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## The natural history of the marsh rice rat, *Oryzomys palustris*, in eastern Virginia

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### ABSTRACT

The marsh rice rat, *Oryzomys palustris*, is a common rodent in tidal marshes of eastern Virginia, including those on the barrier islands. It also is present in grassy old fields in upland habitats in the coastal plain and parts of the piedmont of Virginia. This report summarizes what has been learned in recent decades about the population biology of this species in Virginia, including aspects of behavior, density, diet, distribution, genetics, habitats, mammal associates, and reproduction.

**Keywords:** barrier islands, Chesapeake, Eastern Shore, old fields, tidal marshes

### INTRODUCTION

The marsh rice rat, *Oryzomys palustris*, is a medium-sized, long-tailed rodent (Figure 1) found in tidal marshes and nearby grassy uplands in the southeastern US. It is semi-aquatic (Esher et al., 1978; Forsy & Dueser, 1993) and readily takes to water to escape danger and to catch some animal components of its diet. In Virginia, coastal saline marshes on the Eastern Shore, lower Chesapeake Bay, and south to Back Bay National Wildlife Refuge are primary habitat. *O. palustris* also is present in brackish marshes and wetlands along the big rivers flowing into the Chesapeake Bay, but the details of its inland distributions, especially on the western shore of the Chesapeake Bay, are not well known. Along the James River, its distribution extends past the fall line west of Richmond (Pagels et al., 1992), and the rice rat is present at Fort A. P. Hill, just south of the Potomac River near Fredericksburg (Bellows et al., 2001a).

In the mid-to-late 1990s, five Old Dominion University graduate students conducted field studies in seaside tidal marshes owned by The Nature Conservancy (TNC) in Northampton County on Virginia's Eastern Shore. Monthly trapping provided capture-mark-recapture (CMR) information on the small mammal community in two marshes, one located south of the village of Oyster and the other east of Townsend. In each marsh, a row by column grid was established so that density (number per hectare) could be determined and information on habitat, movement, and dispersion could be recorded. Part of each grid was flooded each day but the landward parts were flooded only during storm and monthly high tides; these flooding regimes also determined the

types of vegetation on the grid as well as the foods available for the small mammals living in these habitats.



Figure 1. Adult rice rat showing typical coloration and long tail. Photo purchased from Alamy.

A Fitch live trap (Rose, 1994), held by a rubber band to a Styrofoam™ float, was placed at each coordinate on the grids, tethered to a numbered stake with a monofilament line. This system allowed the trap to move up and down with the tide, yet remain within a meter of the stake. Each month, usually during the new moon, bait (bird seed and sunflower seeds) was placed in the traps in the late afternoon and the traps were checked the next two mornings. Each captured mammal was given a numbered ear tag, weighed (g), its reproductive status evaluated, and then it was released at the point of capture. Traps were locked open between periods of trapping. The objective was to evaluate the lives of marked (tagged) individuals, i.e., to examine their changes in reproductive condition, their movement, the vegetation they ate and in which they were captured, their lifespans, and other aspects of their biology. The longest field study, 23 consecutive months (Bloch & Rose, 2005), produced the best information on density for both *Oryzomys palustris* and its codominant species, the meadow vole (*Microtus pennsylvanicus*).

Monthly samples of adult rice rats for necropsy were taken from nearby seaside marshes; these provided information on stomach contents (diet), body measurements, and details of reproduction, such as litter size and seasonal changes in reproductive organs (Rose & Dreelin,

2011). The stomach contents were analyzed for details of plant and animal foods eaten during different months and seasons (Rose & McGurk, 2006). (The skeletons were sent to the National Museum of Natural History). The frequency and distribution of herbaceous and woody plants on the grids were evaluated and the structure of the vegetation was measured; this information made it possible to determine which plants were selected or avoided, and to relate use by the rice rats to the structure and composition of the habitat (Sowell 1995).

In the early 2000s, two 1-ha CMR grids were established in southern Chesapeake, both also on TNC properties. These former agricultural fields were two years removed from cultivation so the vegetation of both was dominated by early-colonizing grasses and sedges. As is typical of agricultural fields in this region, the highly organic soils are made arable by a century-old series of deep and shallower ditches. Winter flooding is common in these fields and as a result many wetlands plants, such as sedges, rushes, and spikerushes, were present in slight depressions or near the ditches in these grassy old fields. Each grid was trapped monthly for 3-4 years until shrubs and saplings mostly replaced the herbaceous vegetation, after which seasonal trapping was used to monitor the decline and disappearance of old field small mammals (including rice rats), and the appearance of forest-dwelling mammals. In all, the small mammal community on each grid was evaluated for 8 or more years (Rose et al., 2018).

## GENERAL CHARACTERISTICS

The marsh rice rat (hereafter “rice rat”) is medium in size, with adult body mass of 40-80 g. The sexes are similar in size, with males often somewhat larger. The dorsal pelage is gray with flecks of brown and white, and the tapered tail, almost as long as the combined length of head and body, is dark above and lighter below, with no clear line separating dark from light. The belly fur is nearly white, as are the toes. Thus, the coloration of this semi-aquatic rodent blends well with its background whether seen from above or from below. The toes, four on front feet and five on hind feet, are long and supple, enabling rice rats to climb into emergent vegetation during times of flooding, to catch insects, or to enter birds’ nests to eat eggs or nestlings, as they sometimes do (e.g., Kale, 1965). The rice rat has no webbing on its toes and no flattening of the tail, features seen in other native semi-aquatic rodents, such as muskrat (*Ondatra zibethicus*) and beaver (*Castor canadensis*).

## DISTRIBUTION

*Oryzomys* is a South American genus with only three species reaching into the US, *O. couesi* just barely into southern Texas and *O. argentatus* in southern Florida. *O. palustris* has a broader US distribution, with populations along the Gulf Coast and southeastern states, with coastal populations in the mid-Atlantic region extending as far north as Delaware (Schantz, 1943) and southern New Jersey (Wolfe, 1982). Inland populations often are associated with the Mississippi and Ohio rivers and their larger tributaries; some even extend to southern Illinois (Hoffman et al., 1990; Eubanks et al., 2011). In Virginia, the rice rat is found throughout the coastal plain, including the barrier islands (Dueser et al., 1979) and in the piedmont as far west as Cumberland County, about 65 km west of Richmond (Pagels et al., 1992). Rice rats are common in the freshwater marshes of the Potomac River at George Washington Birthplace National Monument in Westmoreland County (Painter & Eckerlin, 1993), and Bellows et al. (2001b) trapped a small number of rice rats in upland forest in Caroline County, south of Fredericksburg.

Much remains to be learned about its distribution along the rivers and marshes of piedmont Virginia.

Rice rats are the most numerous small mammal on the barrier islands of Virginia, being found on 9 of 11 islands trapped by Dueser and his colleagues (Dueser et al., 1979) and later known from 21 of 24 islands (Loxterman et al., 1998). Experimental studies revealed rice rats were able to swim from one island to another, crossing water barriers as great as 300 m (Forys and Dueser, 1993), likely explaining why rice rats are present on many more islands than poorer swimmers, such as meadow voles or white-footed mice (*Peromyscus leucopus*).

### ONTOGENY AND REPRODUCTION

Early studies of growth and development date from those of Svihla (1931), who collected rice rats in the bayou country of coastal Louisiana and raised them in the laboratory to learn about their diets, mating behavior, gestation length, and growth and development of young. Like the young of most rodents, rice rats are born naked, blind, and helpless. The weight of neonates ranged from 2.35 – 4.0 g, with an average of 3.14 g. The eyes open at 6 days and young are weaned at 11 days (Svihla, 1931). Vibrissae (whiskers) are present at birth, perhaps to assist in finding a nipple. Neonates from pregnant females collected at Chincoteague Island, Virginia, were slightly heavier (3.7 g), with head and body length of 42 mm and tail of 19 mm (Hamilton, 1946). At two days, weight was about 5 g, the back was becoming darker, and each youngster was active and vocalizing. By four days, the young could crawl, the back was well haired, with shoulders dark gray washed with fulvous (reddish), but the belly was still naked. Average weight was 6.3 g, head-body length was 52 mm, and the tail 30 mm (Hamilton, 1946). At six days, the body length was 59 mm, and the body was well furred with grizzled brownish gray above and white belly. By eight days, each young, now with juvenile pelage, was very active and fled the nest if disturbed. With a mean weight of 8.9 g, the average head-body length was 62 mm and the tail 41 mm. By 10 days, the young ate solid food, had an average weight of 10.2 g, a head-body length of 69 mm, and tail of 47 mm (Hamilton, 1946). Young are weaned at 11-13 days, after which they gain 1.0 to 1.5 g per day until about three weeks of age. After that, growth rate slows so juveniles become subadults (40 g) at two months and are full grown (50-80 g) at four months (Hamilton 1946). As adults, the head-body length is only slightly longer than the tail length. It is likely that slow growth continues as long as the animal lives; few rice rats live as long as 12 months in Virginia (Bloch & Rose 2005).

Details of litter size and reproductive indices of both sexes for rice rats from eastern Virginia are derived from the 103 rice rats whose stomachs were analyzed for diet, plus 26 other rice rats from nearby tidal marshes, and 41 rice rats collected on Fisherman Island in January and February 1982. No rice rats were caught for necropsy in January-February 1996 (when population density was very low on the contemporaneous grids trapped by Bloch & Rose [2005]) so the samples from Fisherman Island (7 km from Townsend) provided information on reproduction during January-February.

Females with embryos were collected from April to October, and there was almost no evidence of breeding activity in either sex during the other 4-5 months (Rose & Dreelin, 2011). The average litter size for the 16 pregnant females was 4.63 and litter size did not vary among months, between females having one or multiple litters, or between subadult and adult females.

The smallest pregnant female weighed 34 g and because embryonic bumps in the uterus do not appear until about day 11 or 12 of pregnancy, this female probably weighed about 25 g when inseminated.

Fertility in male rodents is determined by the presence of convolutions (rather than loops) in the cauda epididymides (Jameson, 1950), the structures in which mature sperm are stored. Convolutions were present in males 2-4 weeks before and after the April-October breeding season of females (Rose & Dreelin, 2011), a pattern often seen in seasonally breeding rodents in temperate latitudes (e.g., Bergstrom and Rose, 2004; Rose and Gaines, 1978). Both testes and seminal vesicles showed substantial regression with the approach of winter, an energy-saving adaptation that is especially valuable for rodents with a tropical origin (such as *O. palustris*) but now living in temperate environments. The average mass (weight) of paired testes, expressed in mg/10 g of body mass, was greater in spring and summer (50.9 to 113.7) than during November (14.1) and December (7.3 - Rose & Dreelin, 2011). The values for the males from Fisherman Island from January 1982 were  $11.73 \pm 8.2$  (SE) but increased to  $51.17 \pm 4.6$  (SE) for February 1982, when growth of testes foretells the coming breeding season. The seminal vesicles (also in mg/10 g of body mass) showed similar patterns: greater in spring and summer (36.7 to 139.6) than in November (13.9) and December (2.5 - Rose & Dreelin, 2011). Thus, in eastern Virginia, rice rats are seasonal breeders with almost no adults breeding during the 4 or 5 coldest months.

In other locations, such as near Raleigh, NC, pregnant rice rats were collected from March-November so the reproductive period was longer there (Brimley, 1923) than on the Eastern Shore. In a study near Galveston, Texas, reproductive indices of both sexes showed evidence of moderate reproduction in winter, in both wetland and upland plant communities (Kruchek, 2004). Overall, higher proportions of breeders lived in wetlands than in uplands. In coastal Louisiana, breeding ended in October of one year but continued throughout the next winter (Negus et al., 1961). In a tidal marsh of southern Delaware, pregnant and lactating females were observed from March to late summer, which represents the length of the breeding season at this northernmost location on the Atlantic Coast (Edmonds and Stetson, 1993).

## ECOLOGY

**DENSITY:** The density of *Oryzomys palustris* populations fluctuated during the annual cycle in the Eastern Shore tidal marshes, with highest densities achieved mostly in October or into early winter (Bloch & Rose, 2005: Figure 1; Rose & March, 2013). Density averaged  $9.3 \pm 0.8$  (SE) individuals/ha and never exceeded 15/ha at Oyster, but averaged  $48.2 \pm 5.6$  per ha at Townsend. The peak density at Townsend was greater than 60/ha in October 1995 but was  $\geq 80$ /ha the next autumn, extending from September 1996 through February 1997 (The average densities of meadow voles were similar on both grids across the study, so these two rodents were truly co-dominants in these seaside tidal marshes). The average residency times for rice rats were similar at the two sites:  $3.78 \pm 0.6$  (SE) months (Oyster) and  $4.40 \pm 0.3$  (SE) months (Townsend - Bloch & Rose, 2005). The maximum residency (or trap-revealed lifespan) of *O. palustris* was 12 months at Oyster and 18 months at Townsend. Overall, average body mass did not differ between sexes, sites, or among seasons, but individuals at Townsend were heavier than those from Oyster in summer and autumn, but not in winter or spring (Bloch & Rose, 2005). The sex ratio was male-biased (214:148) at Townsend but not at Oyster (38:23). The largest proportion of males in breeding condition at Townsend was observed in summer and lowest proportion in winter, but

females had similar proportions in every season. At Oyster, small sample sizes prevented an analysis of seasons but 18 of 19 males and 15 of 16 females were potential breeders in summer (Bloch & Rose, 2005).

Densities in other studies also are highly variable, perhaps due in part to different methodologies. In 0.64 ha grids trapped monthly on Assateague Island, Virginia, the highest densities, of 20-30/ha, also were seen in late autumn (Cranford & Maly, 1990). But Porter and Dueser (1982), who trapped along transects across Assateague Island, from beach dunes to tidal marshes, caught only 5 rice rats in tidal marshes. In the wetlands near Galveston, Texas, high densities of 11-13/ha were recorded in summer and autumn but in the nearby uplands, high densities of only 4-5/ha were seen in winter and spring (Kruchek, 2004). Densities in Louisiana were similar: mostly 4-6/ha but ranging up to 18/ha in mid-winter (Negus et al., 1961).

**HABITATS:** In southeastern Virginia, rice rats can be expected in all habitats dominated by grasses and sedges, their principal foods in our region. They are more predictably found in salt and freshwater tidal marshes than in upland old fields, but dispersing rice rats can be found in almost any habitat in Virginia, including (rarely) in upland forests (e.g., Pagels et al., 1992; Bellows et al., 2001b). In upland communities in southern Chesapeake, rice rats were early colonizers of grassy fields but disappeared from one grid after three years, perhaps due to the numerical dominance by meadow voles and hispid cotton rats (Rose et al., 2018). On the other grid, where the transition from old field to forest was much slower, they persisted in low numbers to the end of the 9-year study.

In the tidal marshes of the Eastern Shore, the dominant plants are *Salicornia europaea* (glasswort) in the intertidal zone and *Spartina patens* (salt cordgrass), *Baccharis halimifolia* (saltbush) and *Phragmites australis* (common reed) in the landward area (Sowell, 1995). The herbaceous vegetation at Steelman's Landing (Townsend) was both taller and denser than the vegetation at Oyster, but Oyster had a higher proportion of woody vegetation. Based on trapping results, rice rats moved significantly farther into the open marsh in summer than they did in the cool months, and they used areas with less dense vegetation compared to areas used by meadow voles, especially in summer (Sowell, 1995).

**COMMUNITY COMPOSITION:** In the Eastern Shore tidal marshes we found equal numbers of meadow voles and rice rats, plus much smaller numbers of white-footed mice, house mice (*Mus musculus*), short-tailed shrews (*Blarina brevicauda*), and eastern mole (*Scalopus aquaticus*), the latter a rarity in live traps (Bloch & Rose, 2005; Rose and March, 2013). In the upland habitats of southern Chesapeake, other common species were hispid cotton rats (*Sigmodon hispidus*), eastern harvest mice (*Reithrodontomys humulis*), short-tailed shrews, and more rarely golden mice (*Ochrotomys nuttalli*), woodland voles (*Pitymys pinetorum*), and least shrews (*Cryptotis parva* – Rose et al., 2018).

**DIET:** Detailed information on diet is based on the rice rats collected in every month from Eastern Shore tidal marshes (Rose & McGurk, 2006). All 103 stomachs contained dicotyledonous plants and 82 percent had monocotyledonous plants in their stomachs, so plants were important dietary components in these habitats that were flooded twice each day. The principal dicots were glasswort (*Salicornia* sp.), a succulent that gets inundated each tidal cycle, and cattail (*Typha latifolia*) and saltbush (*Baccharis halimifolia*), both located farther landward and only inundated during storm or monthly high tides. The four commonly eaten monocots were salt grass (*Spartina alterniflora*), salt meadow hay (*S. patens*), panic grasses (*Panicum* sp.), and black needle-rush

(*Juncus roemerianus*). Of these, the last species can withstand the longest periods of inundation. The distribution and frequencies of these common plants in the of inundation. The distribution of tidal marshes were evaluated by Sowell (1995). In general, numbers of captured small mammals closely tracked the density of the vegetation: denser vegetation, more mammals.

Further, 61% of stomachs had crabs and insects and 38 percent had snails in the stomach (Rose and McGurk, 2006). The crabs were fiddler crabs (*Uca minax*) and the insects were a mix of grasshoppers, crickets, and other small soft-bodied arthropods. The common snail was the periwinkle, *Littorina irrorata*, which is attached to vegetation and often is stranded above the mud during low tide. The catholic diet of rice rats was evident because 38% of stomachs contained all five classes of food. Unlike the diet in other rice rat studies (e.g., Sharp, 1987), no fish were detected.

Eighty-four percent of stomachs had hairs but these seem likely to have been consumed during auto-grooming rather from eating other small rodents, such as *Mus musculus*, the house mouse, which is a common part of the small mammal community in Virginia tidal marshes. If house mice had been eaten by rice rats, some bone fragments or teeth would have been present in stomachs; none was found.

The heavy reliance on herbaceous vegetation in the diet of Virginia rice rats contrasts sharply with diets in other populations. For example, the diet of rice rats in tidal marshes near Galveston, Texas, was 65% aquatic organisms (mostly killifish, grass shrimp, fiddler crabs, periwinkles), 5% insects, and only 30% wetland vegetation (Kruchek, 2004). In the nearby upland, the diet shifted somewhat (40% aquatic organisms and 55% wetland plants), but still consisted heavily of animal foods.

Rice rats in Texas coastal prairies ate 90% or more animal foods in all seasons except summer, when animal foods dropped to 54%, and energy-rich dicots were 37%; the rest of the diet was 4% monocots and 5% dicot fruits (Kincaid and Cameron, 1982). Animal foods were mostly insects, including pupae in winter.

Rice rats in Georgia salt marshes were even more carnivorous, with some animals having almost 100% of stomach contents consisting of animal foods (Sharp, 1967). The animal foods were mostly insects and small crabs (*Uca* and *Sesarma*), plus larvae of the rice borer (*Chilo* spp), which rice rats had to extract from *Spartina* stems. When fed only plant foods in the lab, young adult rice rats lost weight whereas those on animal foods, or even grains, did not (Sharp, 1967). Rice rats certainly are opportunistic carnivores, eating eggs and nestlings of ground- or marsh-nesting birds (Brunjes & Webster, 2003; Kale, 1965; Nesmith & Cox, 1985; Post, 1981). Birds that nest in marsh grasses, reeds, or cattails are especially vulnerable. In one study, rice rats moved into a colony of nesting Boat-tailed Grackles near Tampa, Florida, where they destroyed many nests, eating eggs, nestlings, and twice even partially eating adult female grackles on the nest, resulting in the colony abandoning the site (Bancroft, 1986). In brief, rice rat diets are variable and probably tend heavily to animal foods when those are abundant.

**PREDATORS:** As with other small mammals, rice rats are prey for a host of avian and terrestrial predators. Wolfe (1982) lists many of these predators but that list has since been expanded to include bobcats (Tumlison & McDaniel, 1990). In Virginia, barn owls are major predators of rice rats, as revealed by studies of owl pellets collected on Fisherman Island (Blem & Pagels, 1973) and Presquile National Wildlife Refuge, 12 miles downriver from Richmond



(Jackson et al., 1976). Elsewhere, rice rats are major foods of owls, as expected for nocturnal mammals (Wolfe, 1982), and Northern Harriers (*Circus hudsonius*), which hunt by gliding just over the tops of grasslands or tidal marshes, are important predators too (Harris, 1953). We have no new information on predators of rice rats either in Northampton County but owls, red foxes (*Vulpes vulpes*), and feral cats (*Felis catus*) likely are important ones. In southern Chesapeake, a rice rat was among the six mammal species eaten by timber rattlesnakes (*Crotalus horridus* - Goetz et al. 2016).

**PARASITES:** Their omnivorous diet exposes rice rats to more parasites than infect herbivorous rodents, and indeed rice rats are host to many kinds of ecto- and endoparasites. In his examination of the parasites of rice rats in Florida, Kinsella (1988 and references therein) showed that although nematodes are common in rice rats from both fresh- and saltwater marshes, rice rats in saltwater marshes also have large burdens of trematodes, a class of parasites mostly absent in freshwater marshes. Little is known of the parasites of rice rats in eastern Virginia, except for being occasional hosts to the dog ticks (*Dermacentor variabilis*) and Gulf coast ticks, *Amblyomma maculatum* (H. Gaff, pers. comm.). Also, R. Eckerlin (pers. comm.) has collected the flea *Stenoponia americana* from a rice rat in Accomack County and the flea *Orchopeas leucopus* from a rice rat in the Dismal Swamp.

### BEHAVIOR

*O. palustris* is considered to be the most carnivorous rodent in eastern North America. Among US rodents, only grasshopper mice in the genus *Onychomys*, common in the semi-deserts of the Southwest, eat a higher proportion of animal foods than does the rice rat (Wilson & Ruff, 1999).

Auto-grooming is an important behavior, in part because when rice rats are in the water, groomed and oiled fur prevents water from reaching the body surface. Furthermore, the bubble of air around the outer fur of a diving rice rat provides insulation from the usually colder surrounding water. The observation that 84 percent of stomachs contained hairs (Rose & McGurk, 2006) supports the notion that auto-grooming is an important and potentially time-consuming behavior of everyday life for rice rats.

Several studies have examined the swimming ability of rice rats, starting with those in the lab by Esher and colleagues (Esher et al., 1978). In a study of rice rats on three islands on the Eastern Shore of Virginia, 11 rice rats of all sex and age categories swam from the smallest island (with the highest population density) to the larger islands across a saltwater gap of 50 to 300 m; none returned to the smallest island (Forys and Dueser, 1993). Bellows et al. (2001b) caught a rice rat in a minnow trap set in a beaver pond at Fort A. P. Hill, indicating its readiness to hunt for prey in shallow water.

At least four times I have caught one each of rice rat and cotton rat in a very full Fitch trap. (Fitch traps are multiple-capture traps and a second animal can enter by pushing up and slithering under the dropped door, now also being captured.) Because the rice rat is so pugnacious while being handled and the cotton rat so docile by comparison, I would have expected the rice rat to attack the larger cotton rat but in all cases, neither rat was injured.

Unlike other small mammals in our region, almost no rice rats are captured in late pregnancy, and few juveniles are trapped either. This indirect evidence suggests that pregnant and

lactating rice rats may alter their behavior, especially their foraging behaviors, in late pregnancy, perhaps about the time nests are built to hold the young and during early days of nursing their young. The details of peri-natal behaviors may be important to understand in evaluating the transmission of ticks and their associated diseases.

## GENETICS

Some research has been conducted on the genetics of rice rats from eastern Virginia. Forsy and Moncrief (1994) used two methods to evaluate gene flow among mainland rice rats and those from four nearby barrier islands by: (1) monitoring the movement of tagged, dispersing animals from one place to another and (2) using genetic information from 13 polymorphic loci of these rice rats. The results of the two methods were not congruent; the former method estimated dispersal at 0.75 migrants per generation whereas the indirect (genetic) method estimated 0.09 migrants per generation. The other genetic study (Loxterman et al., 1998) compared mainland and barrier island populations of *O. palustris* for their amounts of genetic variation. The populations of rice rats from nine islands had an average heterozygosity of 2.4% with 6.7% polymorphic loci. These levels of variation were greater than for rice rats from mainland populations, reflecting the higher levels of gene flow due to the ability of rice rats to move among islands.

## CONSERVATION STATUS

Nationally, *Oryzomys palustris* is a species of least concern (G5), except perhaps at the northern limits of its distribution in the Midwest (Illinois and Ohio) and on the East Coast, where populations might be moving northward in recent decades but recent surveys are lacking. In Virginia, the marsh rice rat is considered a species of Least Concern (S5).

## REMARKS

The name, *Oryzomys palustris*, is derived from the Latin genus for rice, *Oryza*, and the Latin name for mouse, *mys*. The name “*palustris*” in Latin means “marshy” or “swampy,” referring to these rodents being caught in rice fields of coastal South Carolina in the 1830s.

Much of the information in this report is based on the research conducted in partial fulfillment of requirements for M. S. degrees in the Department of Biological Sciences at Old Dominion University by Christopher P. Bloch, Erin A. Dreelin, John A. March, Allison L. Sowell, and Shannon Wright McGurk, all of whom conducted their research in tidal marshes in Northampton County. Numerous fellow graduate students assisted in this field research conducted on the Eastern Shore and in southern Chesapeake (the latter are coauthors in Rose et al., 2018). Thanks to Ralph Eckerlin for providing information on fleas he has collected from rice rats over the years. I am grateful to The Nature Conservancy for permission to use of their land for these ecological studies. These studies were conducted under permits issued by the Virginia Department of Game and Inland Fisheries (thanks, Shirl Dressler) and before the Old Dominion University Animal Care and Use Committee evaluated research proposals for the study of wild mammals in nature. We followed the guidelines for ethical conduct of field research on mammals as recommended by the American Society of Mammalogists, the latest of which is Sikes et al. (2016).

Since 2008, field research protocols have been evaluated and approved by the ODU Animal Care and Use Committee.

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