily sperm production (daily sperm production = gonadal spermatid number/C). $C = 8 \cdot 1$ is calculated from Ortavant (1958); $C = 3 \cdot 56$ is from Amann (1970). Mean values are shown ± s.e. C.V., Coefficient of variation

Age group		$10^{-9} \times$ Gonadal spermatid number	$10^{-6} \times$ Spermatid number per gram of parenchyma	$10^{-9} \times$ Daily sperm production $C = 8 \cdot 1$	$C = 3 \cdot 56$	$10^{-6} \times$ Daily sperm prodn per gram parenchyma $C = 8 \cdot 1$	$C = 3 \cdot 56$
A	Range	10·7–26·2	55·4–165·1				
	Mean	15·9±2·2	102·8	1·9	4·5	12·7	28·9
	C.V. (%)	33·5	36·5				
B	Range	15·8–32·4	92·3–152·1				
	Mean	22·1±2·9	113·9	2·7	6·2	14·1	33·0
	C.V. (%)	29·3	22·0				
C	Range	42·5–67·81	169·0–214·1				
	Mean	55·8±4·7	185·0	6·9	15·7	22·8	52·0
	C.V. (%)	19·0	14·8				
Overall mean		30·3±4·8	142·4	3·7	8·5	17·6	40·0

The most important relationships between various testicular measurements and gonadal sperm reserves are presented in Table 3. Paired testis weight and testicular parenchyma weight were correlated significantly ($P < 0 \cdot 001$) with 'empirical' testis

Table 3. Relationship between various testicular measurements and gonadal sperm reserves

r, Correlation coefficient; b, regression coefficient

Independent variables		Dependent variables: Paired testis weight[A]	Paired parenchyma weight[A]	Paired testis volume[A]	Total spermatid number[A]	Spermatid No. per gram parenchyma[B]
Paired testis weight	r		0·99		0·91	0·63
	b		0·98		0·24	0·41
Paired parenchyma weight	r				0·91	0·63
	b				0·25	0·42
Paired circumference	r	0·93	0·93	0·92	0·87	0·64
	b	22·64	22·43	23·34	5·73	10·25
Paired length × depth	r	0·99	0·99	0·99	0·92	0·66
	b	1·92	1·89	1·98	0·48	0·83
Paired testis volume	r	0·99	0·99		0·92	0·64
	b	0·97	0·95		0·24	0·41
Paired theoretical volume	r	0·98	0·98	0·98	0·91	0·65
	b	0·97	0·96	1·01	0·24	0·42

[A] All values in these columns are significant at $P < 0 \cdot 001$, d.f. = 14.
[B] All values in this column are significant at $P < 0 \cdot 01$, d.f. = 14.

volume, 'theoretical' volume and with the other testicular measurements, particularly paired length × depth and circumference. Regression equations were calculated for the prediction of paired testicular parenchyma weight (Y) from paired length × depth

($Y = -96 \cdot 964 + 1 \cdot 893\,X$), circumference ($Y = -514 \cdot 128 + 22 \cdot 429\,X$) and paired 'theoretical' testis volume ($Y = 18 \cdot 871 + 0 \cdot 964\,X$). The prediction equation for 'empirical' volume from the 'theoretical' volume of the paired testes was $Y = 20 \cdot 118 + 1 \cdot 006\,X$; these parameters were significantly and linearly ($P < 0 \cdot 001$) correlated.

Paired testis weight, parenchyma weight, paired testis volume (empirical and theoretical), paired testis length × depth, and circumference were significantly correlated with gonadal spermatid number ($P < 0 \cdot 001$) as well as with spermatid concentration ($P < 0 \cdot 01$).

Table 4. Age differences in epididymis weight and epididymal sperm reserves of Awassi rams

Values expressed are means ± s.e.

	Age group (years)		
	A (1)	*B* (1·5)	*C* (2·5)
No. of organs	12	10	10
Single epididymis weight (g)	11·7±0·5	17·6±0·4	22·5±1·1
Caput weight (g)	4·9±0·3	7·6±0·2	9·0±0·3
Corpus weight (g)	1·8±0·1	2·2±0·2	2·9±0·4
Cauda weight (g)	4·9±0·2	7·8±0·4	10·6±0·7
Percentage of total weight			
Caput	41·7	43·2	40·1
Corpus	15·8	12·5	12·7
Cauda	42·5	44·3	47·2
10^{-9} × Combined sperm reserves			
Epididymis	11·1±5·7	21·8±5·0	98·8±23·1
Caput	2·9±1·3	5·0±1·4	19·5± 2·4
Corpus	0·9±0·3	1·4±0·4	6·7± 1·0
Cauda	7·4±4·2	15·3±3·2	72·5±20·4
Contribution (%) to total reserves			
Caput	25·8	23·1	19·8
Corpus	7·8	6·6	6·8
Cauda	66·4	70·3	73·4
10^{-6} × Caudal sperm No./gram caudal tissue	743	982	3422

The regression equations for the prediction of total gonadal spermatid numbers $\times 10^9$ (Y) or concentration $\times 10^6$ (Y_1) from various testicular parameters taken as the independent variables (X) are listed below.

Paired testis weight (X):

$$Y = -24 \cdot 758 + 0 \cdot 244\,X, \qquad Y_1 = 40 \cdot 608 + 0 \cdot 410\,X.$$

Paired testis parenchyma weight (X):

$$Y = -22 \cdot 252 + 0 \cdot 247\,X, \qquad Y_1 = 44 \cdot 827 + 0 \cdot 415\,X.$$

Empirical testis volume (X):

$$Y = -22 \cdot 867 + 0 \cdot 239\,X, \qquad Y_1 = 42 \cdot 584 + 0 \cdot 407\,X.$$

Theoretical testis volume (X):

$$Y = -18 \cdot 575 + 0 \cdot 243\,X, \qquad Y_1 = 48 \cdot 448 + 0 \cdot 421\,X.$$

Paired testis length × depth (X):

$$Y = -47 \cdot 581 + 0 \cdot 476\,X, \qquad Y_1 = -3 \cdot 004 + 0 \cdot 832\,X.$$

Paired testis circumference (X):

$$Y = -155 \cdot 400 + 5 \cdot 730\,X, \qquad Y_1 = -199 \cdot 256 + 10 \cdot 256\,X.$$

Table 4 shows the average weights of the epididymis and the epididymal sperm reserves in the three groups of rams. The total single epididymis weight as well as

Table 5. Relationships between testis weight, testicular spermatid numbers and epididymal weight and sperm reserves

Superscripts: a, $P<0\cdot001$; b, $P<0\cdot01$; c, $P<0\cdot05$. d.f. = 14

Correlated variables	Epididymis weight	Caput weight	Corpus weight	Caudal weight	Epididymal sperm	Caput sperm	Corpus sperm	Caudal sperm
Paired parenchyma weight	0·82[a]	0·72[b]	0·57[b]	0·83[a]	0·76[a]	0·83[a]	0·92[a]	0·72[b]
Paired testis weight	0·83[a]	0·73[b]	0·57[b]	0·84[a]	0·76[a]	0·83[a]	0·91[a]	0·72[b]
Paired epididymis weight					0·73[b]	0·75[a]	0·73[a]	0·70[b]
Caput weight						0·73[b]	0·66[b]	0·69[b]
Corpus weight						0·18	0·54[c]	0·20
Cauda weight						0·74[a]	0·73[b]	0·73[b]
Testicular spermatid No.					0·70[b]	0·85[a]	0·91[a]	0·64[b]
Spermatid No./gram testicular parenchyma					0·56[b]	0·75[a]	0·72[b]	0·49[c]

the weight of each of its three segments in rams aged 2·5 years (group *C*) was almost twice that recorded in rams aged 1 year (group *A*). The cauda epididymides constituted 47·2% of the total epididymis weight in group *C* rams compared to 42·5% in rams of group *A*. Epididymal sperm numbers increased dramatically with age. Thus, at 2·5 years the number of spermatozoa detected in both right and left epididymides was $98 \cdot 8 \times 10^9$ compared to $11 \cdot 1 \times 10^9$ and $21 \cdot 8 \times 10^9$ in rams aged 1 and 1·5 years respectively. The sperm number ($\times 10^6$) per gram of caudal tissue increased markedly from 743 in group *A* to 982 in group *B* and 3422 in group *C*.

The right and left epididymides did not vary significantly either in the weight or in the sperm content of the various segments.

The correlation coefficients between testis weight, gonadal sperm numbers, and epididymal weight and reserves are shown in Table 5. The increase in testis weight was concomitant with significant ($P < 0 \cdot 001$) increases in the weights of the three segments of the epididymis, particularly the cauda. The total epididymal sperm reserves, and the caput, corpus and caudal sperm numbers were significantly correlated with testis weight (with and without tunica albuginea), epididymal weight and with testicular spermatid numbers. Higher gonadal spermatid numbers were associated more with caput and corpus ($P < 0 \cdot 001$) than with caudal ($P < 0 \cdot 01$) sperm reserves.

Discussion

Several authors (Phillips and Andrews 1936; Carmon and Green 1952; Skinner *et al.* 1968) have described the growth of the ram testis during the early postnatal period. However, there is little published information on the rate of testicular growth between the early postpubertal period and sexual maturity. According to Watson *et al.* (1956), the testis growth curve in sheep is sigmoid in shape, the period of rapid weight increase corresponding to the period of establishment of spermatogenesis and sexual maturation leading to puberty. The present results show that in Awassi rams the testis weight at 2·5 years of age is almost twice that at 1 year. The average single testis weight in Awassi rams aged 2·5 years ($157 \cdot 6 \pm 7 \cdot 4$ g) is lower than the weight recorded for 2–3-year-old Suffolk rams (Dott and Skinner 1967) and for 4-year-old fine wool Saxon Merino rams (Lino 1972). Breed differences are likely to exist. Braden *et al.* (1974) observed that the testis weight of Merino rams at 2 years of age varied significantly between strains.

At 1·5 and 2·5 years of age the gonadal spermatid numbers were respectively about 150 and 300% higher than the corresponding numbers found in rams aged 1 year. Courot *et al.* (1970) concluded that the establishment of the spermatogenic process is a long and progressive phenomenon with several phases occurring after puberty. The average gonadal spermatid numbers in the 16 Awassi rams ($30 \cdot 3 \times 10^9$) compares favourably with the values obtained by Ortavant (1952) and Ortavant and Thibault (1956) in Ile-de-France rams. The average spermatid concentration obtained in the present study ($142 \cdot 4 \times 10^6$) is higher than the values ($87–96 \times 10^6$) calculated by Amann (1970) from the data of Ortavant (1952) and Ortavant and Thibault (1956).

The highly significant correlation and regression coefficients between gonadal spermatid numbers and testis weight in Awassi rams aged 1–2·5 years indicate that sperm production in this breed is an essentially linear function of testis weight. Thus, 82% of the variability in testicular spermatid numbers and 40% of the spermatid number per gram of parenchyma are accounted for by variations in the testis weight. For Ile-de-France rams during the breeding season, Ortavant (1958) found a correlation of 0·84 ($P < 0 \cdot 01$) between the number of spermatid nuclei in a testis and testicular weight, whilst for rams in the non-breeding season this correlation was 0·77 ($P < 0 \cdot 05$). A similarly high correlation seems to exist in bulls, buffaloes, boars and rabbits (Amann 1970).

A limitation in calculating daily sperm production from testicular homogenates is the potential inaccuracy arising from the use of a constant conversion factor (or factors) which presumes varied spermatid resistance to homogenization at certain stages in spermiogenesis. These spermatids were assumed to represent those in stages II–VIII (Ortavant 1958) or only those in stages VI–VIII (Amann 1970) of the seminiferous epithelial cycle. The respective constants would, thus, be 8·1 (as calculated by us from Ortavant's data) or 3·56 (Amann 1970). Both constants were used in an attempt to quantify the daily sperm production in Awassi rams.

The estimated daily sperm production irrespective of age would vary from $3 \cdot 7 \times 10^9$ to $8 \cdot 5 \times 10^9$ (i.e. $17 \cdot 6 \times 10^6$ to $40 \cdot 0 \times 10^6$ per gram of testicular parenchyma) for constants of 8·1 and 3·56 respectively. Both daily sperm production values are within the range reported by Chang (1945) for Suffolk rams ($4 \cdot 4 – 8 \cdot 8 \times 10^9$) and by Ortavant (1958) for Ile-de-France rams ($5 \cdot 5 \times 10^9$). It is difficult to predict which one of the values calculated in the present study is closer to the actual daily sperm production. However, the rates of daily sperm production per gram of testicular parenchyma of 12·7, 14·1 and $22 \cdot 8 \times 10^6$ (average $17 \cdot 6 \times 10^6$) in 1, 1·5, and 2·5-year-old rams (Table 2) would seem more accurate for rams at these young ages. These values vary slightly from those previously reported for other breeds of sheep using other estimation techniques. By counting spermatozoa passed through a rete testis catheter, Australian workers (Voglmayr *et al.* 1966, 1967; Setchell *et al.* 1969) indicated that a typical Merino ram testis would produce about $16 \times 10^6 – 18 \times 10^6$ sperm per gram of parenchyma per day. According to Lino and Braden (1972), sexually rested Merino rams aged 4–5 years produced on the average $5 \cdot 8 \times 10^9$ sperm per day as counted from daily sperm output from the urogenital tract.

Our data indicate that sufficiently reliable estimates of gonadal spermatid number and production rate per gram of parenchyma can be obtained in Awassi rams from testicular volume, determined by displacement or theoretically calculated, as well as from the paired testis length × depth value. The circumference of the excised testis, however, appeared to be of less value in predicting the gonadal spermatid numbers. Lino (1972) observed that in rams the scrotal circumference was significantly correlated with testicular weight, although not as highly significantly as in bulls (Willett and Ohms 1957), but it failed to give a significant correlation with the daily sperm production as determined from output from the urogenital tract.

Parallel to the significant increase in testis and epididymis weight with age there is a rapid increase in the epididymal sperm reserves. Comparison of the present results with those of other authors is difficult since most previous reports either did not refer to the age of animals examined, or gave the epididymal reserves of animals varying widely in age (Polovceva 1938; Chang 1945; Ortavant 1952, 1958; Ortavant and Thibault 1956).

Investigation of the sperm distribution in the three segments of the epididymis indicates that the storage efficiency of the cauda epididymides, as judged by the caudal sperm numbers per gram of caudal tissue, increases noticeably with age.

The cauda epididymides of older rams (2·5 years old) could store 73% of the total epididymal sperm reserves compared to 66% in 1-year-old rams (Table 4). This was associated with a decline in the percentages of sperm present in the caput and corpus epididymides. This finding suggests an improved efficiency of the contractile mechanism of the epididymis in older rams; this mechanism may not be fully mature by 1 year of age. A similar proposition has been made for bulls by Macmillan and Hafs (1968). The percentage of spermatozoa in the cauda epididymides in each of the three age groups is within the range of previous reports (68·9–78·5%) of Ortavant (1958) and Lino (1972).

The significant positive correlation between the testis weight and the epididymal sperm reserves agrees with the data of Lino (1972) for Merino rams and with the data of Amann and Almquist (1961*b*) for bulls. This is related to the significant direct relationship observed, in the present study, between testis and epididymis weights. In addition, a highly significant correlation between epididymis weight and epididymal sperm reserves was apparent. However, non-significant correlations between testis or epididymis weight and epididymal sperm numbers have been reported for bulls (Almquist *et al.* 1958; Macmillan *et al.* 1972) and buffaloes (Verma *et al.* 1965).

There is conflicting evidence in the literature as to whether the number of spermatozoa stored in the epididymis is a direct function of the sperm production rate (Amann 1970). The present results show a highly significant relationship between the number of spermatid nuclei in the testis and the number of spermatozoa in the whole epididymis as well as in any of its three segments. Thus, differences in total testicular spermatid numbers and accordingly daily sperm production rate account for almost 49% of the variation in the epididymal sperm reserves ($r = 0 \cdot 70$). Similar highly significant correlation coefficients of 0·73 (Ortavant 1952) and 0·69 (Ortavant 1958) were observed in sexually rested rams during the breeding and non-breeding seasons. However, in young Friesian bulls aged 15–17 months Macmillan *et al.* (1972) found that the sperm content of the cauda epididymides was not strongly correlated with the total number of testicular sperm ($r = 0 \cdot 31$).

In the present study an attempt was made to relate the age trends in testis weight, daily sperm production and sperm reserves in the cauda epididymides in the same manner as that made for bulls by Amann (1970). Although the testes of 2·5-year-old Awassi rams were about twice the weight of the testes of the 1-year-old rams, the caudal epididymal sperm reserves increased about 10-fold with the increase in age from 1 to 2·5 years. The ratio of testes weight (in grams) to the number of spermatozoa in the cauda epididymides ($\times 10^7$) increased from 1:4·5 in 1-year-old rams to 1:7·2 in 1·5-year-old rams and to 1:23 in 2·5-year-old rams. The storage capacity of the cauda epididymides, expressed as the ratio of caudal sperm numbers to daily sperm production (Amann 1970), in older rams (2·5 years) was 1·5 and 2·8 times that in rams aged 1·5 and 1 year respectively. Amann (1970) showed that the storage capacity of the cauda epididymides and ductus deferens in bulls aged 7 years was twice that in bulls aged 12 months. In corroboration, the data of Macmillan *et al.* (1972) suggested that in young Friesian bulls the cauda epididymides had only partly developed the storage role. Therefore, it seems that in rams the storage capacity of the cauda epididymides develops more slowly than does the sperm production rate, as was suggested for bulls by Amann (1970).

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Manuscript received 1 December 1976, revised 20 February 1978