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Morphological and physiological characteristics of Muskrats from three different physiographic regions of Maryland, USA

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Abstract

Between 1977 and 1979, 210 muskrats (*Ondatra zibethicus*) were trapped from 3 different physiographic regions of Maryland: Allegheny Plateau, Piedmont Plateau, and coastal plain. Two subspecies are found in Maryland, *O. z. zibethicus* (Western Maryland) and *O. z. macrodon* (Eastern Shore). The muskrats of Central Maryland are considered to be an intergrade, but data from this study show that they closely resemble the Western Maryland subspecies. Seasonal and subspecific changes in metabolic

and physiological indices are discussed. Testicular weights and lengths of adult muskrats peaked in May. Sperm was found in the testes and epididymides of at least some portion of the male population every month of the year except October. During the breeding season, adult males began producing sperm several months before subadult males. Ovulatory activity was first observed near the end of March. Breeding activity ceased by October in Eastern Shore females, with Western Maryland females probably becoming reproductively inactive several weeks before eastern shore animals. Based on embryo and corpora lutea counts, Western Maryland litters average 6.0 young, while eastern shore litters average 4.8 young. An average placental scar count of 13.6 was observed for Western Maryland females while central Maryland females average 11.6.

Introduction

There are 16 subspecies of muskrats (*Ondatra zibethicus*) abundantly distributed throughout most of the United States and Canada (WILLNER et al. 1980). Because of the species' notable availability and value as a furbearer resource, a substantial amount of literature describes the biology and management of this semi-aquatic rodent. In addition to a multitude of investigations characterizing the various North American muskrat populations, many reports are presently appearing from Europe and the Soviet Union where the muskrat has become a significant furbearing and pest species since its introduction into Czechoslovakia during the early 1900's (MOHR 1928).

Two subspecies of muskrats occur in Maryland. *O. z. macrodon* inhabits the coastal marshes and waterways of the Eastern Shore region; its range extending from the southeastern edge of Pennsylvania, southward through Delaware and central Maryland, to southeastern North Carolina. *O. z. zibethicus* is found in the Appalachian Mountain region of Western Maryland. The range of this subspecies extends through most of the eastern half of the United States and Canada (WILLNER et al. 1980). Muskrat populations inhabiting the central Piedmont Plateau area of Maryland are considered intergrades of *O. z. macrodon* and *O. z. zibethicus* (PARADISO 1969).

The objective of this study is to describe differences in Maryland's muskrat populations, particularly in their morphology, reproductive activity, and physiological responses to their respective environments.

Study area

The State of Maryland, though relatively small in area, varies significantly in its topography. In the eastern part of the State, low lying coastal plains surround the Chesapeake Bay. Central Maryland is

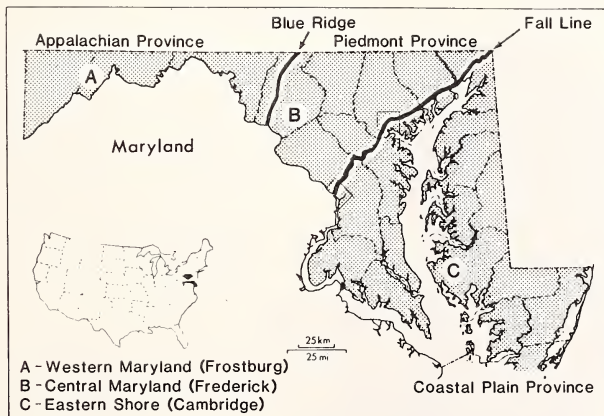


Fig. 1. Study areas and physiographic regions in Maryland, USA

characterized by the rolling hills and valleys of the Piedmont Plateau, while mountainous terrain occurs in the most western parts of the State (Fig. 1). The muskrat is abundant throughout all 3 physiographic provinces, with the annual state harvest presently averaging over 200 000 pelts (DEEMS and PURSLEY 1978).

Throughout the year, average temperatures of Western Maryland generally run 3 to 5 °C lower than those occurring on the Eastern Shore. The average temperatures of the central Piedmont Plateau area are intermediate between the former 2 physiographic regions. While the total amount of winter precipitation is similar for all three regions, in Western Maryland higher amounts occur as snowfall. Western Maryland's freeze-free period is several weeks shorter than that of the central Piedmont Plateau region and at least a month shorter than the freeze-free period of the Eastern Shore (RUFFNER 1979; VOKES and EDWARDS 1974).

Materials and methods

Specimen collections

Between July 1977 and May 1979, a total of 210 muskrats were collected from the 3 regions of Maryland. The majority of the muskrats were trapped using Conibear 110 and 120 steel traps; however, leg hold traps were used occasionally.

During the legal trapping season (November 15 to February 15 in the western and central counties; January 1 to March 15 on the Eastern Shore), the majority of the muskrats were obtained from local trappers. The carcasses of those skinned specimens were frozen until they could be transported to the laboratory.

Reproductive organs

Each testicle was measured for length, width, and breadth and weighed on a top-loading Mettler balance. The caudal epididymides were also weighed separately. Smears were made of fluid extruded from the testes and epididymides. These were examined under the microscope for the presence of sperm. If sperm were found, the amount was noted as being few, moderate, or abundant.

Female muskrats were examined for visible signs of pregnancy. The ovaries and uterus were removed from the carcass, separated, and cleaned of excess tissue. The ovaries were measured for length and width, weighed, and then placed in Bouin's preservative for histological preparation. Both ovaries of each female were mounted in paraffin and cut into 10 μ sec-

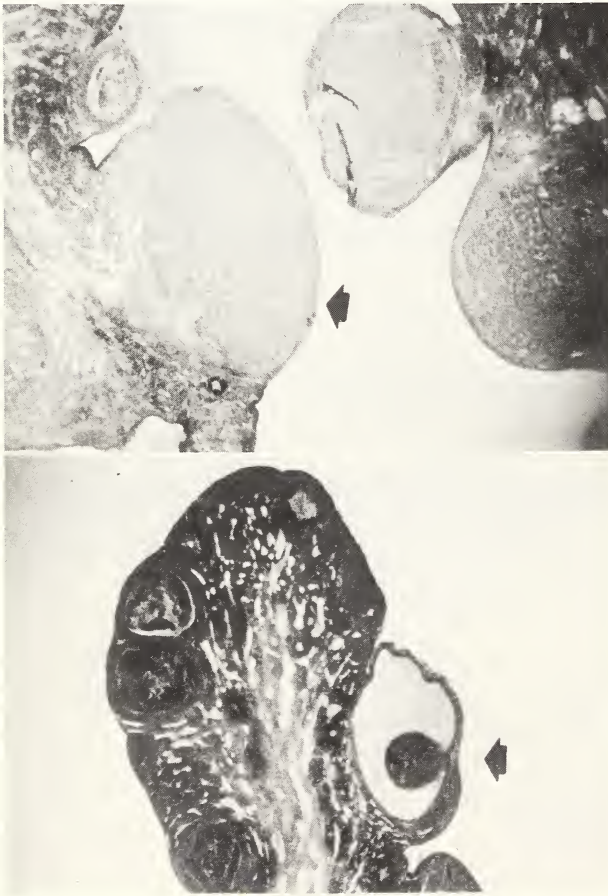


Fig. 2. Histological sections of the ovary of adult female Maryland muskrats showing (top) corpora lutea (28 \times) and (bottom) mature follicle (28 \times)

tions which were examined under a dissecting microscope to determine the extent of follicular development (Fig. 2).

Uteri without visible embryos were examined for placental scars. If scars were present, their numbers were recorded for each uterine horn. All uteri were measured for total length. If a specimen had been collected at a time close to or during the breeding season, the uterus was flushed with a small amount of water and the exudate was examined under the microscope for the presence of sperm.

If a female was visibly pregnant, an embryo count was made for each uterine horn. Each embryo was removed from the uterus, cleaned of the placenta, weighed, and measured for crown-rump, tail, and hindfoot lengths.

Age determination

The age of each specimen was determined according to the technique described by CHEIH et al. (1974). This method involved removal of the first upper molar for examination of root development and enamel patterns. Individuals were then placed into 1 of 6 categories, ranging from juveniles, approximately 2 months of age, to adults over 2 years of age. For the purposes of this study, older animals were classified as either a subadult (5 to 9 months old) or as an adult (over 9 months of age). Ages of kits less than 2-months old were estimated by size comparisons made with weight and length curves developed by ERRINGTON (1939) and ERICKSON (1963).

Occasionally it became necessary to use other criteria in conjunction with the amount of tooth development to reliably discern the age of adult specimens. For example, depending upon the season of its capture, a female specimen could be aged through examination of uterine morphology (ERRINGTON 1963). In the few cases the zygomatic breadth was examined and a specimen having a measurement greater than 40.0 mm was categorized as an adult (ALEXANDER 1951).

Physiological and metabolic indices

Four indices were used to compare some of the physiological and metabolic responses of the 3 muskrat populations to their respective environmental conditions.

The first index was a subjective estimation of internal body fat. At the time of necropsy, each muskrat was assigned to 1 of 4 categories based on the amount of fat found around the kidneys, gastro-intestinal areas and reproductive organs. An arbitrary scale of 1 to 4 was used: 1. no fat around any of the organs, 2. small amounts of fat around any or all of the above organs, 3. moderate amounts of fat around a majority of the organs, 4. large amounts of fat around a majority of the organs.

The second was an adrenal index which may be useful as an indicator of environmental stress on a mammalian population (CHRISTIAN and DAVIS 1956; CHAPMAN et al. 1977).

For this study, total body weight was replaced by total body length because total body weight of many muskrats obtained from local trappers was unavailable (see NELSON and CHAPMAN 1982). Use of total body length increased sample sizes. A linear regression was performed to correlate body weights (total and carcass separately) with total body length. There was a 83.4 % correlation of total length with total weight and an 83.3 % correlation of carcass weight with total length. These results were considered satisfactory for the purposes of this study.

The computational formula for the adrenal index is:

$$\text{Adrenal Index} = \frac{\text{paired adrenal weight}}{\text{total body length}} \times 10^4$$

Index calculations were multiplied by 10^4 to obtain values between 1 and 10.

ALEKSIUK and FROHLINGER (1971) recorded organ weights of muskrats collected over a 12-month period and put them on a per gram body weight basis. The correlations obtained suggested that the hypoxic conditions of the winter environment encountered in muskrat habitat may cause a compensatory increase in lung and heart weights and the relatively low kidney and liver weights that they found might be attributed to a suppression of metabolic activities (such as growth) during the harsh conditions of winter.

A similar set of indices were calculated for this study. Heart and kidney weights were divided by total body lengths and seasonal comparisons were made to see if the hypotheses of ALEKSIUK and FROHLINGER (1971) could be substantiated by data from Maryland muskrat populations. Metabolic indices are defined as:

$$\text{Heart Index} = \frac{\text{heart weight (g)}}{\text{total body length (mm)}} \times 10^3$$

$$\text{Kidney Index} = \frac{\text{weight of right kidney (g)}}{\text{total body length (mm)}} \times 10^3$$

Indices were multiplied by 10^3 to obtain values that fell between 1 and 10.

Statistical analysis

Statistical analyses were performed on a Univac 1108 computer, using the Statistical Package for the Social Sciences (SPSS).

External morphological measurements and skull measurements were all analyzed by breaking down the variables into the following sub-sample groupings: 1. sex, 2. age: subadult or adult, 3. geographical region: Western Maryland, Central Maryland, or Eastern Shore.

A 2-way analysis of variance was performed on each age group to detect statistical differences due to sex and/or region. When regional effects were detected (without significant interaction factors), a 1-way analysis of variance in conjunction with a Duncan's Multiple Range test was used to detect significant differences.

For the physiological indices of the adult muskrats, a 3-way analysis was performed. Each index was analyzed for effects from the following 3 variables: 1. sex, 2. geographical region: Western Maryland, Central Maryland, or Eastern Shore, 3. season: Winter, January through March; Spring, April through June; Summer, July through September; Fall, October through December.

Duncan's Multiple Range Test and Student's T-test were used to determine significant differences between index means. By definition, only fall and winter indices could be analyzed for the subadults.

Results

Morphology

There were significant differences in external morphology found among the adult muskrats taken from the 3 physiographic regions of Maryland (Tables 1 and 2). In general, muskrats from Western Maryland (*O. z. zibethicus*) were significantly larger than those from the Eastern Shore (*O. z. macrodon*).

Table 1

Means and standard deviations (g and mm) of morphological measurements found to be significantly different for adult muskrats captured from three physiographic regions of Maryland

	Western Maryland	Central Maryland	Eastern Shore
Total Weight	1382.2 ^a ± 175.1 (25)	1201.0 ^a ± 134.3 (8)	1100.7 ^b ± 154.2 (22)
Carcass Weight	1116.5 ^a ± 136.3 (15)	1048.6 ^a ± 179.8 (9)	877.2 ^b ± 66.5 (14)
Total Length	596.0 ^a ± 32.5 (41)	585.1 ^a ± 29.4 (15)	559.8 ^b ± 24.4 (37)
Tail Length	241.6 ^a ± 17.4 (41)	242.1 ^a ± 19.4 (15)	224.2 ^b ± 14.8 (37)
Hindfoot Length	82.3 ^a ± 3.1 (41)	81.7 ^a ± 4.7 (15)	76.6 ^b ± 4.6 (37)
Nasal Width	9.64 ^a ± 0.51 (38)	9.24 ^b ± 0.61 (15)	9.21 ^b ± 0.56 (34)
Length of Tooth Row	17.19 ^a ± 0.63 (38)	16.94 ^a ± 0.91 (15)	16.60 ^b ± 0.71 (34)
Bulla Length	12.53 ^a ± 0.54 (38)	12.32 ^a ± 0.62 (15)	11.95 ^b ± 0.49 (34)

Values with the same superscripts are not significantly different ($p > .05$). Sample sizes in parenthesis

Physiological and metabolic indices

Lowest body fat values were found in the warmer months of spring and summer, with the highest values seen in the fall and winter. Throughout the year, adult males tended to have slightly higher body fat indices as compared to adult females. Eastern Shore muskrats maintained larger body fat deposits as compared to muskrats from the other 2 physiographic regions (Fig. 3).

Male adrenal weights fell to a low during the summer and then peaked to their highest point during the fall (Fig. 4). The Eastern Shore adult males were found to have significantly lower adrenal indices as compared to those of the males trapped from Western and Central Maryland (Fig. 5).

Table 2

Means and standard deviations (g and mm) of morphological measurements found to be significantly different for subadult muskrats captured from three physiographic regions of Maryland

	Western Maryland	Central Maryland	Eastern Shore
Total Weight	1105.3 ^a ± 154.2 (23)	—	833.3 ^b ± 125.0 (3)
Carcass Weight	823.0 ^a ± 134.5 (42)	876.8 ^a ± 145.9 (21)	697.3 ^b ± 149.3 (22)
Total Length	560.8 ^a ± 24.9 (62)	565.8 ^a ± 30.4 (21)	508.7 ^b ± 41.8 (24)
Tail Length	232.5 ^a ± 14.1 (59)	238.6 ^a ± 30.4 (22)	203.4 ^b ± 21.0 (24)
Hindfoot Length	82.1 ^a ± 2.2 (59)	83.9 ^a ± 3.4 (21)	76.5 ^b ± 4.9 (24)
Basilar Length	56.47 ^a ± 1.84 (57)	57.51 ^a ± 2.51 (22)	55.27 ^b ± 2.63 (24)
Nasal Width	8.93 ^a ± 0.53 (60)	8.67 ^b ± 0.57 (22)	8.17 ^c ± 0.52 (24)
Nasal Length	20.30 ^a ± 1.05 (60)	20.20 ^a ± 1.34 (22)	19.24 ^b ± 0.92 (24)
Length of Tooth Row	16.26 ^a ± 1.02 (60)	15.99 ^a ± 0.59 (22)	15.49 ^b ± 0.67 (24)
Bulla Length	11.97 ^a ± 0.51 (58)	11.94 ^a ± 0.58 (22)	11.43 ^b ± 0.53 (24)

Values with the same superscripts are not significantly different ($p > .05$). Sample sizes in parenthesis

When the adrenal index data from the adult females of all 3 study areas were grouped together, a seasonal trend resulted that was similar to the one found for the combined sample of the adult males. The lowest adrenal index values of the females occurred in the winter, a significant increase was observed in the spring weights, summer weights were

Fig. 3. Mean seasonal body fat indices for adult muskrats from three physiographic regions of Maryland. Numbers are sample sizes

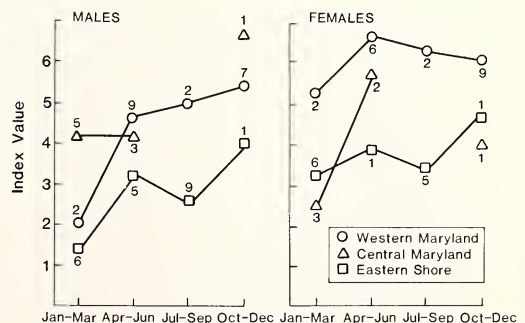
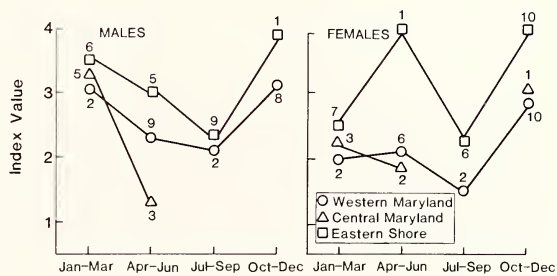


Fig. 4 (left). Seasonal variations in mean adrenal indices for adult muskrats from Maryland. Vertical bars represent standard deviations, vertical lines represent ranges, and numbers are sample sizes. — Fig. 5 (right). Mean seasonal adrenal indices for adult muskrats from three physiographic regions of Maryland. Numbers are sample sizes

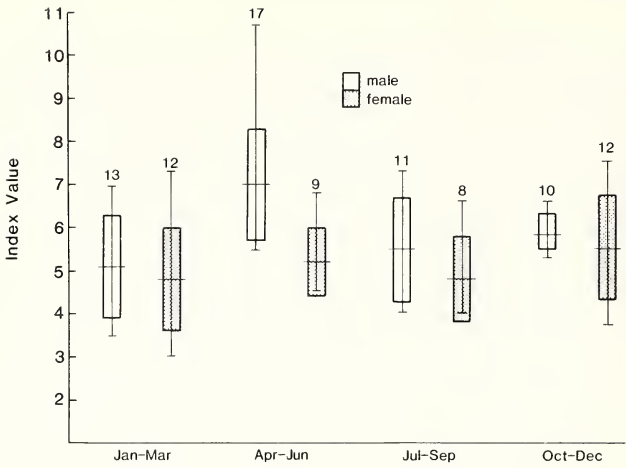


Fig. 6. Seasonal variation in mean kidney indices for adult muskrats from Maryland. Vertical bars represent standard deviations, vertical lines represent ranges, and numbers are sample sizes

quite reduced, and then another peak in adrenal weights followed in the fall (Fig. 4). Eastern Shore and Central Maryland adult females had significantly lower adrenal indices than did the Western Maryland females (Fig. 5).

There were no statistically significant effects due to sex, season or region in the heart indices of Maryland muskrats. Significant effects due to sex and season were found for the kidney indices calculated for the adult Maryland muskrats. Adult males showed distinctly higher values in the spring season.

There was no seasonal variation in the indices of the adult females. Except for the spring season, adult male and adult females did not differ in their kidney indices (Fig. 6).

Reproduction

Male reproductive cycle

Testicular weights and lengths of adult male muskrats increased from winter to spring and peaked in weight in May. After May, a gradual decrease occurred which continued over the summer months into the fall when the lowest values were recorded in October. Weights began to increase after October (Table 3). Epididymis weights of adult males increased from winter to spring, however, the pattern was not as distinct as that of the testicular

Table 3

Means and standard deviations of testicular weights and lengths and epididymides weights of adult male Maryland muskrats

	Testicle weight g	Testicle length mm	Epididymides g
January	1.0 ± .3	19.3 ± 2.3	.18 ± .07 (6)
February	1.4 ± .2	21.5 ± 1.9	.25 ± .04 (4)
March	1.8 ± .5	22.7 ± 1.5	.29 ± .13 (3)
April	2.0 ± .6	22.6 ± 1.9	.34 ± .17 (5)
May	2.3 ± .2	23.0 ± 2.2	.31 ± .11 (4)
June	2.1 ± .3	22.6 ± 2.1	.35 ± .08 (7)
July	1.9 ± .4	22.5 ± 0.7	.34 ± .25 (2)
August	1.5 ± .6	21.5 ± 2.7	.26 ± .07 (8)
September	1.6 ± 0	22.0 ± 0	.35 ± .00 (1)
October	0.4 ± .1	15.5 ± .7	.06 ± .04 (2)
November	0.5 ± .2	16.2 ± 1.4	.11 ± .04 (6)
December	0.6 ± .4	17.5 ± 3.5	.08 ± .04 (2)

Numbers in parenthesis are sample sizes

Table 4

Means and standard deviations of testicular weights and lengths and epididymides weights of subadult male Maryland muskrats

	Testicle weight g	Testicle length mm	Epididymides g
September	0.06 ± .02	8.0 ± 1.7	.02 ± .00 (3)
October	0.08 ± .02	8.0 ± 0.0	.03 ± .01 (3)
November	0.08 ± .04	7.8 ± 1.4	.03 ± .02 (22)
December	0.44 ± .22	13.3 ± 2.8	.08 ± .04 (7)
January	0.7 ± .6	14.8 ± 3.7	.11 ± .09 (18)
February	1.0 ± .6	17.4 ± 3.8	.15 ± .08 (5)
March	1.3 ± .5	18.3 ± 3.0	.18 ± .03 (4)

Numbers in parentheses are sample sizes

dimensions. The largest epididymis weights were recorded in June and July and the lowest weights in October (Table 3).

Sperm was found in the testes of at least some portion of the adult male Maryland populations every month of the year except October.

Testicular weights of the subadults showed a continuous increase from September through March. Testicular lengths recorded for the months of September, October and November were all similar (approx. 8 mm) for the subadult males, however, a marked increase was seen in the December lengths. This increase continued until March (Table 4). Epididymis weights of subadults showed a continuous increase from September until March.

Subadult males captured in September, October and November did not show evidence of spermatogenesis. In December, however, 1 of the 7 young males trapped in the western area had sperm in its testes but not in its epididymis. Of the subadults obtained in January, all of the eastern shore males and 17 central area males showed evidence of spermatogenesis. The only subadult male taken from the western region in January did not have sperm in either organ. In February, the single male taken from the western area and 75 % of the eastern male subadults had sperm. All the Eastern Shore subadult males trapped in March were in breeding condition.

Female reproductive cycle

Ovarian weights of adult female muskrats were relatively low during the winter months of January and February, and began to increase in March (Table 5). The highest weights were recorded in April. From April through July the weights remained high, while a general decrease was observed from July through August into fall until the lowest values were recorded in November. The only adult female collected in December was from the western area, and this animal showed an unusually high ovarian weight, due to a large fluid-filled cyst on its left ovary.

Adult ovarian lengths did not show a distinct seasonal variation. Lengths ranged between 8.5 to 10.5 mm; the highest in July and the lowest recorded in August (Table 5).

Adult uterine horn lengths varied with season. The shortest lengths for adult females were observed in winter, these increased in the spring and largest lengths occurred in the summer months. Lengths dropped again in the fall (Table 5).

Fall trapped subadult females showed low ovarian weights; the values were similar for September, October and November. Two animals caught in the western region in December had high mean ovarian weights. The subadult ovarian weights increased from January to March. Subadult ovarian lengths showed an increase from January to March

Table 5

Means and standard deviations of ovarian weights and lengths and uterine horn lengths of adult female Maryland muskrats

	Ovarian weight g	Ovarian length mm	Uterine Horn length mm
January	.05 ± .01	9.2 ± 1.8 (5)	January–March 77.8 ± 9 (9)
February	.04 ± 0.1	9.3 ± 1.8 (4)	
March	.06 ± .04	8.7 ± 2.3 (3)	
April	.13 ± .07	9.5 ± 1.0 (4)	April–June 97.3 ± 18 (8)
May	.09 ± 0	9.0 ± 0 (1)	
June	.09 ± .03	9.5 ± 1.9 (4)	
July	.09 ± .03	10.3 ± 0.6 (3)	July–September 100.7 ± 23 (7)
August	.06 ± .03	8.5 ± 1.3 (4)	
September	.08 ± 0	10.0 ± 0 (1)	
October	.06 ± .03	9.0 ± 1 (3)	October–December 93.3 ± 9 (11)
November	.04 ± .01	8.9 ± 1.1 (8)	
December	.13 ± 0	10.0 ± 0 (1)	

Numbers in parentheses are sample sizes

Table 6

Means and standard deviations of ovarian weights and lengths and uterine horn lengths of adult female Maryland muskrats

	Ovarian weight g	Ovarian length mm	Uterine Horn length mm
January	.03 ± .01	6.9 ± 1.2 (7)	January–March 63.4 ± 10 (9)
February	.04 ± .04	7.0 ± 3.6 (3)	
March	.06 ± .02	8.0 ± 1.0 (3)	
August	.04 ± 0	6.0 ± 0 (1)	August–September 72.0 ± 17 (2)
September	.03 ± 0	7.0 ± 0 (1)	
October	.02 ± 0	5.4 ± 3.0 (5)	
November	.02 ± .02	6.7 ± 1.3 (20)	October–December 63.1 ± 8 (26)
December	.05 ± .03	8.5 ± 0.7 (2)	

Numbers in parentheses are sample sizes

which paralleled the increase seen in ovarian weights. Late summer and early fall values varied, but a distinct increase in lengths was seen from a low in October to a relatively high value in December. Uterine horn lengths were very similar for the fall and winter trapped subadult females (Table 6).

Eighteen females collected between August and December had placental scars distinct enough to count. A total of 163 scars were counted from 12 western region females, resulting in an average of 13.6 scars per female. A total of 58 scars were recorded for 5 central region females, all trapped between October and February (average 11.6). One female taken on the eastern shore in October had 13 scars. Four females trapped in Western Maryland were found to have an average of 6.0 distinct corpora lutea.

The number of litters produced in a season for western Maryland muskrats was estimated by dividing the mean number of placental scars found per female (13.6) by the average litter size taken from corpora lutea counts (6). Thus an average of 2.3 litters per female was calculated. This suggests that Western Maryland females usually produce 2 litters a season, with some bearing 3 litters.

Discussion

Morphology

The external skeletal measurements taken on muskrats indicate that Western and Central Maryland muskrats are significantly larger in body size than the muskrats inhabiting Maryland's Eastern Shore (Tables 1 and 2).

The ranges of the 2 subspecies *O. z. macrodon* and *O. z. zibethicus* merge within the borders of Maryland (PARADISO 1969). The muskrats inhabiting the Piedmont Plateau area of the state are reportedly an intergrade of the 2 subspecies. However, our data suggest that muskrats inhabiting the central Piedmont Plateau region are more closely related to Western Maryland muskrats in skeletal characteristics.

The data describing body size of Maryland muskrats could be used to support the hypothesis of BOYCE (1978) who used the geographic variability seen in the morphology of North American muskrats to provide evidence that "seasonal variation in resource availability results in selection for large body size". BOYCE (1978) contends that in highly seasonal environments there are periods where food depletions occur and mortality from famine is imminent. Natural selection might favor those individuals that could survive periods of resource shortage through increased growth rates and larger body size.

The muskrats found in the distinctly seasonal climate of the mountainous areas of Western Maryland are significantly larger than muskrats located in the milder region of the Eastern Shore of the Chesapeake Bay. This suggests that there may be a climatic influence on body size as BOYCE (1978) suggests.

Salinity is another environmental factor that must be considered in explaining the regional disparity in body size found for Maryland's muskrat populations. The larger and heavier Western and Central Maryland muskrats are found in freshwater areas. Even within the same subspecies there is evidence that average muskrat body size may be reduced in populations located in environments of increased salinity. Total body weights of Eastern Shore muskrats are quite similar to weights recorded for members of the same subspecies (*O. z. macrodon*) trapped from the coastal marshes of North Carolina (WILSON 1956). In contrast, weight and skeletal measurements recorded for the specimens of *O. z. macrodon* taken from the freshwater Dismal Swamp (HOLLISTER 1911) are distinctly larger than comparable measurements taken for the Eastern Shore muskrats.

DOZIER et al. (1948) observed lower average body weights for groups of muskrats trapped from brackish and highly saline Eastern Shore marshes as compared to animals obtained from fresh or slightly brackish areas. In addition, the more saline marshes consistently showed lower annual harvests, DOZIER et al. (1948) attributes the lower productivity of the saline areas to a lack of preferred and quality vegetation.

Physiological and metabolic indices

Adult females from both Western Maryland (*O. z. zibethicus*) and the Eastern Shore (*O. z. macrodon*) had adrenal indices that were significantly higher than the indices of the males from these 2 regions. Sexual dimorphism showing heavier adrenal weights for females has been reported for other rodent species including the Norway rat (LATTANZIO and CHAPMAN 1980), the cotton rat (GOERTZ 1965) and the house mouse (LIDICKER 1966), and is considered a "morphophysiological standard" (SHVARTS 1975).

When the adrenal index data from this study were combined for the 3 regional populations and partitioned by season, it was found that only during spring female muskrats showed a statistically significant higher index than the males. This indicates that the sexual dimorphism seen in adrenal weights may be related to breeding activity (GOERTZ 1965).

Throughout the year, *O. z. zibethicus* tended to show higher adrenal indices as compared to *O. z. macrodon*. Harsh environmental conditions could be contributing to the higher *O. z. zibethicus* adrenal weights. However, another environmental factor, sodium levels may also be affecting the adrenal morphology of Maryland muskrats. Several past studies have shown that certain herbivorous mammals living in sodium deficient environments have increased adrenal weights (BLAIR-WEST et al. 1968; SCOGGINS et al. 1970). The percentage of the adrenal cortex occupied by the zona glomerulosa increases in sodium depleted animals (SCOGGINS et al. 1970) as response to an intensified production of mineralocorticoids (WEEKS and KIRKPATRICK 1976). The Eastern Shore marshes are replete with sodium, whereas the inland environment of Western Maryland is most probably generally low in soil and water sodium levels. The heavier adrenal weights seen in the Western Maryland muskrats may be a physiological adaptation to a sodium deficient environment.

Along with a increase in lung weights, hematocrits, and hemoglobin counts, ALEKSIUK and FROHLINGER (1971) found a relative increase in the heart weights muskrats trapped during the winter months in Manitoba, Canada. They hypothesized that this increase was due to the hypoxic environmental conditions that muskrats must endure in Canada when the water resources are covered with ice.

The Maryland muskrats did not show a similar increase in heart weights during the winter months. Even in the mountainous regions of Western Maryland, where winter is relatively severe, muskrat heart indices remained unchanged throughout the year. These results indicate that the environmental conditions, particularly ice cover, affecting Maryland muskrats may not be stressful enough to induce the effects seen in the Canadian muskrats. It is also possible that some other physiological or environmental factors were involved in producing the seasonal enlargements of hearts observed by ALEKSIUK and FROHLINGER (1971).

In this study, adult male Maryland muskrats showed significantly larger kidney indices in the spring season. Females did not show a season variation (Fig. 6). The enlargement of the males' kidneys occurred when the reproductive season had begun and testicular weights and lengths were at their peaks. It has been demonstrated in the laboratory mouse that endogenous and exogenous androgen treatments cause cellular enlargement in the kidneys (BARDIN and CATTERALL 1981). Increased androgen levels may be affecting the kidney size of male Maryland muskrats at the beginning of the breeding season. While ALEKSIUK and FROHLINGER (1971) did not statistically analyze their data on relative kidney weights, there was a obvious increase in kidney weights seen in the warmer months of their study period.

Reproduction

Male reproductive cycle

BEER and MEYER (1951) found that Wisconsin male muskrats had maximum testicular weights in May and minimum weights in October. This pattern was also in Maryland muskrats. During the breeding season (February through September), the testicular weights and lengths of Maryland muskrats exceeded those of males trapped in east Tennessee (SCHACHER and PELTON 1975). However, from October through January, Maryland males showed much smaller testicular measurements than the east Tennessee males. This may be explained by the fact that east Tennessee winters are milder than the winters of Maryland. BECKER (1970) explained that seasonal temperatures can modify testicular development in muskrats. Decreased temperatures inhibit testicular growth and spermatogenesis while relatively higher temperatures may enhance testicular development.

ERRINGTON (1963) indicated that male muskrats that had testicles weighing greater than 1 g were capable of reproductive activity. In this study, Maryland male muskrats had

testicles weighing as little as 0.464 g that contained copious amounts of sperm. However, it is not known if these males were behaviorally capable of breeding.

FORBES (1942) found that the majority of male muskrats trapped on the Eastern Shore from early January to early October had large quantities of sperm in their testes, none of the 24 males trapped between 24 October and 26 November showed evidence of spermatogenesis. Only 3 of 24 males captured between 27 November and 11 December exhibited spermatogenic activity.

Female reproductive cycle

BEER and MEYER (1951) and SCHACHER and PELTON (1975) found that the ovarian weights of female muskrats in Wisconsin and east Tennessee, respectively, started to increase from February to March. A similar increase was observed in Maryland muskrats. The ovarian weights of Maryland females peaked in April when corpora lutea were first observed. SCHACHER and PELTON (1975) found maximum ovarian weights in April and May, but BEER and MEYER (1951) did not see maximum weights until May.

Geographic and climatological conditions are probably the major determinants of the initiation and duration of the breeding season of muskrats (ERRINGTON 1963). Populations of muskrats inhabiting more southerly latitudes of the United States breed throughout the year, with peak reproductive activity occurring in the winter months. A winter breeding regime has been reported for muskrats in Louisiana (O'NEIL 1949), and the coastal marshes of Texas (LAY 1945).

In more northern latitudes, reproductive activities are confined to the spring and summer months. McLEOD and BONDAR (1952) reported that the breeding season of muskrats in Manitoba, Canada, is from May to August. This timetable was also found for populations in New Brunswick (PARKER and MAXWELL 1980). In Wisconsin, MATHIAK (1966) observed first litters being born in early April, however, both he and BEER (1950) found that peak litter production of Wisconsin muskrats occurs from May to July. ERICKSON (1963) reported that muskrats in New York state initiate their breeding in late March, however, most litters are produced from late April to early August.

ERRINGTON (1963) points out that litter size may be influenced by the genetics of a subspecies. Most authors that have studied *O. z. ziethicus* reported a mean litter size of 6 or 7 young (ERICKSON 1963; DONOHUE 1966; STEWART and BIDER 1974; PARKER and MAXWELL 1980). An average litter size of 6 was found for the populations of *O. z. zibethicus* inhabiting Western Maryland.

The corpora lutea count of 4.9 used to determine the litter size of Eastern Shore muskrats trapped for this study is consistent with litter size data reported in past investigations on *O. z. macrondon*. HARRIS (1952) stated that an average of 4 or 5 embryos for 10 wild females trapped from Eastern Shore marshes, as well as an average litter size of 5 for 25 muskrat houses opened in mid-May. From his concurrent study on captive Eastern Shore muskrats, SMITH (1938) found an average of 3 young for the 27 litters born in cages.

A latitudinal gradient seen in muskrat litter sizes could be considered evidence for a climatic influence on muskrat productivity (SCHACHER and PELTON 1975). Muskrats located in more northern areas, where breeding is confined to the spring and summer seasons, seem to produce larger litters than muskrats found in southern climates where reproductive activity extends throughout most of the year (ERRINGTON 1963; SCHACHER and PELTON 1975). A similar set of arguments could be used to explain the different litter sizes of the Eastern Shore and Western Maryland muskrat populations. Because of the severe winters and potentially high mortality rates encountered in the mountains of Western Maryland, there may be a selective advantage for resident muskrats to produce more young in a breeding season through increased litter sizes.

In Louisiana, where muskrat populations breed year round, O'NEIL (1949) reported that females usually produce 5 or 6 litters per year. In more northern regions of North

America, a general pattern of 2 or occasionally 3 litters per season is more common (ERICKSON 1963; DONOHOE 1966; STEWART and BIDER 1974). In some northern areas 4 litters are reported, but only infrequently (OLSEN 1959). In Maryland, we calculated 2 to 3 litters are produced annually.

Evidence of precocial breeding was found to occur in the Eastern Shore muskrat populations, but not in the Western and Central Maryland populations. Precocial breeding would probably be expected to occur more frequently in the Eastern Shore region because the climate of that area is considerably milder, and the breeding season could easily be extended into late fall or early winter. However, as MATHIAK (1966) pointed out for Wisconsin muskrats, the extent of precocial breeding is probably not significant enough to affect population growth. SMITH et al. (1981) found little precocial breeding in a heavily harvested muskrat population in the Quinnipiac River estuary, Connecticut.

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Zusammenfassung

Morphologische und physiologische Eigenschaften von Bisamratten aus verschiedenen Gebieten Marylands

Zwischen 1977 und 1979 wurden 210 Bisamratten (*Ondatra zibethicus*) in drei Teilen des Bundesstaates Maryland (USA) gefangen. Die folgenden physiographischen Gebiete waren in der Stichprobe vertreten: die Alleghani- und Piedmonthochebenen sowie die atlantische Küstenebene. Zwei Unterarten der Bisamratte kommen in Maryland vor, nämlich *O. z. zibethicus* im westlichen Staatenteil und *O. z. macrodon* an der Küste. Exemplare aus dem zentralen Teil des Staates, die bisher als Zwischenform betrachtet wurden, wiesen nach Ergebnissen dieser Untersuchung starke Ähnlichkeiten mit der westlichen Unterart auf. Die Gewichte und Längen der Hoden von erwachsenen Männchen erreichten die höchsten Werte im Mai. Die Hoden und Nebenhoden mancher Männchen enthielten in jedem Monat des Jahres Samen außer im Oktober. Während der Ranzzeit lag der Beginn der Spermatogenese bei erwachsenen Männchen einige Monate früher als bei den subadulten Tieren.

Die ersten Anzeichen der Brunst wurden gegen Ende März beobachtet, im Oktober hörte sie bei den von der Küste stammenden Weibchen auf, bei den Tieren aus dem westlichen Teil des Staates wahrscheinlich einige Wochen früher. Die Anzahl der Embryonen und Gelbkörper wiesen auf durchschnittliche Wurfgrößen von 6.0 und 4.8 für Tiere des westlichen bzw. östlichen Teiles des Staates hin. Entsprechend betrug die Anzahl der Plazentanarben 13.5 und 11.6 bei Weibchen aus den betreffenden Gegenden.

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Zur Taxonomie der Gattung *Rattus* (Rodentia, Muridae)

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Abstract

On the taxonomy of the genus Rattus (Rodentia, Muridae)

Investigated the relations between 12 taxa of murine rodents of the genus *Rattus* and similar forms according to the distribution of some morphological characters and differences in proteins demonstrated by gel electrophoresis. Both methods had some major results in common:

1. *Maxomys surifer* has to be excluded from the genus *Rattus*, if *Bandicota* is recognized as a separate genus.
2. The delimitation of the genus *Bandicota* and of the species included is correct for the forms considered.
3. The degree of kinship with *Rattus rattus* decreases in the following order: *Rattus tiomanicus*, *R. argentiventer*, *R. exulans* or *R. norvegicus*, *R. berdmorei*, *Bandicota*, *Maxomys surifer*.

The results for the Australian *Rattus villosissimus* are controversial. The electrophoretic distance to typical *Rattus* is great, whereas the morphological distance seems to be smaller.

Einleitung

Die Gattung *Rattus* gehört trotz fortschreitender Präzisierung und Einschränkung auch heute noch zu den artenreichsten und unübersichtlichsten Taxa der Muriden. So werden nach WALKER (1975) etwa 570 benannte Formen hierzu gerechnet. ELLERMAN (1941) vereinigte hier eine Vielzahl nicht besonders spezialisierter Muriden mit Gewichten zwischen 50 und 500 g aus Afrika, Asien und Australien. Später wurden zunehmend Arten ausgegliedert und in eine eigene Gattungen gestellt, so alle ursprünglich zu *Rattus* gezählten afrikanischen Muriden (MISONNE 1969) und die Gattungen *Niviventer* und *Maxomys* in Asien (MUSSEY 1981).

Auf der anderen Seite sind auch die Beziehungen von *Rattus* zu den übrigen Muriden unklar. So glaubt NIETHAMMER (1977), daß stark wühlende südasiatische Muriden, die nur in Grabanpassungen von *Rattus* stark abweichen, nämlich *Bandicota* und *Nesokia*, nähere Verwandte von *Rattus* sind, da andere Merkmale wie Karyotyp und Alveolenmuster erhebliche Ähnlichkeiten zeigen.

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