MUSKRAT PREDATION ON ENDANGERED FRESHWATER MUSSELS IN VIRGINIA

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Abstract: We assessed foraging by muskrats (*Ondatra zibethicus*) on freshwater mussels at North Holston Ford (NHF), North Fork Holston River (NFHR), by comparing the mussel assemblage in fall 1981 to shell middens collected seasonally between 1980 and 1981. Nearly 30,000 adult mussels of 16 species occupied NHF in 1981. Abundance of most prey species in shell middens was generally related to the relative abundance of that species at the site, although 2 mid-size species were selected and the smallest species was not consumed in proportion to availability. From 1979 to 1986, 28% of endangered shiny pigtoes (*Fusconaia cor*) were consumed; other species lost 8.6–24.3% of their demes to muskrat predation. Shell middens collected quarterly at 12 sites in the NFHR and Clinch River for 1 year (1984–85) contained 623 (13%) endangered mussels. Muskrats appeared to prey on mussels and Asiatic clams (*Corbicula fluminea*) during most of the year, with the greatest consumption at sites with the largest mollusk assemblages. The Asiatic clam is the dominant molluscan prey of muskrats in the Clinch River. Muskrat predation appears to be inhibiting the recovery of endangered mussel species, and likely placing some demes of endangered pigtoe mussel species in further jeopardy of extirpation from sites in both rivers.

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The upper Tennessee River drainage supports remnants of a diverse molluscan fauna with species, endemic to the Cumberland Plateau region, that are endangered (U.S. Fish and Wildl. Serv. 1983). Within the Clinch, Powell, and Holston rivers of southwestern Virginia are approximately 50 species of freshwater mussels, including 9 endangered species. Hydropower dams and industry along the Tennessee River and its tributaries have permanently altered water quality and siltation levels, and eliminated riverine habitat from large sections of the rivers. The impact of these activities on mollusks has been documented (Stansbery and Clench 1974, Dennis 1981, Ahlstedt 1984), and chronic effects of the physical and chemical alterations on rivers continue to be detrimental to the survival and recovery of endangered mollusks. However, ecological interactions such as competition and predation have not been assessed. The exotic Asiatic clam, a potential competitor with mussels, invaded the upper Tennessee drainage in the mid-1970's and is now abundant and widespread (Bates and Dennis 1978). Predation on mussels by muskrats was described >100 years ago (Apgar 1887) but subsequent information has been anecdotal or derived from European studies (Evermann and Clark 1920;

Brander 1955*a,b*; Akkerman 1972). Because recovery plans for endangered mollusks emphasize the preservation of extant populations and the need to assess factors contributing to their decline, an assessment of muskrat predation is pertinent to recovery goals.

The muskrat is herbivorous, although foods and feeding habits vary with habitat, season, and availability (Butler 1940). Perry (1982) identified species of emergent vegetation and macrophytes as the major food items of muskrats in the southeastern United States. However, muskrats in streams and canals eat a greater variety of foods, including animal matter, than muskrats in marshes (Schwartz and Schwartz 1959). Consumption of animal matter is generally considered incidental and insignificant in the diet, although aquatic invertebrates can be important during winter (Bailey 1937, Stearns and Goodwin 1941). The feeding ecology of river populations of muskrats in the southeastern United States is not documented.

Our study was conducted concurrently with life history investigations on freshwater mussels in Virginia (Zale and Neves 1982*a,b*), and was prompted by predation on mussels by muskrats at study sites. The deposition of shells in numerous, discrete middens at feeding sites provided evidence that the muskrat was the major predator on adult mussels and an excellent opportunity to describe and quantify mollusk consumption by muskrats. Our objectives were to quantify the consumption of mollusks by muskrats at river sites in southwestern Virginia, determine possible selectivity of prey species, and evaluate the potential threat of muskrat predation to endangered mussel populations.

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STUDY AREAS AND METHODS

The NFHR was a fourth-order stream originating in Bland County, Virginia, and flowed southwesterly for 218 km before joining the South Fork near Kingsport, Tennessee. Although the NFHR has been substantially degraded from Saltville, Virginia downstream to its confluence with the South Fork (Hill et al. 1974), the upper watershed and its fauna was relatively undisturbed (Stansbery and Clench 1974). The Clinch River was a slightly larger stream that originated in Tazewell County, Virginia and flowed 563 km southwest to its original confluence with the Tennessee River. Only 322 km of its original length remained free-flowing, upstream of Norris Reservoir, Tennessee. The occurrence of a high diversity of mussels (45 species) and 8 endangered species of mussels makes the Clinch River valuable for the preservation and recovery of mussels.

During frequent visits to NHF, NFHR during 1979 we collected shells of mussels preyed upon by muskrats. North Holston Ford at river mile (RM) 86.9 is well-defined, bordered upstream by a large pool and downstream by a ford used by vehicles in summer. Lack of mussels and muskrat activity immediately above and below NHF provided the opportunity to quantify the mussel assemblage and middens from a discrete location.

From September 1979 through July 1981, we collected muskrat middens bimonthly. Muskrat burrows and feeding sites were located by wading along both river banks. Feeding sites occurred at burrow openings, undercut banks, stumps, logs and snags; middens were collected consistently at the same locations among sample dates. Growth of beds of water willow (*Justicia americana*) in the summer provided additional cover for feeding sites and locations for midden collections. Mussels consumed by muskrats usually had characteristic scratches on the periostracum of 1 valve, and had unbroken valves attached by the hinge ligament. Evermann and Clark (1920:50–51) briefly describe how muskrats open and consume mussels. Mussel shells in middens were cleaned, identified, counted, and measured for total length (TL).

The mussel assemblage at NHF was sampled in August–September 1981 to determine species composition and densities at the site. A stratified random sampling design was used: 10 samples along each of 6 transects were taken with a 0.5-m^2 quadrat sampler (Kitchel 1985:21). Substratum within each of the 60 quadrats was removed to a depth of roughly 10 cm. Mussels were identified, measured, and returned with substrata to the quadrat location. Population estimates and variances for each species at the site were calculated by the area-density method (Everhart et al. 1975). Total area of the streambed at NHF, from mean length and width measurements taken at mid-summer flow conditions, was 2,930 m^2.

To assess seasonal changes in species of mussels eaten and species selection by muskrats, we pooled midden data for several dates to increase sample sizes of less abundant species. Three seasons were defined based on when middens were deposited: summer (Jun–Aug 1980), fall (Sep–Oct 1980), and winter (Nov 1980–Feb 1981). Statistical tests were conducted on 8 species that were collected in sufficient numbers ($n > 50$)for analysis. We used a Chi-square contingency table to test whether proportions of these species varied among the 3 seasons and secondary Chi-square statistics to test for differences between each pair of midden groups. For each species that appeared to differ between pairs of midden groups ($P < 0.05$), a 2- × 2- Chi-square statistic (with Yates' correction for continuity) was computed as a third level test, with all other species pooled. Seasonal differences in the size (TL) of each species consumed were checked with a Kruskal-Wallis test, followed by a rank analogue of Fisher's protected least significant difference to identify which seasons differed.

The procedure of Marcum and Loftsgaarden (1980) was used to test for random selection of mussels by muskrats, with pooled quadrat data (fall 1981) representing prey available and pooled winter middens (1980–81) as prey consumed. If significant ($P < 0.05$) selection of a species occurred, a prey-selection index value (C) was computed (Pearre 1982). Size selectivity/species by muskrats was determined by Wilcoxon rank sum statistics, comparing lengths of mussels available and lengths of those consumed.

Visits to NHF were continued at least quarterly from 1981 to 1986 to collect additional middens and to estimate mortality in the endangered shiny pigtoe deme (semi-isolated local population) due to muskrat predation from 1979 to 1986.

To evaluate the possible significance of muskrat predation at other sites with endangered mollusks, 1 additional site on the North Fork and 10 sites on the Clinch River were sampled quarterly for 1 year: October, March, May, and July, 1984–85. The additional site on the North Fork was in Smyth County upstream of Saltville at RM 85.0. Sites on the Clinch River were in Scott County between the Virginia–Tennessee border and Dungannon, Virginia at the following Clinch River Mile (CRM) locations: CRM 206.9, 210.8, 211.1, 212.0, 212.8, 219.1, 223.5, 234.0, 235.1, and 236.4. Sites were selected based on the presence of ≥1 endangered mussel species and the occurrence of pools or substrata unsuitable for mussels immediately upstream and downstream of the site. Each site was roughly 100 ± 20 (SD) m in length except for 2 sites (CRM 211.1 and 223.5) on the Clinch River. These 2 sites were 200 ± 20 m long and were selected because of large mussel populations and known habitat for 4 endangered species (Ahlstedt 1984). Sites were first visited in June 1984 to delineate the proposed sampling area and to remove any midden material accumulated during previous months. Because of high water conditions in the spring of each year, some exposed shell middens were dispersed. At several sites, dead trees or boulders in the river served as feeding sites at appropriate water levels. Some shells of mussels consumed on these structures undoubtedly fell into the water and were dispersed downstream prior to our sampling. Collections of middens therefore provided a minimum estimate of predation by muskrats at all sites.

Muskrat middens from sites on the Clinch River and NHF were processed similarly. Species, numbers, and sizes were summarized for each site and sample date. Midden data from 2 sites with the highest levels of predation on endangered species were evaluated further for size and cohort composition. The 2 most commonly consumed endangered species at NHF and CRM 223.5, shiny pigtoes and fine-rayed pigtoes (*F. cuneolus*), were partitioned into size classes and assigned ages based on previously plotted age-length equations (Moyer 1984:118, Kitchel 1985:72) to determine what cohorts of these demes were most affected by predation.

RESULTS

The mussel assemblage at NHF was composed of 16 species. Ten species were collected in quadrat samples, with computed deme sizes (N ± 95% CI) as follows: Cumberland moccasin (*Medionidus conradicus*), 10,353 ± 779; Alabama rainbow (*Villosa nebulosa*), 5,762 ± 589; mountain creekshell (*Villosa vanuxemi*), 3,516 ± 559; Tennessee clubshell (*Pleurobema oviforme*), 2,960 ± 556; fluted kidneyshell (*Pty-*

Table 1. Number and median length (mm) of common mussel species in muskrat middens and in quadrats at North Holston Ford, North Fork Holston River, Virginia, 1980–81.

Size group Species	Middens				Quadrats	
	n	Summer	Fall	Winter	*n*	Fall
Small						
Cumberland moccasin	405	38.6	39.7	39.7	106	37.2
Mountain creekshell	303	40.2	41.7	40.2	36	35.9
Medium						
Alabama rainbow	454	47.9	48.7	43.4[a]	59	31.7
Tennessee clubshell	329	53.3	49.4[a]	55.0	30	44.4
Shiny pigtoe	278	48.7	46.6	45.3[a]	15	50.6
Slabsided pearly	57	49.4	56.6	51.0	16	49.6
Large						
Fluted kidneyshell	237	60.8	60.3	60.2	21	57.6
Kidneyshell	102	65.7	62.8	66.5	10	48.2

[a] Median length differed significantly ($P < 0.05$) for this season (Kruskal-Wallis test).

chobranchus subtentum), 2,051 ± 480; slabsided pearly (*Lexingtonia dolabelloides*), 1,565 ± 468; shiny pigtoe, 1,465 ± 374; kidneyshell (*Ptychobranchus fasciolaris*), 977 ± 314; wavy-rayed lampmussel (*Lampsilis fasciola*), 391 ± 217; and pheasantshell (*Actinonaias pectorosa*), 391 ± 217 (Kitchell 1985:35). The Tennessee pigtoe (*Fusconaia barnesiana*), pocketbook (*Lampsilis ovata*), slippershell (*Alasmidonta viridis*), elktoe (*Alasmidonta marginata*), purple lilliput (*Toxolasma lividus*), and fluted shell (*Lasmigona costata*) were collected only in muskrat middens. Sixty quadrat samples were inadequate to collect the less abundant species at this site. The Cumberland moccasin was the smallest and most abundant species; conversely, the pheasantshell was the largest but least abundant species of those collected in quadrat samples. An estimated 29,428 ± 7,031 adult mussels were present in NHF in fall 1981.

The 10 species quantitatively sampled were assigned to 3 length groups based on their maximum adult sizes at this site: small species <50 mm (Cumberland moccasin, mountain creekshell), medium-size species between 50 and 70 mm (Alabama rainbow, shiny pigtoe, Tennessee clubshell, slabsided pearly, wavy-rayed lampmussel), and large species >70 mm (fluted kidneyshell, kidneyshell, pheasantshell). Relative abundance of some species in these size groups differed significantly ($P < 0.05$) in muskrat middens among the 3 seasons evaluated. The proportion of shiny pigtoes in the summer middens was significantly higher than that in fall middens, but its frequency of occurrence in winter middens was similar to that in summer and fall. A smaller proportion of the Cumberland moccasin and fluted kidneyshell was present in winter compared to summer and fall middens, whereas the Tennessee clubshell was significantly less abundant in summer middens. Percent composition for all other species in shell middens did not differ among seasons.

Median lengths of 3 of the 8 common species differed significantly among seasons (Table 1). Specimens of the shiny pigtoe and Alabama rainbow were smaller in winter middens, and the Tennessee clubshell was smaller in fall middens. In general, however, muskrats preyed upon the same species and sizes of mussels in summer, fall, and winter.

Results of the Chi-square test for random selection were highly significant ($P < 0.001$) and indicated that muskrats were selecting or avoiding 3 species during the winter. There was selection for 2 mid-size species, shiny pigtoe and Tennessee clubshell ($P = 0.006$), and avoidance of the smallest species, Cumberland moccasin ($P = 0.0001$). The other 5 species were consumed in proportion to their abundance at the site ($P < 0.05$).

A minimum of 4,815 mussels was eaten by muskrats at NHF between 1979 and 1986 (Table 2). Predation was highest in 1980, when nearly half of the total number were consumed. No middens were found in 1982 and 1983, a period when local residents reported muskrat trapping in this river reach. Shell middens were collected again in subsequent years, although in lower numbers. About 75% of the shells in middens for the 8-year period consisted of the 5 small and mid-size species. Ranking species from most

Table 2. Numbers of mussels collected in muskrat middens at North Holston Ford, North Fork Holston River, Virginia, 1979–86. No shell middens were found in 1982–83.

Mussel species	Yr						Total
	1979	1980	1981	1984	1985	1986	
Cumberland mocassin	186	416	32	32	205	1	872
Alabama rainbow	192	472	58	10	116	13	861
Mountain creekshell	221	313	36	15	76	11	672
Tennessee clubshell	83	287	86	11	91	19	577
Shiny pigtoe	172	280	33	11	40	9	545
Fluted kidneyshell	99	247	27	3	23	1	400
Tennessee pigtoe	53	155	15	5	26	1	255
Kidneyshell	57	86	17	13	22	4	199
Wavy-rayed lampmussel	38	118	2	9	17		184
Slabsided pearly	24	62	4	11	32	1	134
Pheasantshell	21	49	13	3	8	1	95
Pocketbook	1	8	4	2			15
Slippershell	1	2					3
Elktoe		1					1
Purple lilliput					1		1
Fluted shell		1					1

to least abundant in middens was similar to the ranked abundance of species at NHF. In general, muskrat predation was related to prey abundance, particularly for the small and midsize species. However, predation on the shiny pigtoe and wavy-rayed lampmussel was higher than expected. During the 8-year period, 545 endangered shiny pigtoes were consumed from the deme at NHF. Similarly, 184 lampmussels were eaten, or 47% of the adults of this species present at NHF in 1981. Other species lost from 8.6 to 24.3% of their demes to muskrat predation. Overall, an estimated 16.4% of the adult mussels at NHF were eaten by muskrats between 1979 and 1986.

Muskrat predation on mollusks at sample sites on the NFHR and Clinch River was highly variable. Highest predation was recorded at CRM 223.5, where 2,080 mussels, including 353 endangered specimens, were removed. Overall, 13% of the mussels eaten at this site were (in order of decreasing abundance) endangered species: fine-rayed pigtoe ($n = 280$), shiny pigtoe ($n = 68$), birdwing pearly (*Conradilla caelata*) ($n = 4$), and dromedary (*Dromus dromas*) ($n = 1$). At NHF, shiny pigtoes in shell middens ranged from 30 to 60 mm TL and 5 to 23 years old; ages 10–19 (46–55 mm) were consumed most often (59%). At CRM 223.5, fine-rayed pigtoes in middens ranged from 35 to 85 mm TL and ages 6 to 35. The age 10–15 cohorts (56–65 mm) were consumed with greatest frequency (54%) at this site.

Between October 1984 and October 1985, 32,873 Asiatic clams and 4,709 mussels were consumed by muskrats at the 12 sites on the NFHR and Clinch River; 623 of these mussels were endangered. Predation on the Asiatic clam was extensive at most sites on the Clinch River, ranging from 267 to 14,442 individuals at the 10 sites. These clams ranged from 12 to 32 mm in length and were often the only species in shell middens. Clam middens were often scattered along streambanks, partly covered with silt, or slightly dispersed by previous water level fluctuations. Total numbers of clams collected in definable shell middens therefore are a minimum estimate of the numbers consumed and probably underestimate the importance of this species in the muskrat diet. Other mollusks occasionally found in middens were snails (*Io fluvialis* and *Anculosa subglobosa*).

DISCUSSION

The extensive collections of shell middens and quantification of the prey assemblage at NHF provide evidence of some size-selective feeding on mussels by muskrats. Selection against the smallest and most abundant Cumberland moccasin mussel may possibly relate to reduced vulnerability or to optimal foraging by muskrats. Small size may reduce the visibility or recognition of this species in the river bottom, although our quantitative sampling and the collection and consumption of smaller Asiatic clams by muskrats in the Clinch River refute this explanation. Selection for some medium-size and against the largest large-size species may indicate that optimal foraging behavior and prey handling time influence prey selection by muskrats (Schoener 1971). Large mussels are burrowed in the river bottom and may be more difficult to extricate, transport, and open than smaller mussels. Time and energy expense of prey capture and handling would therefore be minimized by the preference for mussels of intermediate length. However, without feeding experiments to define the selection process (e.g., Stein 1977), no conclusive explanation for the observed foraging behavior can be presented.

The estimate of shiny pigtoes at NHF in fall 1981 (n = 1,465 ± 374) was made after the greatest predation had occurred in 1979 and 1980. The deme of shiny pigtoes in 1979 was therefore ±1,917 adults, when individuals consumed in 1979–80 are added to the estimate of adults in 1981. Muskrats therefore removed an estimated 28% of the adults between 1979 and 1986. Unfortunately, no estimates of juvenile (≤3 yr) abundance or recruitment could be made because of the difficulty in sampling and identifying juveniles. Previous studies indicate that natural mortality during the first year of life is high (Howard 1922, Neves and Widlak 1987), and annual mortality rates of adult mussels range from 5 to 19% (Negus 1966, Zale 1980). A concurrent study on the life history of the shiny pigtoe at NHF found low fertilization of eggs in females, unlike other species at this and other sites (Kitchel 1985). Results of this latter study suggest that the viability of this deme may already be in jeopardy, exacerbated by muskrat predation on adult (reproducing) cohorts.

Freshwater mollusks are an important item in the diet of muskrats in the upper NFHR and Clinch River, Virginia. If our site-specific data are extrapolated to all reaches in these 2 rivers, then this predator-prey relationship is of ecological and biological significance to predator and prey populations. Present range of the shiny pigtoe in the upper NFHR is roughly 7 km. Shiny and fine-rayed pigtoes are found at >60 sites along 268 km of the Clinch River in Virginia and Tennessee (Ahlstedt 1984). Based on these ranges and that of the muskrat, we estimate that several hundred shiny pigtoes from each river and >1,000 fine-rayed pigtoes from the Clinch River are consumed each year. Because these endangered mussels nearly always occur at sites with an abundant and diverse assemblage of other mussel species, and muskrat predation seems to be common and most frequent at these sites, predation on endangered populations is likely to continue at roughly the same level of intensity.

Differences in the quantity of mollusks consumed among sites were probably due to variations in mollusk or muskrat abundance, and possibly the availability of more traditional foods such as aquatic or riparian vegetation. Evermann and Clark (1920) reported that lake-dwelling muskrats switched to mussel predation in late autumn after vegetation died, but we observed the opposite trend. Shell middens were infrequent or absent at most sites in winter and were most common from spring through fall. It appeared that at least some muskrats preyed on mussels for most of the year, with the highest predation rates recorded at sites with the greatest mussel abundance.

The Asiatic clam, introduced into the Tennessee River drainage in 1959 (Sinclair and Ingram 1961), is now the most abundant bivalve in the Clinch River. Muskrats fed more frequently on this clam than the native bivalves at all sites in the river, probably because of its greater abundance and presence in all riverine habitats (Ahlstedt 1984). Quantitative sampling for mollusks at CRM 223.5 recorded a mean density of 162 Asiatic clams/m^2 in 1985. Results of an earlier mollusk survey (Neves et al. 1980) and shell middens we collected suggest that muskrats have switched molluscan prey, from mussels in the 1970's to principally Asiatic clams now. No Asiatic clams were collected in the upper NFHR until 1983; this species is now common within this river reach and should become an important prey item for muskrats in this river as in the Clinch River.

MANAGEMENT IMPLICATIONS

The general decline in most mussel populations in the upper Tennessee River drainage has been attributed to water quality degradation and habitat loss (Bates 1962, Fuller 1974). Predation by muskrats is viewed as a secondary mortality factor. Distribution of endangered mussels in these rivers is now disjunct, with demes isolated in refugia least disturbed by human activities. Sites with diverse and abundant assemblages of mussel species in combination with suitable habitat requirements appear to sustain resident muskrats that threaten to reduce demes of endangered pigtoes to the point of extirpation. Historically, muskrat predation probably had little, if any, effect on healthy mussel populations widely distributed throughout each river system. However, similar or even lower levels of predation today pose a serious threat to endangered species already reduced to low abundance and isolated locations because of environmental degradation. Available information indicates that annual recruitment in mussel populations is typically low and sporadic (Neves and Widlak 1987). Population stability and viability is seemingly sustained by the many cohorts and occasionally good year-classes, as are other mollusk populations (Tompa et al. 1984). Consequences of continued predation on endangered mussel populations cannot be predicted without knowledge of minimum viable population sizes, values difficult to obtain even for intensively studied species (Lacava and Hughes 1984). However, muskrat predation is retarding species recovery at minimum, and likely contributing to further declines of these endangered populations throughout the Tennessee River drainage. Removal of muskrats by fur trappers or specifically for predator control, particularly at sites identified as important refugia for endangered mussels, would likely assist in maintaining those demes and be in agreement with the goals and objectives of recovery plans for these species (U.S. Fish and Wildl. Serv. 1983, 1984).

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