SPERMATOGENESIS IN THE TAIGA-MOOSE OF NORTH CENTRAL ONTARIO*

A PILOT STUDY

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Abstract : Testes of 128 moose between the ages of 6 months and 15 years were collected in June (1), September (4), October (108), November (11) and December (4) of 1977 and 1978. Weights of testes and epididymides and the pattern of spermiogenic activity (SA) were investigated. A wide individual variation of testicular weight and SA-pattern occurred within each age class. Some yearlings may have achieved puberty at the end of September, but most exhibited this stage in October. With increasing age (2 1/2 to 4 1/2 yr.) the peak of SA shifted gradually from mid-October to mid-September. In 5 1/2 yr. bulls the peak could be in early September. The most stabilized trend of SA is in the class of 6 1/2 - 9 1/2 yr., with a maximum reached speculatively around the end of August or by the beginning of September. The longest period of SA was found in the 4 1/2 - 5 1/2 yr. class. In primes (6 1/2 - 9 1/2 yr.) and older seniors (greater than 10 yr.) the SA declined sharply by the end of November and terminated in December. The relatively high frequency of partially or completely emptied tubules of epidiymal ductuli and vas deferens was surprising. We concluded that bulls of this population matured at 5 1/2 yr., and the 6 1/2 - 9 1/2 yr. group was fully prime. The results are compared with data from Minnesota and the USSR.

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*According to Peterson (1955) this is the geographic area where the alleged subspecies of Acles a. andersoni and A. a. americana overlap and the oligogamous mating of taiga moose might exert additional search effort on bulls when compared to the polygamous breeding in the tundra strain A. a. gigas .

There is virtually no published record concerning spermatogenesis in moose (Bubenik 1981a). The statement of Peek (1962) that bulls older than 1.5 yr. have sperm in October and November was the only reference found. Kaplanov (1948), Jazan (1959) and Cheruvimov (1969) report on the combined weights of testes and epididymides of USSR moose (A. a. alces) in relation to age, season and body weight. None of the authors could agree whether testicular activity achieved its maximum before or after 4 yr. of age. This might be due to a rather large individual variability which Jazan (1962) relates to individual differences in body weight; a finding not accepted by Cheruvimov (1969). Both authors although lacking material from Aug. concluded that testicular activity peaked in Sept., co-incident with active rutting behaviour. Mature bulls whose testicular activity generally peaks before the first overt estrus as demonstrated in red deer Cervus elaphus by Pinsker (1978) should attain heightened testicular activity somewhat earlier and may conceivably service and even fertilize cows during this period.

The ovarian analysis of Swedish moose Alces a. alces (Markgren 1952, 1974), Bubenik's personal observations in Alaska (1969) and Ontario (1972 - 1982), J. L. Frund from Mt. McKinley National Park, Alaska (pers. comm. 1981) and R. Henderson's and H. Irvine's from northern British Columbia prior to 1975 (pers. comm. 1981) confirm that many moose cows experience estrus with a receptive phase (Beach 1976) during the first half of Sept.

The onset and duration of testicular activity in free ranging boreal zone ungulates depends on age, maturation stage, social structure and environmental conditions (Bubenik 1983a). Reliable conclusions therefore concerning testicular activity in relation to age can only be derived from animals of a distinct population having a stable social structure, relatively similar environmental conditions and if the data are collected over a one year period. Otherwise a disparity of results, ie. asynchronny in physical and sexual maturation can be expected for all, if testes from well organized and disorganized populations are compared. A bull can be considered as mature only, when he is fully grown, has maximum volume or weight of testes and epididymides and has the earliest onset of spermatogenesis. At this stage he stores the largest amount of viable sperm and is capable of fertilizing the greatest number of cows in the shortest possible period.

The current data on moose maturation are incomplete. Beside the progress in dentition replacement (Flerov 1952, Peterson 1955), body weight gain (Cheruvimov 1969, Krorre 1959, Knorre and Knorre 1956, Timmermann 1972), and skull grow_h (Bubenik and Bellhouse 1980), we have only indirect indices of physiological maturation, derived from antlerogenesis (Bubenik et al. 1978b, Cheruvimov 1969, Heptner and Nasimovic 1974, Peterson 1955, Timmermann 1972, Timofejeva 1974), bell development (Timmermann 1979), timing of pheromon secretion, and hoof wear (Bubenik et al. 1979 and 1978a respectively). From these records and Jazan's data (1959) on testes weight we can conclude that bulls may reach maturity by 4 1/2 or 5 1/2 yr. (Bubenik et al. 1975).

With respect to identifying sexual maturity or the speed of sexual maturation, the gravimetrical and histological investigation of testicular activy are considered the most suitable indicators. One might argue that the cycle of the seminiferous epithelium could render histology an unreliable tool in attempting to differentiate the onset of the rut among age classes, especially if influenced by nutrition and range conditions.

We reject this premise for a number of reasons as follows: The sexual maturation is a stepwise process, due to the yearly repetition of puberty, stepwise gain in weight of testes and corresponding increase of testosteron secretion. It requires a certain number of years dependent generally on the demographic structure and environmental conditions. Biologically significant deviations from this standard might be considered as indicators of some type of stress for the individual or its age class. Therefore a statistical analysis of testicular activity per year class could be used as a reliable indicator of the relationship between social classes of either sex.

We attempted to gain an insight into the sexual maturation of male moose by collecting and studying testes from the 1977 and 1978 hunting season.

MATERIALS AND METHODS

Pairs of testis from 169 bulls of various age classes were collected by co-operating hunters in N. C. Ontario during the open seasons of Oct. 11 to Dec. 15 of 1977 and 1978. Additional testes originated from summer road kills and 1 pair of testis came from a bull found dying of unknown causes in Sept. 1979.

Ages were determined by dentition pattern (less than 1.5 yr.) and cementum annuli (greater than 1.5 yr.).

The date, hour of shooting, antler size, degree of head pigmentation and behavioural circumstances were recorded as well for each specimen.

Collectors were instructed to remove the testes with epididymides immediately after death, and cut two deep incisions (Fig. 1) through each

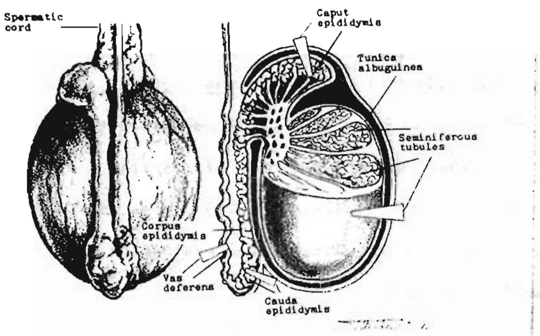

Fig. 1. Testes of moose showing a portion of epididymis and testes in cross section as well as location of sections cut for histological study.

before submerging into 500 ml of formalin diluted to 10%.

Due to a variety of reasons, only 15% of all testes were handled correctly. The balance only permitted a partial histological evaluation. Altogether testes from 128 bulls were studied histologically.

Preserved specimens were examined in the laboratory. The tunica albuguinea (Fig. 1) was removed and the weight of each testis and epididymis was recorded to the nearest centigram (Table 1). Thereafter a portion of the central segment of testis, from caput and cauda epididymis and if available the adjacent part of vas deferens was removed and embedded in paraffin. Sections of 8 to 10 μm were cut and stained with haematoxylin-eosin. The discrimination of subtle differences in spermatogenesis (Bloom and Fawcett 1975) were difficult due to overstaining and forced us to limit the evaluation to the following criteria (see legend to Table 1):

A) Testes : The size of the interstitia and proportion of active to inactive Leydig cells (Lc) were examined. Considered as inactive Lc were those containing dark pycnotic nuclei and occassional vacuols rather than the fibroblast-like Lc's described by Lincoln (1981). The diameter of seminiferous tubules was measured in μm and the status of the germinative epithelium was subjectively determined by the relative proportion of spermatogonia, spermatocytes and spermatids. The relative thickness of the epithelium was expressed in ranges of μm: (low $<$ 200, medium 200 - 315, high 316 - 420, very high $>$ 421+). The following 6 stages were distinguished and recorded on special forms (Table 1):

(1) Prepubertal - when only interstitium was activated and gametes maturated at most to secondary spermatocytes.

Table 1. Typical examples of gravimetric and histological parameters of testicular activity.

Class	Code Nr	Date	Month	Measurements	Testis	Epididymis caput	Epididymis cauda	Vas deferens	STATUS
CALVES	C-2000	10.10.77	OCTOBER I	Testes g 18.7 Epididym. g 4.8 ø um 126 E/T % 25.7	I la LA me C me Z ø	EP lo ety	ety	ety	PR
2½ yr	025-MH	21.09.77	SEPTEMBER	Testes g 115.6* Epididym. g 18.4 ø um 210 E/T % 12.5	I vla LA vhi SP me	EP hi Z hi CO me	Z hi R vhi	Z hi R vhi	A
CALVES	643-2501	23.11.77	NOVEMBER II	Testes g 36.5 Epididym. g ø ø um ø E/T % ø	I la LA me C me	EP lo ety	ety	ety	
2½ yr	639	17.11.78	NOVEMBER II	Testes g 99.1 Epididym. g ø ø um ø E/T % ø	I la LA vhi SP me	EP me Z lo CO lo	Z vvfw R lo	ø	T
1½ yr	002-SSR	11.10.77	OCTOBER I	Testes g 94.0 Epididym. g 15.0 ø um 231 E/T % 15.9	I vla LA hi SP lo	EP hi Z fw CO me	Z me R me	ø	B
3½ yr	1-GF	11.10.78	OCTOBER I	Testes g 184.7 Epididym. g 21.7 ø um 252 E/T % 11.7	BB I vla LA vhi T vhi SP lo	BB EP me Z lo CO lo	BB Z me R re	BB ety	P S
3½ yr	6-BS	11.10.78	OCTOBER I	Testes g 124.4* Epididym. g 14.0* ø um ø E/T % 11.3	I vla LA vhi SP lo	EP hi Z vlo Z vlo	Z [illegible] R me	ø	T
3½ yr	4-GF	11.10.78	OCTOBER I	Testes g 132.2* Epididym. g 19.6 ø um 260 E/T % 14.8	I la LA hi SP me	EP vhi Z ø CO ø	Z me R me	Z hi R hi	A S
4½ yr	500-GE	29.09.78	SEPTEMBER II	Testes g 154.3 Epididym. g 22.3 ø um 290 E/T % 12.6	I vla LA vhi SP hi	EP vhi C fw Z vhi CO hi	C vvf Z hi R me	Z hi R me	B
7½ yr	503-GE	27.09.78	SEPTEMBER II	Testes g 185.0 Epididym. g 29.0 ø um 235 E/T % 15.7	BB I la LA vhi L O SP lo	EP vhi Z vvfw CO vvlo	Z me R lo	ø	T
4½ yr	11-SK	12.10.78	OCTOBER I	Testes g 157.1 Epididym. g 20.5 ø um 223 E/T % 13.0	I vla LA hi SP me	EP hi Z hi CO hi	Z vhi R me	Z vhi R lo	A
8½ yr	270-84	11.10.77	OCTOBER I	Testes g 67.1 Epididym. g 10.1 ø um 160 E/T % 15.2	BB I hi LA me L O SP hi	EP me C ? Z vhi CO hi	Z vhi R hi	Z vhi R vhi	A
5½ yr	20-SK	13.10.77	OCTOBER I	Testes g 111.1 Epididym. g 20.7 ø um 195 E/T % 18.6	I la LA hi L O SP lo	EP hi C vfw Z vhi CO hi	C vfw Z vhi R hi	C vvfw Z vhi R me	T
8½ yr	501-GE	08.10.77	OCTOBER I	Testes g 130.4 Epididym. g 19.8 ø um 252 E/T % 15.2	I vla LA vhi L O SP lo T+Z floating	EP hi Z me CO me	Z me R lo	ø	D?
5½ yr	077	14.10.78	OCTOBER I	Testes g 132.4* Epididym. g 22.3* ø um 237 E/T % 16.4	I la LA hi SP lo	C fw Z me CO hi	C fw Z me R hi	Z vhi R vhi	D
12½ yr	72-BS	20.10.78	OCTOBER II	Testes g 97.1 Epididym. g 17.9 ø um 277 E/T % 17.4	I me LA hi SP lo	EP hi C me Z me CO lo	ety	Z lo R lo	E

Table 1. (continued)

Class	Code Nr	Date	Month	Measurements	Testis	Epididymis caput	Epididymis cauda	Vas deferens	STATUS
12½ yr	219	16.10.77	OCTOBER II	Testes g 114.5 Epididym. g 18.1 ø um 223 E/T % 15.9	I vla LA vhi SP lo	EP me Z vvfw CO vvlo	Z me R me	Z vhi R hi	T

Legend to Table 1.

Measurements

g = gram, D = both glands damaged, *) = one gland was damaged, the weight calculated by multiplying the intact gland by 2, because the error was found to be <10% of the combined weight.

ø µm = average diameter of seminiferous tubuli

E/T % = Epididymides/Testes ratio

Histology:

BB = tissue poorly preserved, ø not available , ? uncertain, questionable

Testis

I = size of interstitia: sm = small, me + medium, la = large, vla = very large

LA = activity of Leydig cells: lo = low <5 %, me = medium <30 %, hi =<high >60 %, vhi = very high 60 %.

L = lumen of seminiferous tubuli: ○ = open, closed to ¼◔ , ½◑, 3/4◕ , completely ●

SP = spermiogenesis: vlo = very low, lo = low, me = medium, etc.

G = spermatogonia, C = spermatocytes (I + II), T = spermatidi, Z = spermatozoa fw, me, hi, vhi - their occurence in seminiferous tubuli or in the canuli of epididymides or vas deferens.

Epididymis

EP = thickness of epithelium of canuli in ranges of µm : low <200, medium 200-315, high 316-420, very high > 421.

CO = content of canuli of epididymides: lo, me, hi, vhi, ety = empty.

Vas deferens

R = reserve of spermatozoa: lo, me, hi, vhi, ety.

Status of testicular activity

PR = prepubertal, P = pubertal, B = beginning, A = active, D = declining, T = terminating, E = end of spermiogenetic activity , S = may be in distress

(2) Pubertal - when all stages of spermatogenesis were present however the number of spermatids and spermatozoa was low and the interstitium was activated to a low grade only.

(3) Full Active - the seminiferous tubules showed the typical "radial" design, with dynamic production of gametes and a high number of spermatozoa in relation to spermatids and secondary spermatocytes. Interstitial areas were very large and Lc cells highly activated.

(4) Declining Activity - the number of secondary spermatocytes was reduced, all spermatids and spermatozoa were located more centrally and lumina of seminiferous tubules were visible. Interstitium was either high (less than 60% of Lc active) or medium (less than 30% respectively).

(5) Terminating Activity - germinal epithelium was regressing, lumina of seminiferous tubules were enlarged. All spermatids and spermatozoa in epithelium were almost or totally absent, some of them "floating" in the seminiferous fluid. Interstitium was diminishing in size, percentage of active Lc was low.

(6) End of Activity - only spermatogonia with few spermatocytes were present. Interstitium was returning to quiescent stage.

B) Caput Epididymis : Average thickness of epithelium was estimated in μm and classified similarly to those in testis. The relative frequency of spermatids and spermatozoa was estimated subjectively. The terminating or end phase of activity was indicated by the presence of immature gametes (ie. secondary spermatocytes and spermatids) in the tubular lumina or epididymis and the disappearance of spermatozoa from all parts of the reproductive tract respectively.

C) Cauda Epididymis and Vas Deferens : The same criteria as above were used.

Due to lack of representative samples from Sept. and Dec. we were unable to follow the spermatogenetic progress extensively from beginning to end. Our data deal mainly with the period from Oct.and Nov. We therefore pooled the testes for each age class in the first or second half of the month, designated as (i) or (ii) respectively.

The sample size of testes from each period and age class as well as the individual variation and quality of preservation restricted the depth of this study, and limited the statistical evaluation to correlations between testicular and epididymial weights. Altogether the following eight age classes were examined: ie. calves less than one yr. old, 1 1/2, 2 1/2, 3 1/2, 4 1/2, 5 1/2, 6 1/2 to 9 1/2 yr. and older than 10 1/2 yr.

Trends in testicular weights related to age from this study were compared to fresh weights from Minnesota (due to courtesy of P. Karns) and those of unknown conditions from the USSR (Jazan 1959, Cheruvimov 1969).

RESULTS

A) Gravimetric Relationships Between Testes And Epididymides (Fig. 2)

Calves : The testes and epididymides gained rapidly in weight from Oct. (i) to Nov. (i) and then dropped in Nov. (ii) to the Oct. (i) value.

1 1/2 yr. - The trend in testicular and epididymides weight gain proceeded from Sept. to Oct. (ii), then decreased dramatically towards Nov. (ii). The only specimen from Dec. had a weight above the maximum of the three specimens from Nov. (ii).

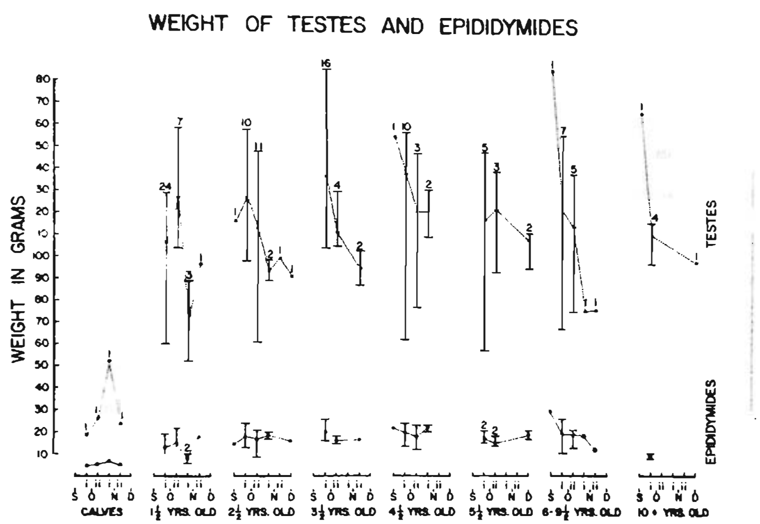

Fig. 2. Weight of testes and epididymides for N. C. Ontario moose.

2 1/2 yr. - The peak of testicular weight occurred in Oct. (i). Beginning with Oct. (ii) there was a permanent decline to Dec. The epididymes weight remained constant, despite variation in individual amount of spermatozoa content and testicular weight.

3 1/2 yr. - The sharp decline in mean testicular weight from Sept. to Nov. (ii) suggests that most bulls may have achieved their peak weight earlier, probably in Sept. (ii). Declining weights of both 3 1/2 and 2 1/2 yr. testes from the Nov. (ii) period suggest a terminating stage of spermatogenesis. The weight of epididymides followed the declining weight of testes towards Oct. (ii), however further reduction towards Nov. (ii) was not found.

4 1/2 yr. - The trend in testicular weight indicated that the maximum activity should be associated with mid-Sept. The very low minima recorded in Oct. (i) and (ii) suggest either substantial differences in timing of spermatogenesis or depression due to social distress (Patanelli 1975). The remaining specimens from Nov. (i) exhibited similar mean weight to the Oct. (ii) period. The range and the means of epididymides weight followed the trend in testicular weight.

5 1/2 yr. - Mean weight values for Oct. (i) and (ii) and Dec. were somewhat lower than those from the 4 1/2 yr. class, with the relatively most stable average weight through the whole period, when compared with other classes.

6 1/2 to 9 1/2 yr. - The trend of the testes and epididymides weights varies from those of the younger classes and showed a very sharp decline from Sept. to Dec.

10 1/2 to 15 1/2 yr. - Testicular weights in this class laid in the range of the previous class. Unfortunately, almost all epididymides from Sept. and Dec. were damaged.

Combined Weight of Testes and Epididymides (Fig. 3): The trend in gain and loss of testicular weight and of the timing of the peak of activity during sexual maturation is more obvious in the combined weights.

Epididymides vs. Testes Ratio (E/T %) (Fig. 4a): The inversed trend of E/T in calves as compared to that of their testes is not surprising (See Discussion).

The trend in E/T distinguishes the 1 1/2 yr. class from the 2 1/2, up to the age of 5 1/2. A stagnation or slight decline of the E/T ratio occurs during Oct. in 2 1/2 to 5 1/2 yr., followed by a very sharp rise towards the end of the year. The 6 1/2 and older bulls showed a relatively stable means around 16% up to Dec. with a single exception of 25.8%, which might be an artefact due to improper separation of vas deferens.

Correlation Between the Weight of Testes and Epididymides (Fig. 4b): In calves and yearlings we found a significant correlation of R^2= 0.776. However for all bulls $\geq$ 2 1/2 yr. R^2 dropped to 0.57, apparently due to a substantial individual variation in the 2 1/1 to 5 1/2 yr. classes, albeit the 6 1/2 to 9 1/2 yr. class had the most significant correlation coefficient with R^2 = 0.87.

B) Histology of Testes and Epididymides - (Table 1 and 2)

Calves : All 7 testes examined histologically from Oct. to Nov. were in prepubertal stage, typical of cervids during the phase of pedicle development (Table 1, #643-2501 and G 2000). The interstitia were large, Lc cells activated and canuli of epididymis and vas deferens were empty. No spermatozoa were found. All gravimetric data described earlier support these indicators.

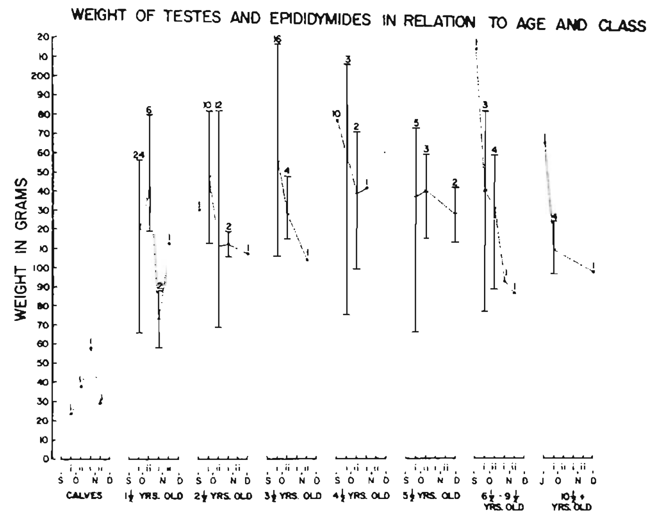

Fig. 3. Weight of combined testes and epididymides in relation to age and class for N. C. Ontario moose.

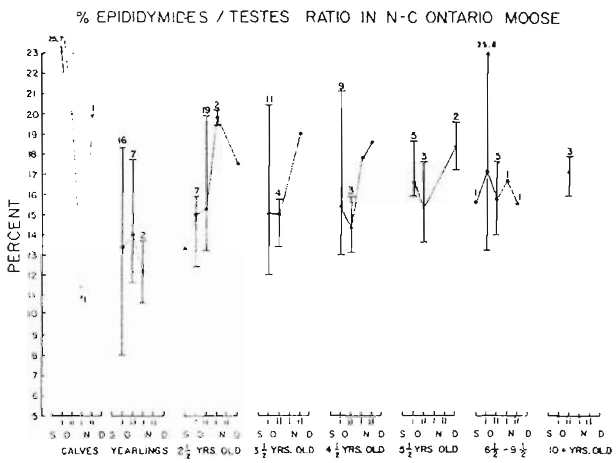

Fig. 4a. Epididymides/testes ratio in N. C. Ontario moose.

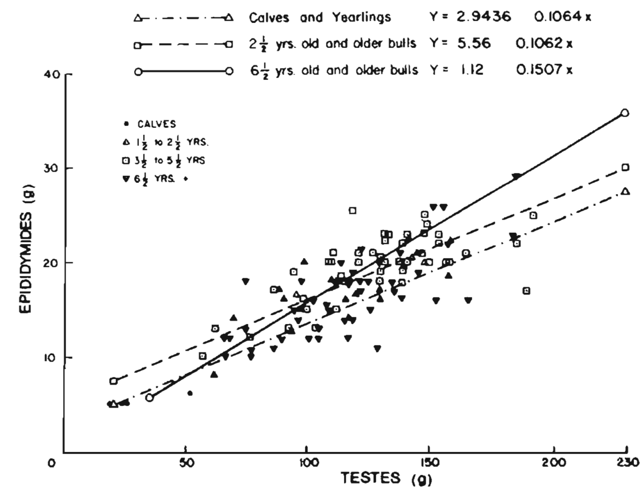

Fig. 4b. Regression of epididymides (Wt.) on testes weight for N. C. Ontario moose.

Table 2. Spermatogenesis in N. C. Ontario moose in relation to age and season.

Number of testes and epididymides per season and their status

Class: CALVES	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.			3	2	1	1	
Pubert.							
Beginn.							
Active							
Declin.							
Termin.							
End							

Class: YEARLINGS	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.							
Pubert.				1			
Beginn.			8				
Active			12	6	1		
Declin.			1	1		1	
Termin.			4		1		
End							

Class: 2 ½ years old	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.							
Pubert.							
Beginn.			2				
Active		1	5	3			
Declin.			4	3	1		
Termin.				3		1	2
End							

Class: 3 ½ years old	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.							
Pubert.							
Beginn.			1				
Active			11	1			
Declin.			3	1		1	
Termin.			1	1			
End							

Class: 4 ½ years old	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.							
Pubert.							
Beginn.		1					
Active			5				
Declin.			2	1			
Termin.				1			
End					1		

Class: 5 ½ years old	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.							
Pubert.							
Beginn.							
Active			1	1			
Declin.				1	1		
Termin.			2				1
End				1			

Class: 6½ to 9 ½ years old	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.							
Pubert.							
Beginn.							
Active			2				
Declin.			5	1			
Termin.		1	1	2	1		
End				2			

Class: 10 ½ to 15 ½ years old	Ju	Se	Octob. I	Octob. II	Novem. I	Novem. II	De
Prepub.	1						
Pubert.							
Beginn.							
Active							
Declin.							
Termin.				2			
End		1		1			1

1 1/2 yr. - The spermatogenesis of this class appears very heterogenous. In Oct. (i), 48% of yearlings had well developed spermatogenic activity, but there were still 38% in the beginning and 16% in the terminating phase. In Oct. (ii) one testis appeared in pubertal and one in a terminating stage while 75% were fully active. Only one of three testes from Nov. was in full spermatogenic activity (Table 1, specimens # 002-SSR, # 6-BS). The overall activity pattern was similar to that found in yearling red deer (Cervus elapus hippelaphus) as shown by Hocherau-de-Reviers and Lincoln (1978), and Pinsker (1978). Fully active testes normally have high semen reserves (Lincoln 1981). However the cannuli of epididymides and vas deferens of those at the beginning phase were empty or only mediocre (me) filled.

2 1/2 yr. - Only one bull from Sept. (ii) had highly active testes. However there were still 18% in beginning phases of spermiogenesis in Oct. (i) in comparison to 45% active and 36% in declining or supressed stages. During Oct. (ii) all specimens examined showed an equal distribution of active, declining and terminating spermiogenesis. The trend in reduction of testicular activity proceeded from the Nov. to Dec. period. One of four specimens examined was in a declining, and three in a terminating stage.

3 1/2 yr. - The onset and peak of testicular activity appeared shifted more into Sept. since of 19 testes examined from Oct., only 63% were active. The remaining were in a declining or terminating phase. The testes from specimens #1-GF and 4-GF (Table 1) demonstrated a low level of spermiogenesis and few if any spermatozoa in the epididymis. This condition is an unusual stage for this class during the Oct I period and may be due to a temporarily distressed condition.

4 1/2 yr. - Moose of this age were probably in full testicular activity during the Sept. (ii) period as exhibited by specimen #500-GE (Table 1). The mediocre sperm reserve in the tail of epididymis and the low reserve in vas deferens of the specimen #11-SK (Table 1) are intriguing. The fact that two testes from Oct. (ii) were in a declining or terminating phase and one from Nov. (i) was at the end of spermatogenesis indicates that in this class the testicular activity was reducing more rapidly during Oct. - Nov. than in the 3 1/2 yr. class.

5 1/2 yr. - The spermatogenesis in bulls from Oct. (i) ranged from a low to a high grade (Table 1, # 20-S and 072). Unfortunately most of these sections were overstained and we can only guess that from Oct. (ii) on, bulls reduced their spermiogenetic activity from a peak in mid-Sept.

6 1/2 to 9 1/2 yr. - The lumina of seminiferous tubules and the low filling grade of epididymal canu'i (Table 1, # 270-84, 219-A and 503) show that beginning with Oct. (i) the bulls of this age reduce their sperm production so rapidly that some had testes in terminal spermatogenesis in Oct. (ii) while others terminated during the end of Sept. (ii), as was the case in specimen # 501-GE (Table 1). Typical of specimens examined, the canuli of the tail appeared half empty and only low sperm reserves remained in the head of the epididymis. The lumina of seminiferous tubules were open and the spermatogenesis was of a low grade. Such a pattern suggests a very early peak of testicular activity, ie. probably in the last week of Aug. or first days of Sept. (see Fig. 2 to 4 ab).

10 1/2 to 15 1/2 yr. - The relatively well preserved testes of two specimens examined (# 72-BS and 219-B, Table 1) exhibited a terminal phase of testicular activity in Oct. (ii). A testi from July 19 revealed a

typical prepubertal stage. This is in accord with very low testosteron levels normally associated with antler growth at this time of year (Bubenik, G. 1982) and low or absent facial pigmentation in bulls less than 10 yr. (Bubenik et al. 1977). A single bull from Dec. had testes exhibiting a quiescent stage and epididymides without spermatozoa.

Diameter of Seminiferous Tubuli (Fig. 5, Table 1) The number of testes preserved well enough that a reliable measurement of the diameter could be taken, was too limited for a secure evaluation. Nevertheless the trend fits into the general pattern of testicular activity in each of the classes and secures for the class of 6 1/2 to 9 1/2 yr. a special position because the tubuli exhibited slower diameter reduction during Oct. compared to the 5 1/2 yr. class.

DISCUSSION

This study attempted to examine sexual maturation in bull moose.

Results are discussed from one single population. It is open to discussion if generalizations can be made because we do not suggest that the testes originated from a well organized population. Therefore, substantial differences from other populations cannot be a priori excluded. The data provided an insight on testicular activity during the Oct.-Nov. period. Changes which occur in Aug.-Sept. and Dec. are inferred but cannot be confirmed exactly. However, using analogical reports on testes of red deer stags (Gibson and Guiness 1980 a, b, Guiness et al. 1978, Hocherau-de-Reviers and Lincoln 1978, Jaczewski and Morstin 1973, Kernstock 1981, Lincoln 1971a, b 1975, Pinsker 1978, Stieve 1952), whose rutting period is almost identical with that of moose, we might hazard to

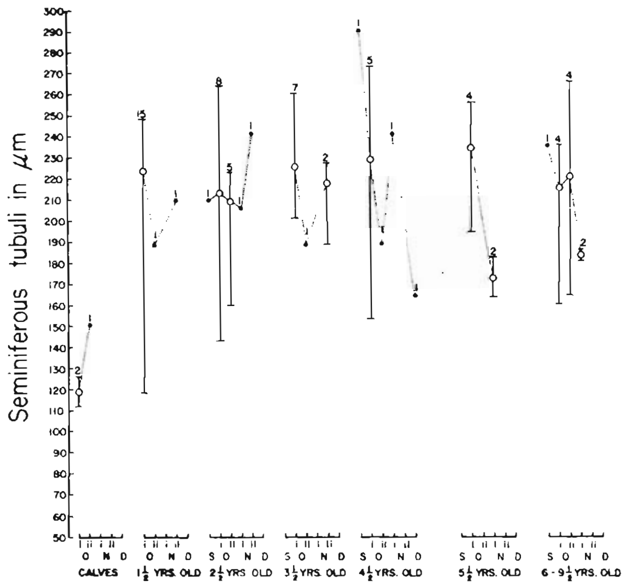

Fig. 5. Diameter of semiferous tubuli in relation to age and class for N. C. Ontario moose.

predict the course of testicular activity in moose with reasonable probability.

The sudden rise in testicular weight of calves toward Nov. with activated Lc cells is related to testosterone production for stimulation of pedicle growth (Bubenik, G. 1982, Frankenberger 1954, 1955, Hartwig 1967).

Concerning the spermatogenesis of bulls of yearling age, the parallelism between moose and red deer is obvious (Pinsker 1978). We deliberately excluded statistical evaluation of our data. Without knowing the personal history and physiological parameters of each individual, and the social status of the population, we cannot presuppose that in such a highly individual species as moose, we could achieve the statistical significance claimed by mathematicians. If a high degree of significance is achieved in such studies, it might be either by chance or resulting from statistical manipulation as shown exquisitely by Feller (1969).

Free living ungulates are not laboratory animals with purified gene pools as demonstrated for cervids by Ryman et al. (1980) and Smith et al. (1982). More over, animals are social beings (Bubenik 1971, 1983b, c, Hediger 1980) and not living machines which must behave as such. In studies related to behavioural physiology of free ranging animals, experience and sound logic are more valuable than statistical results (Hediger 1980). The variance of testicular activity we have found in bulls, was greater than that of red deer populations described by Schwab (1977) and studied by Pinsker (1978) and Kernstock (1981). The differences in the testicular activity between moose and red deer included the lumina of seminiferous tubuli per age class which were larger in moose and the much faster weight increase of testes. If the variance in testicular activity in moose is a norm or a sign of sexual hyperstimulation, due to poor demographic conditions (Bubenik et al. 1975, Markgren 1969, 1971) is open to question since the weather conditions (Markgren 1974) were very similar in both years. However it is important to recognize the short period of spermatogenesis in moose.

The peak of spermatogenesis appears to shift from Oct. into Sept. between the age of 2 1/2 to 4 1/2 yr. Bulls 5 1/2 yr. and older should reach their maximum in early Sept. or late Aug. as indicated by the trend in declining testicular activity (Fig. 3, Table 2). The seven 5 1/2 yr. bulls examined were in relatively good reproductive performance to Dec., albeit those older exhibited a permanent decline in testicular activity. This suggested a much earlier peak and a subsequent separation or avoiding of the mating grounds of cows. The rapid decline of the epididymal weight or epididymis/testes ratio (Figs. 2 and 4a) lends credence to this argument.

We were surprised not only in the relatively short rutting period, but in comparison with red deer or wapiti (J. Haig, pers. comm. 1982), the frequency of epididymides with extremely low sperm reserves in the tail and vas deferens of 4 1/2 yr. bulls. The reason for this is open for discussion, however one may speculate that either these bulls were low ranking and hence their sexual activity was depressed or that they were shot soon after intensive copulation which had depleted their sperm reserves. Surprising was also the early age (> 10 yr.) for attaining seniority, confirmed by such other indicators as facial pigmentation and declining antlerogenesis (Bubenik et al. 1977, 1978b).

In regard to the relative longevity of bulls this appears somewhat early for such large cervids and differs from Alaskan moose (Gasaway

1975), where 10 - 12 yr. old bulls are superior in antler size. Albeit it is known in red deer, of disorganized populations. In contrast, red deer stags from well organized populations end their prime age with 14 - 16 yr. (Bubenik 1983c). In this regard the testes volume of 10 1/2 yr. and older Oct. bulls from Minnesota (Table 3) is surprising, being the largest from all age classes. However the Oct. trend in all classes greater than 10 yr. is relatively similar to that found in Ontario. Despite the similarities mentioned, we have to stress the discrepancy in the trend of decline in spermatogenesis between the N. C. Ontario moose and red deer from Tirol, Austria (Pinsker 1978). In our study, the production of spermatozoa in prime bulls (6 1/2 - 10 yr.) terminated as early as Oct., and epidiymal canuli and sperm reserves in vas deferens were partially or completely evacuated by Nov.-Dec. In red deer, relatively large reserves of mobile sperm are still present as late as Jan. (Jaczewski and Morstin 1973) and activity of germinative epithelium begins to decrease in Dec. (Pinsker 1978).

The comparitively short spermatogenesis and the surprisingly high number of testes with depleted or evacuated sperm reserves was unexpected. An explanation could be either sexual overstimulation, or adaptation to severe environmental conditions, ie. tundra (Bubenik 1973, 1983b), where a long rutting season might severely affect body condition of actively rutting bulls. A comparison of testicular weight and epididymides/testes ratio with five other ungulate species (Table 4) indicates that moose have probably one of the smallest testes and epididymides. Despite that there is probably not an absolute relationship between reproductive capacity and size of testes (Amann and Almquist 1962), the comparison is striking. The reproductive potential of bovids is superior to that of cervids, eg. a ram

Table 3. Combined weight[1] and volume[2] of testes and epididymides of fall shot moose from N. C. Ontario[1] and Minnesota[2]

AGE CLASSES	1½	2½	3½	4½	5½	6½-9½	10½-15½
MINNESOTA 1971 and -72	N: 1	5	16	16	21	30	9
Range in ml	1	150 - 255	65 - 250	100 - 335	150 - 250	125 - 270	155 - 360
Mean in ml	150	188	175	220	197	190	260 (!)
N-C-ONTARIO 1977 and -78	N: 37	25	22	14	10	18	4
Range in g	66 - 180	69 - 182	116 - 217	65 - 206	67 - 173	77 - 182	97 - 125
Mean in g	123	136	148	153	136	108	95

(The volume must be multipied about by 1.1. for to obtain approximative weight.

Table 4. Relationship between epididymides and testes (E/T) and combined testicular weight expressed as a percentage of live body weight in six Pecora at the peak of their rut.

Species	E/T %	combined TE in % of live weight
Ibex (Capra ibex)	% 32 ±	% o.35
Mouflon (Ovis musimon)	22 ±	o.88
Roe deer (Capreolus capreolus)	21 ±	o.25
Fallow deer (Dama dama)	17 ±	o.14
Red deer Cervus elaphus)	20 ±	0.1-0.09
Moose (Alces alces)	18 ±	0.05

can fertilize almost 100 ewes in 14 days (Mattner et al. 1967, and Mattner and Braden 1967), and a red deer stag an average 6 to 8 hinds (Bubenik 1983b, Clutton-Brock et al. 1982).

Testes must be exposed to air currents to keep cool (Gomes et al. 1971), however in subarctic conditions such external organs may have evolved a smaller size to avoid hypothermy of such a critical gland.

There might also be another factor which contributes to rapid depletion of semen reserves in taiga-moose ie. the serial monogamy (Bubenik 1983c). The cow stimulates the bull to as many copulations as he is physiologically or physically capable, despite the fact that two copulations are generally considered sufficient to ensure conception. Semen waste is avoided in the cow assemblages of the tundra-moose because the cows sychronize their estrus, and are simultaneously in a receptive phase (Beach 1975). Hence the bull must court and service each cow and pace himself to maintain sufficient reserves for those remaining. As long as we are unaware of the volume of sperm reserves (for methodology see Jindal and Panda 1980) and the amount used in one ejaculation, it will be difficult to explain the large depletion of semen as found in the histological examination.

Summarizing the results (Fig. 6) we believe bull moose generally mature by 4 or 5 yr. based on testicular activity and therefore several social or maturation classes should be discriminated.

Recommended Social or Maturation Classes in N. C. Ontario Bull Moose

(a) Calves, which are in prepubertal stage.

(b) A class of maturating bulls from 1 to 4 yr. in which the maturation progress and behavior corresponds to that of human 'teenagers' as an

analogous term (Lorenz 1974). Their sexual maturation and behaviour is dictated by their number in relation to primes (5 - 10 yr.). As a minority class, they maturate slowly and do not compete as breeders. As a majority, they are an agressive and competitive group.

The yearlings as youngest "teens" should be separated as a special subclass. They are the class in which age can be reliably estimated and used to predict population trends on the basis of their numbers, antler development and body size.

(c) Bulls older than 5 yr. (exceptions excluded) are considered prime and those older than 6 yr. are apparently the most potential breeders. The percentage of them that actually breed is open to research. Certainly in this regard, the sexual potency of some 5 and 6 yr. old bulls will overlap and the low ranking might become so sexually depressed that they will not try to breed. Generally speaking only bulls from 5 yr. upward should be called 'adult', if this obsolete term (Eabry 1970) is to be used.

(d) Finally we have a class of post-prime or seniors. There is no proof that seniority in moose bulls must begin with 10 yr., should the deterioration of the CNS and endocrine function in moose be dependent on population structure as demonstrated in red deer (Bubenik 1983a).

The range of the social classes cannot be considered an absolute limit. Depending on demographic conditions, we may have in each age class a higher or lower percentage of males, whose testicular activity deviates from the expected speed and intensity (Autrum and Holst 1968, Gordon and Bernstein 1973, Gibson and Guiness 1980b, Guiness et al. 1978, Patanelli 1975, Rose et al. 1972). In red deer or chamois *Rupicapra rupicapra* a psychological castration is not uncommon in low ranking individuals (Kernstock 1981, Dietrich 1979).

From a point of population well-being (Bubenik 1971, 1983a), it is important that all prime bulls are the first in and out of rut, since they are the most effective breeders. This is probably the norm when this class is so numerous that the teen-bulls cannot compete with the primes either physically or behaviourally. Hence teens remain sexually depressed, until the peak of the rut is over. Otherwise the rut may be extended due to inadequate numbers of primes who are incapable of fertilizing the majority (approximately 80%) of cows in their first overt estrus as demonstrated in disorganized populations of wapiti (Prothero et al. 1979).

The variable timing of testicular activity of each social class in turn contributes to a different mobility pattern among these classes. In dealing with this problem we have to exclude yearlings as long as they are not forced to breed. During the fall they are the most mobile class. They are deprived of the company of mothers, on the one hand, and cannot find a bond to other bulls as potential rivals, on the other.

Where selective hunting is not imposed and the season begins in Sept., prime taiga-bulls are the most mobile and therefore the most vulnerable. The fact that during the past decade in Ontario, open season dates were progressively shifted from mid-Sept. to mid-Oct. offered an opportunity to test this prediction using harvest data (Fig. 6). There was a negative linear relationship between the percent prime bulls (correlation coefficent r = -0.77, N = 1225, P < 0.05) and opening season dates 1973 -80. A reduction in the proportion of prime bulls as seasons are opened later corresponds to the observed pattern of testicular activity in teen and prime bulls of wapiti (Prothero et al. 1979,

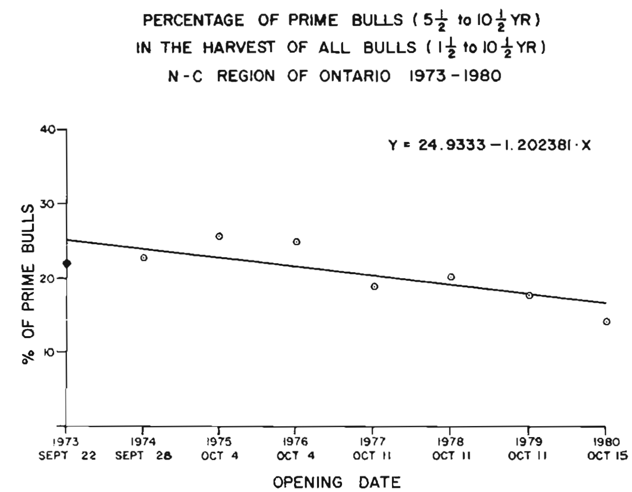

Fig. 6. Regression of percent prime bulls on shifting opening hunting season dates for N. C. Ontario moose ($r = -0.77$, $N = 1225$, $P < 0.05$).

Timmermann and Gollat 1982).

The extent in which demographic and/or environmental conditions may influence the spermatogenesis is shown in Fig. 7 and Table 3. The testicular weights from the USSR (Jazan 1959) are similar to those from N. C. Ontario. Whether these weights relate to testes preserved in formalin is unknown, therefore the similarity might be coincidental. Striking however is the weight from a 3 1/2 yr. bull taken Sept. I which falls in the 6 - 7 1/2 yr. old range from Sept. II. The lack of earlier material from Aug. precludes speculation that this bull might have been sexually hyperstimulated, originated from a disorganized population with a skewed sex and social class ratio or that the actual age may have been under estimated. The trend of converted volume weights found by Karns in Minnesota are similar to our moose up to the age of 9 1/2 yr. However, bulls 10 1/2 yr.+ showed a completely different trend in weight from all younger specimens as well as those from N. C. Ontario. What factors contributed to these differences is unknown and purely speculative. They may have been for example influenced by population structure resulting from specific hunting policies existing in Minnesota during this period.

Our results indicate that knowledge concerning sexual maturation in bull moose is still inadequate to generalize or try to explain aberrant findings. Further study should be a project of highest priority.

CONCLUSIONS

This study has shown that taiga bull moose of N. C. Ontario require at least 4 or 5 yr. to achieve sexual maturity and those between 5 and 10 yr. are regarded as prime breeders. Variability of testicular activity

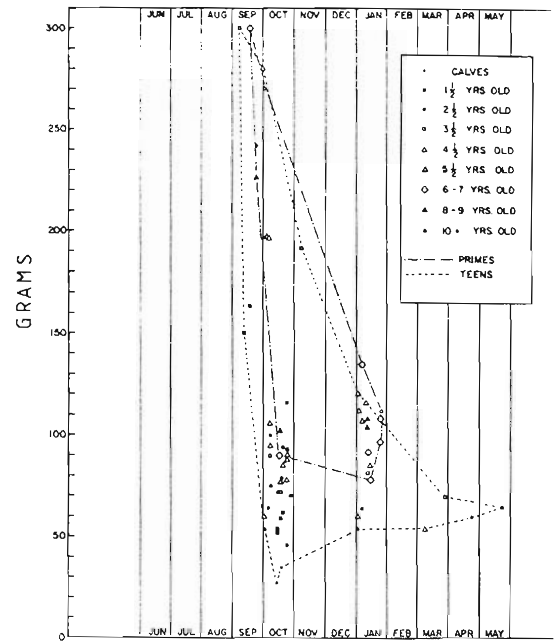

Fig. 7. Combined weight of testicular glands of Petchora-River-taiga-moose after Jazan (1959, Table 1).

among age classes might relate to such factors as physical fitness, rank, and such demographic conditons as a skewed sex ratio and a low percentage of prime bulls. In addition, the relatively short spermiogenesis and the serially monogamous breeding strategy (Bubenik 1983c) must lead to a long breeding and calving period. This leads to a temporary reactivation of spermiogenesis as observed in red deer (Frank et al. 1983), in tame moose (Krzywinski, pers. comm. 1982 and Dudzinski pers. comm. 1982).

We have speculated that the relatively small testes/body weight ratio in moose could indicate a low reserve of viable sperm, which is subject to being wasted by serially monogamous mating. Such reasoning however is questionable without reliable data on sperm production, frequency of mounting with ejaculation and sperm maturation time.

This pilot study has illustrated that much more information concerning male moose sexual maturation, semen reserves and fertilization capacity is needed. Simultaneously, some evidence has suggested that submature bulls (up to 4 1/2 yrs.) are less potent than primes and delay their breeding activity. This in turn may reduce the probability of cows conceiving in their first overt estrus and hence prolongs the rutting and calving season (Gollat et al. 1981).

In order to directly manipulate taiga moose populations, we suggest that an almost equal sex ratio with parity between submature (teenage) and prime moose appears necessary. This ratio should restore the rutting peak to the Sept. period, shorten the rutting and calving period, raise the reproductive success, and allow the majority of adult cows to calve in May. This situation apparently occurred in Norway 70 years ago (Schultz 1931) and after World War II (Lykke pers. comm. 1977). Markgren (1969, 1971) reported early ruts in the exploding Swedish populations and

recently Child (pers. comm. 1982) suggested an apparent improved population structure in Central British Columbian moose was responsible for the rutting period reverting from late Oct. to late Sept.

In summary, the future destiny and well-being of moose populations relies on the careful inventory of the mid-winter structure and full documentation of the hunter kill with emphasis on harvest control of the non-breeding and prime breeding classes.

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