PRODUCTIVITY OF MUSKRATS IN EAST TENNESSEE[1]

by
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ABSTRACT

Muskrats, *Ondatra zibethicus*, (360) were collected from river and creek study areas in East Tennessee from July, 1972 to June, 1973. Data were recorded on reproductive parameters.

Maximum values for testis length and width occurred in August, whereas maxima for testis volume and weight were in May and August, respectively. Evidence indicated that sperm were present in the adult males year-round.

Maturation of follicles began in January in adult females; mature follicles were present in late February and March, and the first corpora lutea of pregnancy were found in April. Maximum values for mean ovarian weights for pregnant and non-pregnant river adults were achieved in July. Ovarian lengths were maximum in April (non-pregnant) and August (pregnant). Average litter size was 5.38 and the average number of litters per year per female was 2.3. Fetal implantations were found until August, and follicular activity ceased by October. The peak months of prevalence of pregnancy were April, May, and July when 50 percent of the females were pregnant by gross examination. It was estimated that 36 to 50 percent of the sample was in the preimplantation stage of pregnancy and thus not accounted for as pregnant animals. Annual productivity in the river females was not significantly greater (5% probability level) than in the creek females and thus did not reflect nutritional differences that apparently exist between the two areas. Records from the present study indicate litter sizes are intermediate between studies from more southern and northern latitudes.

INTRODUCTION

Millions of muskrats are harvested each year and make up a major portion of the fur industry in the United States. A total of 5,164,953 muskrats were harvested in the United States during 1969-70. Of this total, 1,404,974 were trapped in the nine southeastern states (Alabama, Florida, Georgia, Kentucky, Louisiana, Mississippi, North and South Carolina, Tennessee) and 19,448 were harvested in Tennessee (United States Department of Interior 1971). The muskrat is not profitably bred in captivity on a pelting basis; therefore, essentially all of the harvest of muskrats comes from wild populations (Svihla and Svihla 1931, O'Neil 1949, Errington 1961).

The determination of productivity of muskrats is of considerable value as a combined indicator of the success of the breeding season and the effect of mortality factors acting upon a population (Alexander 1951). A great deal of work has already been conducted concerning the reproductive biology of muskrats (Svihla and Svihla 1931, Errington 1937, 1939, 1940, 1954, Enders 1938, 1939, Beer 1950, Beer and Meyer 1951, McLeod and Bondar 1952, Beshears and Haugen 1953, Donohoe 1966). However, as Forbes and Enders (1940) state, not only do reports on the subject differ, but the time of beginning and the duration of the breeding period undoubtedly vary in different parts of the United States. Studies performed in different continental locations involve different subspecies of *Ondatra zibethicus*, each possibly with its own demographic and reproductive characteristics. Information from previous studies has been obtained through trapper-supplied carcasses from late fall, winter, and early spring, and litter observations throughout the remainder of the year. The present study utilized data on a year-round basis to provide a more complete interpretation of muskrat reproduction.

DESCRIPTION OF THE STUDY AREA

Location

The river portion of this study was conducted on a 48km segment of the Holston River extending from the confluence of the North Fork and South Fork of the Holston River near Kingsport, Sullivan County, to the upper end of the John Sevier Lake near Rogersville, Hawkins County, in East Tennessee.

The trapping area for samples collected from creeks encompassed small creek drainages within Blount and Knox Counties in East Tennessee.

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[1] Funds in support of this study were made available through McIntire-Stennis Project No. 11, Department of Forestry, Agricultural Experiment Station and the Ecology Program, the University of Tennessee, Knoxville.

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The Holston River is characterized by long, bending pools intermittently broken by shallow, rocky shoals. The average width of the river channel is 128m, with a floodplain varying from .402 to 1.609km. In summer, much of the river channel contains mats of rooted aquatic vegetation, the dominant species being Sago pondweed *(Potamogeton pectinatus)* and water stargrass *(Heteranthera dubia)* (Minser 1968). During high water, much of this vegetation becomes dislodged and is caught in snags along the shoreline or floats downriver. The high fertility of the Holston River has been considered a major factor in the large quantities of aquatic plant biomass and probably contributes to the apparent high muskrat population. Peltier and Welch (1969) state that "nutrient levels in the Holston River were in excess of optimum levels" for aquatic plant growth. Similarly they rule out water temperature and dissolved CO_2 as limiting factors. The authors further state that "physical factors best explain the (plant) growth through interaction to determine the available light."

In Blount County, the creeks selected as trap sites were within the drainages of the Tennessee River and the Little River. In Knox County, the trap sites were in the drainages of the Tennessee and Clinch Rivers. While the Tennessee Valley Authority performs flood-control operations on some of these creeks, physical dimensions were unavailable. In general, the creeks range from 1.5 to 12m in width, with depths of less than 5m. Characteristically, there is much variation in the stream flow, depending upon season, local precipitation and topography.

The creeks flow through woodland or pasture and are generally not recipients of excessive cropland runoff or urban pollution. The aquatic biomass appears to be small. Applicable data on amounts of soluble phosphates and inorganic nitrogen compounds were not available (Jones Tysinger, personal communication).

MATERIALS AND METHODS

Collections of River Samples

Muskrats from the river were collected by shooting during monthly float-trips. The fluctuation of the level of water in the river and the distance from Knoxville made conventional trapping techniques impractical.

Since muskrats are predominantly crepuscular/nocturnal, night-floats were utilized. A 12-volt battery was rigged with two aircraft landing lights. Three people were needed per float; one to guide the canoe, one to operate the lights and scan the snags and shoreline for muskrats and one to collect the muskrats. Two canoes were outfitted and floats were conducted simultaneously along both shorelines. This modification yielded the highest monthly collections.

Muskrats were collected and tagged; tag data included date and time of collection, and the location of capture according to numbered quartermile divisions along the river. Specimens were examined externally to determine sex (Baumgartner and Bellrose 1943). The specimens were kept on ice until they were transported to the laboratory; they were then frozen until dissection. A total of 215 muskrats were collected from the Holston River over the collection period of 12 months.

Collections of Creek Samples

In order to compare reproductive characteristics between muskrats from the river system and a muskrat population from small creeks, muskrat carcasses were obtained from a local trapper during the legal trapping season, November 15, 1972, to February 15, 1973. All animals were trapped along the numerous small creeks within Knox and Blount Counties in East Tennessee. After the muskrats were skinned, the carcasses were refrigerated until they were picked up by the investigator. A total of 145 muskrats were obtained during the trapping period.

Dissection

The sample of muskrats from the river were obtained as whole specimens. They were skinned and the pelt was stretched, dried, and used as an aging technique (Applegate and Predmore 1947).

On dissection, sex determination was verified by examining the reproductive tract. For males, the right and left testes were removed from the reproductive tract where they join the epididymides. Each testis was measured (mm — length and width) and volume (ml) was determined by water displacement. Other conditions such as turgidity/flaccidity and presence/absence of epididymal convolutions were noted and recorded. The tails of the epididymides were inspected microscopically for the presence or absence of sperm. Male muskrats were separated into adult and subadult age classes based on the presence or absence of convolutions in the epididymides and the relative development of the testes and accessory organs. Breeding condition in the male muskrat was determined by the presence or absence of epididymal convolutions. The penis was measured for length (at complete extrusion) and diameter (at the distal end). Following this examination, the right and left testes were weighed (g) on a Mettler Model No. H 6T Digital Balance and were preserved in Mossman's AFA for future reference.

Prior to skinning females, the vaginal orifice, located at the posterior base of the urethral papilla, was noted as open or closed. Teats were located and measured (basal diameter and length). Upon dissection, gross examination (Forbes and Enders 1940, Gashwiler 1950) of the uterus was performed to determine whether the female was pregnant; the number of fetuses present in the left and right uterine horns was recorded. If the animal was not pregnant, the average uterine width was recorded and the number of placental scars and their location were noted. The uteri of the subadult females were underdeveloped and transparent, and the ovaries showed no follicular activity. These characteristics served to differentiate between the subadult and adult females since the latter had uteri which were thicker, translucent, vascularized and usually contained placental scars and/or fetal implantations. The adult ovaries similarly exhibited present or past follicular activity. The adult female was defined as capable of breeding when the mature follicle stage of the ovulatory cycle was attained (Forbes and Enders 1940). Each ovary was weighed on the Mettler Balance and preserved for future use.

Analysis of Data

Data were analyzed for a total of 360 muskrats, 215 from the river and 145 from the creeks. Data were programmed into an IBM 360 Model 65 Computer which calculated the standard deviation, variance, the maximum, minimum, and total range, and the sample size for each variable.

The river population data were compiled and analyzed as monthly or seasonal samples and the means, and the maximum and minimum ranges of all pertinent variables were plotted over the collection year. The winter river and creek data were segregated into sex, age, and population units (i.e. adult male creek, adult male river, adult female creek, adult female river) for comparative purposes.

An "F Test" (Steel and Torrie 1960) was performed to determine any significant difference between the variances of appropriate creek and river variables. A pooled variance was used in the "t test" to compare means. For those comparisons with significantly different (5% probability level) variances, an approximate t value was calculated for comparison.

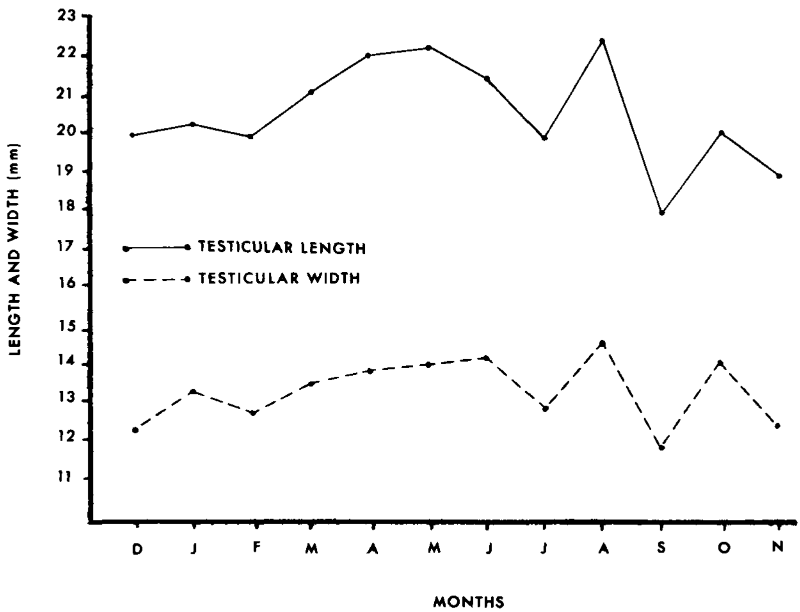

Fig. 1. Mean testicular length and width for adult male muskrats in the combined creek and river samples in East Tennessee.

Table 1. Summary of monthly reproductive parameters, sample sizes, and standard deviations for adult male muskrats from combined creek and river study areas, East Tennessee.

Monthly sample	*Sample size (n)*	*Mean testis length (mm) & S.D.*	*Mean testis width (mm) & S.D.*	*Mean testis weight (g) & S.D.*	*Mean testis volume (ml)*
January	43	20.16 ± 2.57	13.18 ± 1.55	1.53 ± 0.42	1.74
February	44	19.88 ± 2.31	12.63 ± 1.47	1.47 ± 0.34	1.60
March	18	21.06 ± 1.74	13.36 ± 1.18	1.67 ± 0.25	1.78
April	14	22.00 ± 1.20	13.73 ± 1.16	1.78 ± 0.45	1.91
May	9	22.17 ± 1.73	13.89 ± 1.10	1.95 ± 0.41	2.22
June	10	21.45 ± 1.95	14.10 ± 0.86	1.75 ± 0.23	1.74
July	4	19.86 ± 2.15	12.75 ± 3.30	1.90 ± 0.46	1.70
August	5	22.40 ± 1.58	14.50 ± 1.32	2.29 ± 0.82	1.98
September	3	17.83 ± 5.90	11.83 ± 5.00	1.10 ± 0.00	1.27
October	1	20.00 ± 0.00	14.00 ± 0.00	1.36 ± 0.19	1.35
November	7	18.90 ± 0.86	12.30 ± 0.85	1.15 ± 0.51	1.23
December	13	19.92 ± 2.97	12.19 ± 1.79	1.36 ± 0.46	1.49

RESULTS AND DISCUSSION

Reproductive Parameters – Males

Testicular measurements – Since there was no significant difference (5% probability level) in the lengths, widths, weights, and volumes of testes between creek and river muskrats the data for the respective creek and river populations were combined and graphs constructed to illustrate monthly variations (Figs. 1 and 2, Table 1).

Beer and Meyer (1951) state that adult males are capable of breeding in March and the weight of adult male testes attained a maximum value in May, gradually decreased through the summer and fall and decreased to a minimum level in October. Testis weight remained low through January and began to increase in February to the maximum in May. McLeod and Bondar (1952), studying *O. z. alba* in Manitoba, state that the sexual activity of males increased with the onset of warm weather. The authors further state that testis size increased with the mating season, but decreased after three weeks, reducing to one-half the maximum by mid-August. Donohoe (1966) gives testis lengths as 22.73mm and 23.06mm in his controlled and uncontrolled water-level units, respectively. Beer and Meyer (1951) reported that the testes of immature males began to enlarge in December, continued to increase from January through April, when spermatogenesis began, and reached a maximum in May. Errington (1939) contends that Iowa subadults reach sexual maturity between 8 and 9 months and are capable of breeding by December.

The data on testicular size for the November and December muskrats exceed those reported by Errington (1937). The testis length data reported by Donohoe (1966) appear to be larger than those for East Tennessee muskrats. Data in the present study approximate those reported by Sooter (1946). Variations in testicular weights in the present study differ from Beer and Meyer (1951) whose maxima and minima occur in May and October, respectively, and from those reported by McLeod and Bondar (1952).

In the present study, subadult males, as defined by the criterion of unconvoluted epididymides, were captured from May through January. Data on testis length, width, weight, and volume exhibited continuous increase from their capture following birth to the following spring. The above indicates that the previous year's subadult males were approaching values indicative of mature males. These transition adults (subadults developing toward sexual maturity) were classified as adults despite the fact that their reproductive tracts were not yet fully mature and were combined with other adult males. The above situation may account for the slight decrease in testicular values for the January to February period (Figs. 1 and 2).

The penis diameter for the combined winter creek and river adults was 6.3mm; the diameter of the river subadults varied from 3.0mm (spring) to 6.0mm (winter), and the creek subadults measured 5.1mm in the winter.

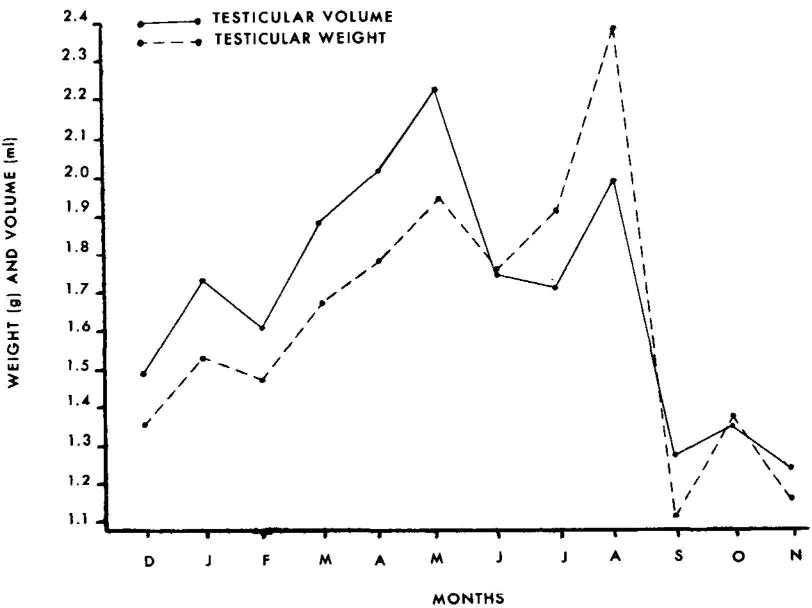

Fig. 2. Mean testicular weight and volume for adult male muskrats in the combined creek and river samples in East Tennessee.

Spermatogenesis — An integrative approach was undertaken to evaluate the presence or absence of sperm in the epididymides of muskrats. The sperm in the epididymides (July to April), stored in Mossman's AFA, were found to be denatured by the preservative and reduced to an unrecognizable state. Pelton (1968) indicates there exists a "close correlation between convolutions in the tail of the epididymides and the presence of viable sperm in the cottontail rabbit *(Sylvilagus floridanus)*." The above observation was verified in adult muskrats by preparing microscopic slides of the contents of convoluted epididymides from May and June; all possessed large quantities of sperm. Under similar examination, the unconvoluted epididymides of subadult males contained no sperm. It therefore appears that epididymal convolutions in muskrats indicate the presence of sperm. The above assertion is reinforced several times throughout the study. Sooter (1946) mentions the presence of sperm plugs on his winter-trapped California muskrats. A total of 30 sperm plugs were found in the samples from the creek and river areas of East Tennessee from December to June. In order to further substantiate the assertion, muskrat carcasses were obtained from a local trapper during the winter, 1973-74. The above carcasses were trapped in December and January from the same creeks as the original creek samples (1972-73). They were analyzed for the presence of sperm and all but one muskrat having convoluted epididymides contained large quantities of sperm. From the above approach, it can be stated with some degree of confidence that adult male muskrats contain quantities of sperm throughout the year in East Tennessee and appear physiologically capable of breeding year-round.

Reproductive Parameters – Female

Ovarian measurements — The ovarian measurements for the creek adults and subadults collected over the winter were not significantly different (5% probability level) from the measurements taken for their appropriate river counterparts. The creek and river data were therefore pooled and graphs exhibiting monthly variations in ovarian weight and ovarian length and width were plotted (Figs. 3 and 4, Table 2). The ovarian weights for pregnant females paralleled those of non-pregnant females but were of greater magnitude. Ovarian lengths for non-pregnant adult females show only moderate monthly variations (Fig. 4). The ovarian length and width of subadult females from December through February are only slightly less than those for adult females for this time period, indicating that they are approaching sexual maturity.

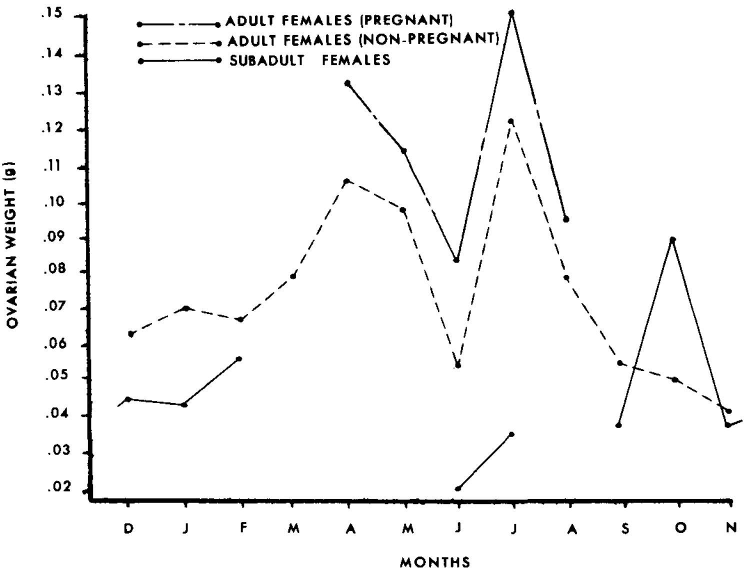

Fig. 3. Mean ovarian weights from the combined samples of creek and river adult and subadult muskrats in East Tennessee.

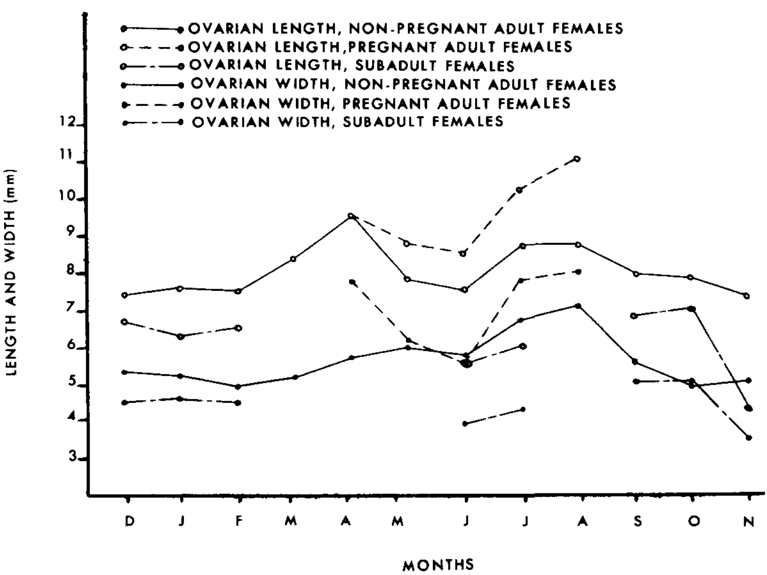

Fig. 4. Mean ovarian lengths and widths from the combined samples of creek and river adult and subadult muskrats in East Tennessee.

Table 2. Summary of monthly reproductive parameters, sample sizes and standard deviations for subadult and adult female muskrats from combined creek and river study areas, East Tennessee.

	December	*January*	*February*	*March*	*April*	*May*
Sample size (n)						
non-pregnant adult	5	26	22	4	2	6
pregnant adult	—	—	—	—	2	6
subadult	15	6	1	—	—	—
Mean ovarian weight (g) and S.D.						
non-pregnant adult	0.064 ± 0.034	0.071 ± 0.023	0.068 ± 0.021	0.080 ± 0.019	0.107 ± 0.032	0.099 ± 0.016
pregnant adult	—	—	—	—	0.134 ± 0.029	0.116 ± 0.025
subadult	0.046 ± 0.019	0.044 ± 0.019	0.057 ± 0.000	—	—	—
Mean ovarian length (mm) and S.D.						
non-pregnant adult	7.40 ± 1.20	7.62 ± 1.16	7.50 ± 1.30	8.38 ± 1.75	9.50 ± 0.70	7.75 ± 1.18
pregnant adult	—	—	—	—	9.50 ± 1.41	8.83 ± 1.79
subadult	6.70 ± 1.15	6.29 ± 1.35	6.50 ± 0.00	—	—	—
Mean ovarian width (mm) and S.D.						
non-pregnant adult	5.30 ± 1.55	5.21 ± 1.14	4.95 ± 1.08	5.13 ± 1.00	5.75 ± 1.05	6.00 ± 0.72
pregnant adult	—	—	—	—	7.75 ± 1.75	6.08 ± 0.95
subadult	4.47 ± 0.97	4.64 ± 1.28	4.50 ± 0.00	—	—	—
$\overline{X}$ teat diameter (mm) and S.D.						
non-pregnant adult	4.00 ± 1.00	1.40 ± 0.89	2.20 ± 0.83	2.25 ± 0.50	5.25 ± 0.00	6.58 ± 1.86
$\overline{X}$ teat length (mm) and S.D.						
non-pregnant adult	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00	2.00 ± 0.00	2.83 ± 2.04
Mean uterine width (mm) and S.D.						
non-pregnant adult	3.80 ± 0.84	2.85 ± 0.92	3.09 ± 0.87	4.00 ± 0.82	11.50 ± 9.19	5.00 ± 1.09
subadult	2.00 ± 0.00	2.00 ± 0.00	2.00 ± 0.00	—	—	—

Table 2. (continued)

	June	July	August	September	October	November
Sample size (n)						
non-pregnant adult	7	3	5	7	4	2
pregnant adult	1	3	1	—	—	—
subadult	4	3	—	2	1	2
Mean ovarian weight (g) and S.D.						
non-pregnant adult	0.054 ± 0.017	0.124 ± 0.032	0.080 ± 0.025	0.056 ± 0.021	0.051 ± 0.021	0.042 ± 0.006
pregnant adult	0.084 ± 0.000	0.154 ± 0.080	0.096 ± 0.000	—	—	—
subadult	0.020 ± 0.006	0.036 ± 0.001	—	0.038 ± 0.004	0.091 ± 0.000	0.038 ± 0.007
Mean ovarian length (mm) and S.D.						
non-pregnant adult	7.50 ± 0.75	8.67 ± 0.57	8.70 ± 1.10	7.79 ± 1.14	7.75 ± 0.50	7.25 ± 2.45
pregnant adult	8.50 ± 0.00	10.17 ± 2.50	11.00 ± 0.00	—	—	—
subadult	5.50 ± 0.73	6.00 ± 0.57	—	6.75 ± 0.35	7.00 ± 0.00	4.25 ± 0.35
Mean ovarian width (mm) and S.D.						
non-pregnant adult	5.64 ± 0.71	6.67 ± 0.57	7.10 ± 0.90	5.50 ± 1.40	4.88 ± 1.15	5.00 ± 2.10
pregnant adult	5.50 ± 0.00	7.83 ± 1.65	8.00 ± 0.00	—	—	—
subadult	3.88 ± 0.65	4.33 ± 1.10	—	5.00 ± 1.41	5.00 ± 0.00	3.50 ± 0.00
$\overline{X}$ teat diameter (mm) and S.D.						
non-pregnant adult	5.63 ± 1.49	6.00 ± 2.30	5.50 ± 1.92	4.83 ± 1.47	4.25 ± 1.71	3.00 ± 2.83
$\overline{X}$ teat length (mm) and S.D.						
non-pregnant adult	2.00 ± 0.89	2.33 ± 2.00	1.50 ± 0.54	2.00 ± 0.81	1.25 ± 0.50	1.50 ± 0.70
Mean uterine width (mm) and S.D.						
non-pregnant adult	4.57 ± 0.77	7.00 ± 0.00	7.40 ± 2.30	5.00 ± 0.00	3.75 ± 0.50	3.50 ± 2.12
subadult	2.25 ± 0.50	2.00 ± 0.00	—	2.00 ± 0.00	5.00 ± 0.00	2.50 ± 0.70

In both the present study and that of Beer and Meyer (1951), weight increases of ovaries began in February. Beer and Meyer's (1951) "near peak in March" is in advance of the East Tennessee peak in April and May. The maximum peak of ovarian weights of Wisconsin muskrats is attained in May, continues through June and declines in July; this is well in advance of the maximum for East Tennessee females which occurs in July and declines in August. Variations in ovarian activity in muskrats in Wisconsin indicate that breeding activity is more restricted, extending from February to July, than the ovarian weight variations of East Tennessee muskrats, which extend from February to late August. This shorter breeding season is possible considering that the latitudinal difference and associated harsher northern climate have a restrictive effect on productivity.

From the data on ovarian weights, lengths, and widths (Figs. 3 and 4) it is apparent that most ovarian activity occurs within two peak periods in East Tennessee. The first period occurs from late March to May; the second from July to August. These peaks indicate the presence of two periods of intense ovarian activity, probably resulting from hormone production associated with pregnancy.

Teat measurement, uterine widths, and vaginal orifices — The patterns of monthly variation in teat diameter and length coincide with the high peaks of reproductive activity from April to May and July to August, periods of litter production (Fig. 5). The teats increase in length and diameter due to hormonal stimulation and the suckling activity of the young.

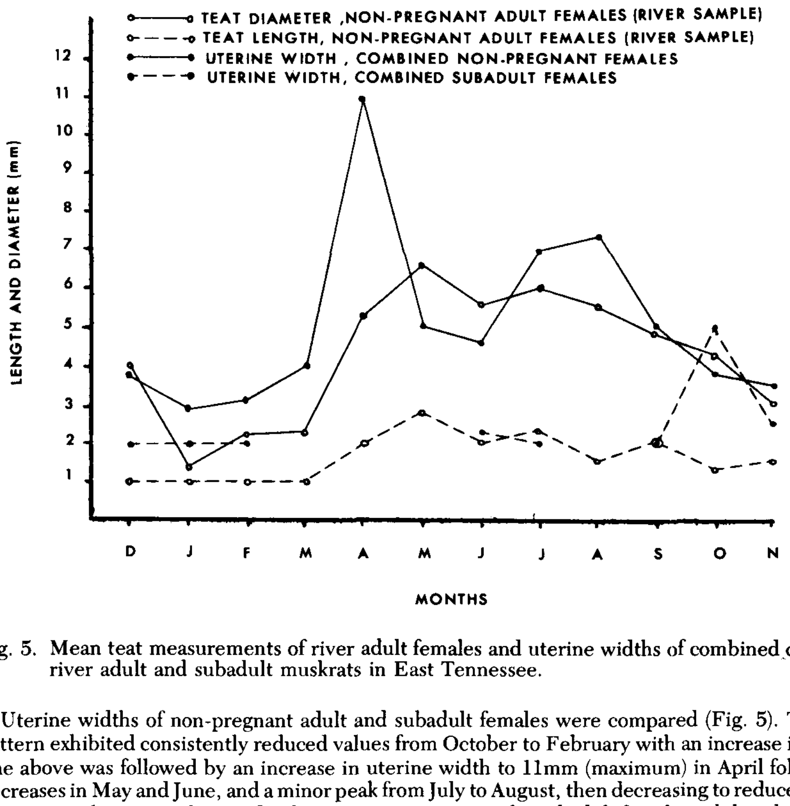

Fig. 5. Mean teat measurements of river adult females and uterine widths of combined creek and river adult and subadult muskrats in East Tennessee.

Uterine widths of non-pregnant adult and subadult females were compared (Fig. 5). The adult pattern exhibited consistently reduced values from October to February with an increase in March. The above was followed by an increase in uterine width to 11mm (maximum) in April followed by decreases in May and June, and a minor peak from July to August, then decreasing to reduced values. Here again the two peak periods of activity are apparent. The subadult females exhibited consistent uterine widths (approximately 2mm) from June to February, followed by increases with maturity and continued increase with litter production.

The vaginal orifices of all subadult females are closed throughout the year, initially opening during January and February of the following breeding season. Data indicate that reclosure of the vaginal orifice of adult females does occur occasionally after breeding (one fall female with a closed vaginal orifice contained six placental scars).

Placental scars — Placental scars of pregnant animals were not considered since scars were often unclear or obscured by the implanted fetuses. To obtain a complete annual picture of productivity for each adult female, scar counts were not begun until September, after the termination of the breeding season. Counts of placental scars were made on the river sample from September to February and from December to January on the creek sample. Seventeen females from the river had placental scars averaging 12.71 per female; 53.2 percent of the scars were found on the right horn of the uterus. Eleven creek females had placental scars which averaged 11.82 scars per female; 52.3 percent of the scars occurred on the right horn of the uterus. Counts of placental scars in muskrats from the creek and river samples were combined since no significant difference (5% probability level) was found. In the total of 28 females placental scars averaged 12.36 scars per female; 52.9 percent occurred on the right horn of the uterus. The range of placental scars per uterus was 4 to 24.

With regard to reliability of placental scar counts, Errington (1963) states, "For muskrats breeding more or less in all months of the year, or with much seasonal irregularity, I would consider placental scar counts to be of limited utility . . . but for northern muskrats in which the annual breeding season is essentially restricted to a block of months, fall and early winter specimens yield far more satisfactory data. Even so, the fading of the older sets of placental scars may make counts in Iowa specimens unreliable after about the end of the calendar year." Nevertheless, data from the present study indicate that the numbers of placental scars from muskrats in East Tennessee are within the ranges of productivity reported previously (Table 3).

Litter sizes and litters per year — An estimate of litter size was made from 13 pregnant muskrats from the river area. These females contained a total of 70 fetal implantations, indicating an average of 5.38 fetuses per litter. The number of fetuses ranged from three to seven for the 13 animals, with five the most frequent litter size (four cases) and six and seven (three cases) the next most frequent. Fifty percent (35 of 70) of the fetuses were implanted in each uterine horn. The average number of litters per year per female was calculated by dividing 5.38 (mean litter size) into 12.36 (mean counts of placental scars). The above provided an average of 2.3 litters per year and indicates that some adult females in East Tennessee produce more than two litters per year.

Comparisons of previous studies (Table 3) with the present study indicate that litter sizes and litters per year in muskrats from East Tennessee are intermediate between northern and southern locations. Lord (1960) establishes a correlation between litter sizes and the duration of the breeding season with changes in latitude. Colder temperatures and greater numbers of days of snow cover with concomitant less availability of food and cover result in more severe environment in areas further north than Tennessee. The higher potential productivity (number of young produced per breeding season) of more northern areas would therefore appear to be a selective advantage to populations where severe climatic conditions might cause greater mortality. Conversely, a lower potential productivity is apparently adequate for survival of muskrat populations in areas of more moderate winter weather (Pelton and Jenkins 1970).

Apparent discrepancies (Smith 1938, Gashwiler 1950, Alexander 1951, Arata 1959) in the application of Lord's (1960) hypothesis to muskrat productivities have several possible explanations. Differences could be the result of genetic differences characteristic of different subspecies. Stevens (1962) and Negus (1956) discuss the difference in regional productivity of cottontails as related to soil fertility. They indicate that decreased soil fertility can have the effect of decreasing annual productivity. The above possibility (Negus 1956, Stevens 1962) was not found to hold in the creek and river study areas of the present study. The annual productivity of muskrats of the creek and river areas, despite differences in stream fertility and the resultant effects on aquatic vegetation, were not significantly different (5% probability level).

Errington (1954) states that 23 percent of the adult females examined conceived four or more litters per year. Two of the East Tennessee muskrats captured contained placental scar totals of 22 and 24; the average number of fetuses per litter was previously established at 5.38. Dividing the mean litter size into 22 and 24 results in litters per year averaging 4.09 and 4.46, respectively. This suggests the production of four litters per year in some cases within East Tennessee.

No evidence was found of subadults, born during the breeding season, mating that same year. However, since no mark-recapture data were available in the present study, the possibility of precocial breeding remains speculative. The incidence of barren females was low and is apparently of little significance in East Tennessee. The influence of resorption of embryos on muskrat productivity was not felt to be significant in the present study. This conclusion is consistent with that of Dozier (1947) in his Maryland study.

Table 3. A summary of productivity data on muskrats from previous studies.

Author	Date	Location	Subspecies	Placental scars per adult female	Average litter size	Number of litters per year	Breeding season
Alexander	1951	New York	zibethicus	—	5.6	2-3	—
Arata	1959	Illinois	zibethicus	6.9	3.4	2	—
Beer	1950	Wisconsin	zibethicus	—	—	2-3	Early April to early July (female); March to August (male)
Beshears and Haugen	1953	Alabama	zibethicus	12.7	4	3	Year-round
Donohoe	1966	Lake Erie	zibethicus	12.06, 10.93	7.03, 6.33	2-3	
Enders	1939	Maryland	macrodon	—	—	—	Female begins first week of February
Errington	1954	Iowa	zibethicus	—	7.6	2.49	Litters born April to August; most born in May to July
Gashwiler	1950	Maine	zibethicus	14.8	5.4	2-3	Most litters born in April and May; last litter in August
Highby	1943	Maine	zibethicus	11.5(1941) 15.2(1942)	—	—	—
Lay	1945	Texas	rivalicius	—	—	—	Year-round
Marshall	1937	Utah	osoyoosensis	—	—	—	Litters found until October 15; no beginning given
McCann	1944	Minnesota	zibethicus	11.5	6	2	Begins in late March
McLeod and Bondar	1952	Manitoba	alba	—	7	1.7	Females enter breeding before males
Olsen	1959	Manitoba	alba — zibethicus — cinnamominus	—	7.1(1955) 7.3(1956)	— —	and remain active longer; no young born before May 18, none after August

Reeves and Williams	1956	Idaho	osoyoosensis	—	7.1	1.6 2.4	—
Seamans	1941	Vermont	zibethicus	—	6.8	—	—
Smith	1938	Maryland	macrodon	—	4.4	3	January to October; most young born mid-April to mid-September
Sooter	1946	California	bernardi	14.1	—	—	Begins in late January and early February
Svihla and Svihla	1931	Louisiana	rivalicius	—	3.7	—	Year-round; most young born between November and April

Breeding season — Beer (1950) defined the breeding season as the period when the mature males and females are sexually active. Enders (1938) indicates the importance of the male reproductive cycle to be that males with active sex glands must be available when the females are ready to ovulate. In the present study, this period was determined separately for males and females. As previously discussed, the adult male muskrat, based on the correlation between the presence of sperm and epididymal convolutions, was judged capable of breeding (physiologically) throughout the year. The behavioral aspects of male courtship and mating are beyond the objectives of this study. Therefore, whether these aspects present a barrier to successful breeding at any time during the year is not known.

Forbes (1942) states that "study of the . . ovaries involved a search for ripe follicles and particularly for corpora lutea as indicators of imminent or actual ovulation, respectively." Enders (1939) reports that ova are only mature during the breeding season in rodents, and, if ova are present, the females are in breeding condition. These criteria for sexual activity for the adult females were used. In examination of the ovaries of females, notes were taken regarding the chronology of the following stages: initial follicular activity and development, the presence of mature follicles, the presence of ovulation (corpora haemorrhagica, Donohoe 1966) sites, the presence of corpora lutea.

The initial activity in maturation of ripe follicles was observed to occur in late December and early January. Mature follicles were first encountered in late February. By the second week of March, nearly all adult females examined contained mature follicles. Corpora lutea of pregnancy were first encountered during the second week of April. Fifty percent of the adult females collected during April, May and July were pregnant, while 14 percent in June were pregnant and 20 percent in August (Fig. 6). The above percentages are probably low because a portion of the adult females were likely in a preimplantation stage of pregnancy. This stage of pregnancy would not be noticeable through observations of the uterus. Based on a gestation period of approximately 28 days and a preimplantation period of approximately 10-14 days (Gashwiler 1950), a random sample of adult females of a population would result in 36-50 percent of this sample being pregnant, but not visibly so.

Gashwiler (1950) states that 9.1 percent of the adult females were pregnant during April and May in Maine, while Svihla and Svihla (1931) report that the months of greatest litter production in Louisiana were from November to April. Errington (1954) indicates that the number of litters born later than mid-July in Iowa was 22 percent (481 of 2139 litters).

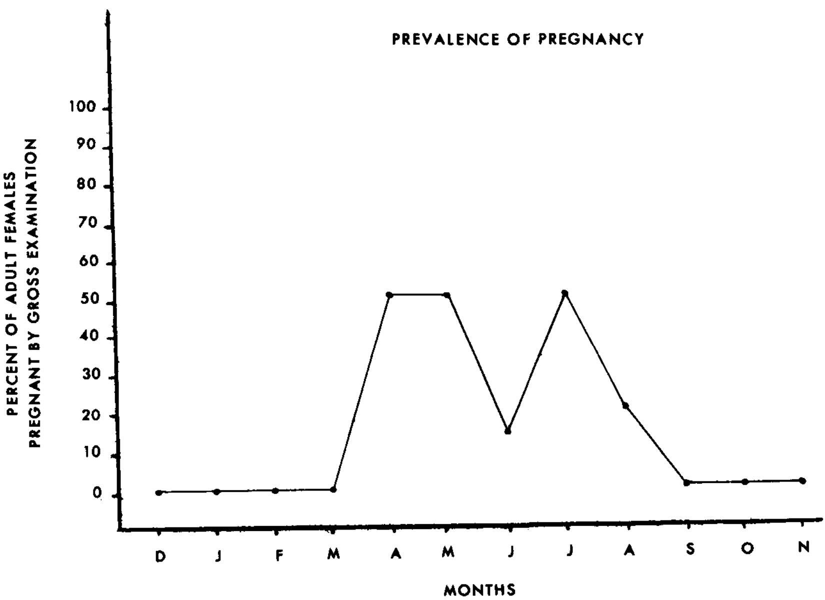

Fig. 6. Prevalence of pregnancy of adult female muskrats in East Tennessee.

The monthly sample sizes of females were insufficient to document ensuing characteristics of ovulatory cycles, but follicular activity continued with varying ratios of ripe follicles: developing follicles in the individual females. General decrease in the number of mature follicles were evident through August and September and follicular activity ceased completely by October. Adult female muskrats in East Tennessee are initially capable of breeding (possess mature follicles) in late February and early March and remain capable until mid-September. The peak of production of muskrat litters in East Tennessee is between April and July (Fig. 6).

There is considerable variation in the timetables and intensity of breeding of muskrats throughout the North American continent (Table 3). Many of these reported timetables deal with subspecies other than the one present in East Tennessee, *Ondatra zibethicus zibethicus,* and comparisons between subspecies are questionable due to possible genetic differences. When considering the other reports pertaining to *O. z. zibethicus,* however, a certain consistency does appear. Beer (1950) states that Wisconsin females commence breeding the first week of April and continue through early July. This period is shorter than the late February-early March to September timetable of the females in East Tennessee. As discussed previously (Lord 1960), the shortened breeding season in Wisconsin seems to reflect the more restricted period of breeding brought on by harsher weather. Errington (1937) in Iowa and Gashwiler (1950) in Maine give the months from mid-April to August as the months in which pregnant animals were found. These timetables correspond precisely with that of the present study. The above authors present no information on the onset or cessation of follicle maturation; these data may reflect the expected differences in the breeding season. McCann (1944) indicates that late March was the period of the onset of breeding in Minnesota. He made no reference to the termination of breeding, nor did he define his criteria for breeding, so comparison with the present study is impossible. The year-round breeding timetable given by Beshears and Haugen (1953) is reasonable due to the more southerly latitude and more suitable conditions for year-round breeding (Lord 1960).

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