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The Population Dynamics of Two Rodents in Two Coastal Marshes in Virginia

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ABSTRACT

The communities of small mammals were evaluated for 13 months with capture-mark-recapture methods in two *Spartina-Juncus* marshes of the Atlantic coast in Northampton County, Virginia. Small mammals were trapped for three days each month using live traps placed on floats on two study grids. Two rodents were numerically dominant (~90% of small mammals) there: marsh rice rat, *Oryzomys palustris*, and meadow vole, *Microtus pennsylvanicus*. Monthly estimates of population density were greater for rice rats (peak: 45/ha) than for those of meadow voles (peak: 30/ha). Survival rates were generally low, especially for rice rats, indicating highly vagile populations. Both species had greatest breeding activity in spring and autumn, with lower rates in summer and winter. Sex ratios favored males in rice rats but were unity in meadow voles. Although marsh rice rats, being semi-aquatic and capable swimmers, are more highly adapted to living in flooded marsh environments, meadow voles can thrive there too.

INTRODUCTION

Two species of rodent, marsh rice rat, *Oryzomys palustris*, and meadow vole, *Microtus pennsylvanicus*, are dominant in the marshes of the coast and the nearby barrier islands in eastern Virginia (Bloch and Rose 2005, Cranford and Maly 1990, Dueser et al. 1979). These species have been frequently studied elsewhere, but rarely together because the meadow vole is a boreal species near its southern limit in eastern Virginia and *Oryzomys,* a tropical genus, is widespread only from coastal Delaware southward.

Early studies reporting the presence of the marsh rice rat in Virginia tidal marshes include Goldman (1918) on Wreck and Smith islands and Bailey (1946) on Wallops Island. Later, Paradiso and Handley (1965) found rice rats and meadow voles as the dominant marsh rodents in their survey of the small mammal fauna of the northernmost barrier island, Assateague Island. But the most complete survey of tidal marsh and island mammals was conducted in the mid-1970s by Dueser et al. (1979), who trapped on 11 islands; nine had marsh rice rats but only three islands also had meadow voles.

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All studies confirm the numerical dominance of marsh rice rats and, when present, meadow voles in the grass- and sedge-dominated tidal marshes.

Two studies used regular trapping on study grids to obtain density estimates of small mammals on barrier islands: Adkins (1980) in an Assateague Island marsh and Cranford and Maly (1990), on Wallops Island. Adkins (1980) found modest densities (10-15/ha) of both species in late autumn of two years with few or none of either species during the summer months. Cranford and Maly (1990) reported densities of 25 and 30/ha in two Novembers for rice rats but higher peaks in late winter (45 and 50/ha in March) for meadow voles. Later, Bloch and Rose (2005), also using capture-mark-recapture (CMR) methods on two study grids, report density estimates for both species in mainland tidal marshes in Northampton County, Virginia, with populations of both species fluctuating around a mean of 10/ha on one grid but on the second grid meadow voles had August-September peaks of 65 and 75/ha and rice rats had comparable densities but with peaks 3-4 months later. This paper describes the dynamics of populations of both species on the sites used by Bloch and Rose (2005) immediately after our study ended.

Meadow voles and marsh rice rats differ in two important ways: their diets and their activity periods. The meadow vole is considered a strict herbivore and the marsh rice rat an omnivore. Wolfe (1982) and others believe the marsh rice rat to be the second-most carnivorous North American rodent, behind the grasshopper mice (genus *Onychomys*) of the western US. However, a recent study of the diet of marsh rice rats in mainland marshes of Northampton County, Virginia indicates that local rice rat populations rely heavily on plant material throughout the year (Rose and McGurk, 2006), suggesting that Virginia populations may be more herbivorous than those living farther south (Negus et al., 1961; Wolfe, 1982). Regarding activity patterns, the marsh rice rat is strictly nocturnal, in part confirmed by being common in the diets of owls (e.g., Blem and Pagels 1973, Harris 1953, Jemison and Chabreck 1962), whereas meadow voles are intermittently active both day and night (e.g., Webster and Brooks 1981). Both species are similar in size, with fully adult meadow voles weighing 40-60 g and marsh rice rat adults slightly larger, up to 80 g.

The objectives of our study were to evaluate the population dynamics of the two species, including such features as density, survival rates, and reproduction, and to compare these patterns to those of other geographic populations. Our study lasted for a calendar year, from May 1994 through May 1995.

MATERIALS AND METHODS

The Study Sites

The two study sites were seaside marshes on Nature Conservancy property in Northampton County, Virginia. At Grid 1, located 4.4 km east of US Highway 13 at the southern edge of the village of Oyster, the vegetation was representative of the salt grass community. The dominant plants were *Spartina alterniflora, S. patens, Iva frutescens, Juncus roemarianus*, and on slightly higher ground, *Phragmites australis (communis*). Low-lying areas were subject to more frequent flooding, but most of the grid was on higher ground and remained relatively dry except during the high tides associated with the full moon. A thick ground cover of *S. patens* blanketed most of Grid 1. Grid 2 was located in a marsh locally known as Steelman's Landing, east of Townsend. A larger grid could be placed in this marsh, but the three rows closest to the mud flats had sparse vegetation and deeper water during the periods of daily flooding. Grid 2 flooded less often than did Grid 1 because it was farther away from the shoreline. But the surface was flatter and so it flooded more uniformly, and was usually wetter than Grid 1 when flooding did occur.

Trapping Procedures

After preliminary trapping in March 1994 confirmed the presence of both species, grids were established at both sites, and monthly trapping began in May 1994. Grid 1 was irregular in shape to conform to the area of herbaceous vegetation; its 75 trapping stations were placed at 10-m intervals (maximum of 7 rows, 14 columns) for an effective trapping area of 0.75 ha. Grid 2 had 130 traps on a 13 X 10 grid, for a trapping area of 1.3 ha. One Fitch live trap (Rose, 1994) was placed at each grid coordinate (= station). However, because of the daily flooding or danger of flooding, traps were strapped onto floats made of 31 cm by 21 cm rectangles of 1.6 cm thick insulation Styrofoam, using large rubber bands. Wire ties and monofilament line secured each float to the wooden stake marking each coordinate on the grid. Thus, during periods of flooding the float raised the trap, enabling a rodent to swim to the trap or preventing trapped animals from drowning.

Each grid was trapped for three days per month, for a total of 1872 trap-nights on Grid 1 and 3584 trap-nights on Grid 2 (1 trap set for 1 night = 1 trap-night). Traps baited with mixed bird seed and sunflower seeds were set in the late afternoon and then checked early in the next three mornings. In summer, traps were locked open in the morning and set again in late afternoon to prevent death from confinement to a trap during the heat of the day. In winter, polyfill was added to each trap for insulation.

At first capture, each rodent was given a uniquely numbered ear tag, examined for its reproductive condition, weighed with a Pesola® scale, and released at the point of capture. Reproductive information included position of testes (abdominal or descended/scrotal) for males and for females we evaluated condition of the vagina (perforate or not), size of nipples (small, medium, large) and the condition of the pubic symphysis (closed, slightly open, open). Heavily pregnant females were recorded as such. We defined the age classes of meadow voles using the criteria of Krebs et al. (1969), with juveniles ($<$22g), sub-adults (22-29g), and adults ($\geq$ 30 g). For rice rats, we used the criteria of Wolfe (1985), with juveniles ($\leq$30g), sub-adults (31-50g), and adults ($>$ 50 g). The trapping methods followed the animal handling guidelines of the American Society of Mammalogists (most recent: Sikes, Gannon et al. 2011). This study was conducted before Old Dominion University had established an IACUC protocol for the field study of wild mammals.

Statistical analysis

We used the Minimum Number Alive (MNA) method to estimate density of the populations (Krebs, 1966) and the statistical package JOLLYAGE to calculate time-specific survival rates of both adults and young and recruitment (Pollock et al., 1990). These parameters were analyzed using a Model-II 3-factor analysis of variance (ANOVA), with the factors being grid, season, and species. Where necessary, a Ryan-Einot-Gabriel-Welsch (REGWF) test was used to investigate the role of significant factors. Seasons were defined as summer (June-August), autumn (September-November), winter (December-February), and spring (March-May). Chi-Square tests

TABLE 1. Numbers of tagged *Oryzomys palustris* and *Microtus pennsylvanicus* and the other members of the small mammal communities at two locations in tidal marshes of the Atlantic coast in eastern Virginia. The numbers in parentheses are the number of captures for each sex and "unk" means the sex is unknown.

	Grid 1			Grid 2		
	Males	Females	Unk	Males	Females	Unk
Oryzomys palustris	30 (40)	28 (40)	3	118 (173)	72 (105)	28
Microtus pennsylvanicus	34 (35)	24 (29)	4	94 (115)	67 (83)	19
Peromyscus leucopus	6 (11)	6 (9)	4	2 (2)	1 (1)	0
Mus musculus	6 (7)	0	0	2 (2)	0	0
Blarina brevicauda	0	1 (1)	0	6 (11)	1 (1)	5

were used to determine whether sex ratios were unity. The $p \leq 0.05$ level of significance was used for all statistical tests.

RESULTS

The Small Mammal Community

During the 13-month study period, 185 small mammals of five species were identified on Grid 1 (Table 1), of which 65 were rice rats and 62 were meadow voles; together these species constituted 84.7% of mammals. The other small mammals were white-footed mice (*Peromyscus leucopus*), house mouse (*Mus musculus*), and short-tailed shrew (*Blarina brevicauda*). Grid 2 yielded 218 rice rats and 180 meadow voles, comprising 96.8% of small mammals, and many fewer of the same three minor species (Table 1). Thus, rice rats and meadow voles numerically dominated both communities of small mammals.

Population Density

The MNA density of *Oryzomys palustris* each month ranged from < 5/ha to 23/ha on Grid 1 (Figure 1a), showing no seasonal pattern, whereas on Grid 2 the population density rose steadily from September into winter, reaching a peak of nearly 45/ha in January (Figure 1b). Monthly changes in population density were similar for *Microtus pennsylvanicus,* i.e., mostly low densities and no seasonal pattern on Grid 1 but with highest density (30/ha) being attained in April on Grid 2.

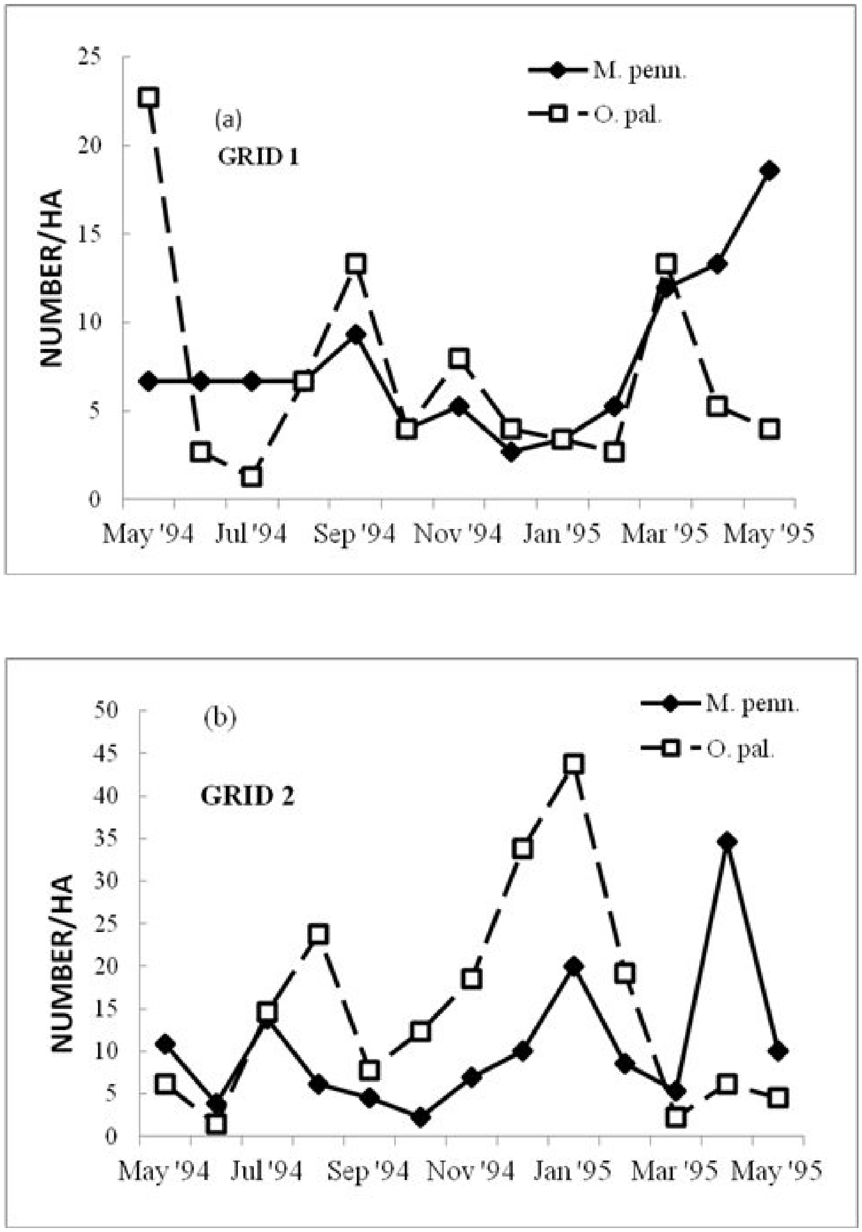

FIGURE 1. Monthly density changes for *Microtus pennsylvanicus* and *Oryzomys palustris* on Grids 1 (a, Oyster) and 2 (b, Steelman's Landing) in two coastal marshes in eastern Virginia.

Survival Rates

Time-specific survival rates were calculated for juveniles and adults of both species. Grid (F=17.01, df=1), species (F=2.94, df=1), and the interaction of grid with species (F=39.62, df=1) all had significant ($P < 0.05$) effects on adult survival. Mean monthly survival rate of adult meadow voles (0.524) was significantly ($P < 0.05$) greater than that of rice rats (0.397). Summer survival rates (0.535 per month) were significantly higher than winter rates (0.372) but no other seasons differed. The interaction of grid and species also showed levels of significance in monthly survival rates (Grid 1: 0.753 for voles, 0.351 for rice rats; Grid 2: 0.316 and 0.438, respectively). Thus, survival rates of adult voles were much higher on Grid 1 than on Grid 2, whereas those of rice rats were more similar between grids. Except for meadow voles on Grid 1, the mean monthly survival rate was substantially less than 50 percent per month.

Juvenile survival rates could not be calculated for either species on Grid 1 because of small sample sizes. On Grid 2, the mean survival rate was 0.164 per month for juvenile *Oryzomys palustris* and 0.309 for juvenile meadow voles.

Recruitment and Age Structure

The age structure of the *Oryzomys* population seemingly differed between grids, with juveniles being present on Grid 1 in May 1994, September, November, and March and April, whereas on Grid 2 juveniles were recorded in May 1994, July, August, September, November and December. No clear time of recruitment of young is evident, except that the absence of juveniles in January and February suggests no breeding in winter. For meadow voles, juveniles were observed on Grid 1 in May 1994 and April and May 1995, but on Grid 2 small numbers of juveniles were present in July, December, January, February, April and May 1995. Sub-adults dominated the age structure of both species during most months for populations on both grids.

Sex Ratios

Although males of both species predominated on both grids (Table 1), significantly more males were observed only on Grid 2, the grid with higher densities of both species. The deviation from unity was greater for *Oryzomys palustris* (118:72, $p < 0.001$) than for *Microtus pennsylvanicus* (94:67, $p < 0.05$).

Reproduction

Monthly changes in reproduction were analyzed using the position of the testes in males and nipple size in females as estimators of reproductive activity. Descended (scrotal) testes is a good (87-94%) predictor of reproductive status in male small mammals, but the best estimator for females of several rodent species is medium-large nipple size, with much less predictability at 72% (McCravy and Rose, 1992).

For meadow voles, males had peaks of breeding activity from late summer through autumn on both grids, with all males having descended testes during this period. Low rates were observed in early summer and mid-winter for male voles. Females showed a similar pattern, with low rates in early summer, increasing through autumn and peaking in October and November. June, with 0% with medium-to-large nipples, was the month of least breeding activity in female meadow voles.

Male rice rats showed greatest breeding activity in May, June, and November (100%) and lowest levels in late summer and late winter. Female reproductive activity in rice rats was low in late summer and in winter, and highest in April, May, and November, with lows later in summer and in winter, suggesting a bimodal pattern of breeding for the species in eastern Virginia.

DISCUSSION

The composition of the small mammal communities in the two tidal marshes was identical. Rice rats and meadow voles predominated across the grids. Bloch and Rose (2005) later found these same five species, plus one mole at Grid 1; they also recorded nearly equal proportions of rice rats and meadow voles on each grid. Harris (1953) also found these two species as co-dominants in tidal marshes of the Chesapeake Bay in Maryland. These three studies on the mid-Atlantic coast represent the examples of these two rodents coexisting in mainland marshes where their distributions overlap.

The highest densities of marsh rice rats ranged up to 23/ha on Grid 1 and 45/ha on Grid 2 (Figure 1), whereas those of meadow voles peaked somewhat lower at 18/ha and 25/ha, respectively. Densities on Grid 1 were uniformly lower than on Grid 2, being greater than 10/ha only for 3 months by both species. By contrast, densities of 10 or more per ha were observed in half of the months on Grid 2: 7 times for rice rats and 6 times for meadow voles. Later, Bloch and Rose (2005) observed the same pattern of lower densities of both species on Grid 1 than on Grid 2. At Grid 1, they report densities for rice rats mostly in the 5-15/ha range, whereas densities of meadow voles were twice those values, with the high of about 40/ha in June 1995 resulting from the continued upswing in numbers seen earlier that spring. Bloch and Rose (2005, Fig. 1) recorded much higher densities of both species on Grid 2, with rice rats showing peaks of more than 60 and 80/ha in the two autumns. By contrast, high meadow vole densities, mostly in the 40-60/ha range, were less related to season. The densities observed by Adkins (1980) were similar to those on our Grid 1 for both species but Cranford and Maly (1990), also working on Assateague Island, reported higher densities of both species compared to our results on Grid 2. Thus, it seems likely that densities of both species vary in similar ways from year to year in both mainland and island marshes.

Survival can only be calculated for animals caught the next or a succeeding month, because only recaptured animals are known to have survived an interval of time. Animals caught in only one month (=transients), although they can be counted in estimates of density, contribute no information on survival. In our study, survival rates were highly variable, differing between grids and species. The survival rates of meadow voles on Grid 1 were twice those observed on Grid 2, whereas rates of rice rats were more similar between grids but low. Many studies (e.g., Krebs et al. 1969; Green and Rose 2009) have measured survival rates of small mammals, especially of voles and cotton rats; monthly survival rates are mostly in the 60-70% range. For our study, except for meadow voles on Grid 1, the other survival rates were 0.32-0.44, much lower than reported in studies conducted in upland habitats. Whether the low survival is attributable to mortality or migration is moot, but the dynamic nature of the tidal environment likely was an important factor too. Neither Bloch and Rose (2005) nor Harris (1953) reported survival rates.

The proportion of juvenile rice rats reached 50 percent of captures during the April-July period, especially in May of both years, but juveniles were absent in January and February. By contrast, juvenile meadow voles comprised about 25% of captures during the March-May period on Grid 1 but on Grid 2 only once exceeded 10 percent of captures. Juvenile meadow voles were absent from both grids from August through November, suggesting that breeding occurs mainly during the winter and spring months. Populations of both species were dominated by sub-adults during many months, especially summer months. Adults often were missing from monthly estimates of age structure; only meadow voles on Grid 2 had adults present every month, and usually at 20-30 percent levels. One explanation for the relative lack of adult rice rats is that the 50-g criterion for adult weight is set too high for Virginia animals.

More males than females of both species were present on both grids, but significance was observed only on Grid 2. Bloch and Rose (2005) also found significantly more male rice rats than females on Grid 2 but not on Grid 1. Sex ratios for meadow voles were unity on both grids, a common finding across many geographic populations of this species (Reich 1981; Rose and Birney 1985). Harris (1953) reports catching significantly more male than female rice rats but equal numbers of each sex of meadow vole, results that conform to ours.

Reproduction in wild-caught rice rats is more difficult to assess than for many kinds of rodents, due in part to the dense fur in the inguinal region of both sexes and also to apparent changes in behavior in heavily pregnant females, which rarely enter live traps (RKR, personal observations). Rose and Dreelin (2011) report a relatively poor correspondence between external features of reproduction and the true reproductive condition of the rice rat as revealed at necropsy. For example, six of the 16 females found to be pregnant during necropsy had no external sign of pregnancy: no perforate vagina, small nipples, and no separation of pubic bones. Rose and Dreelin (2011) learned, using logistic regression, that perforate vagina was the best predictor of breeding status for female rice rats and descended testes for males. Large body mass also was useful in predicting breeding status in rice rats. Using these external indicators, rice rats bred mostly in spring and autumn in our study, with a lull in mid-summer and no breeding in winter, a pattern similar to that observed in a Delaware marsh by Edmonds and Stetson (1993). The timing of the entry of juveniles into the trappable population also supports this assessment.

By contrast, the highest proportion of reproductively ready male meadow voles was observed from late summer through autumn, with lower indices in the other months, especially in summer. Female voles had high reproductive indices in spring and autumn, and lowest values in summer. Thus, a mid-summer breeding lull was apparent in both sexes of meadow vole. Interestingly, no juvenile meadow voles were trapped from late summer through autumn, suggesting that their rates of survival were poor then.

In conclusion, marsh rice rats and meadow voles are the dominant small mammals in mainland marshes in eastern Virginia, both species having made accommodations to the daily flooding cycle. Rice rats generally had higher densities than meadow voles, both species had breeding peaks in spring and autumn with less breeding in summer and especially in winter, and sex ratios favored male rice rats but were unity in meadow voles.

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