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Population Dynamics of *Oryzomys palustris* and *Microtus pennsylvanicus* in Virginia Tidal Marshes

CHRISTOPHER P. BLOCH^{1,2,*} AND ROBERT K. ROSE¹

Abstract - *Oryzomys palustris* (marsh rice rat) and *Microtus pennsylvanicus* (meadow vole) cohabit coastal marshes in the mid-Atlantic US. Both were live-trapped for 23 months at two tidal marsh sites in Virginia to assess their demography near the margins of their distributions. In the presence of dense vegetation, population dynamics of the two species were seasonal and positively correlated, with densities declining through the winter. At the more sparsely vegetated site, densities of both species were lower, and densities of *M. pennsylvanicus* were negatively correlated with those of *O. palustris*. Patterns of reproduction differed between the species. *O. palustris* was reproductively most active in summer and least so in winter, whereas female *M. pennsylvanicus* decreased reproductive activity during summer.

Introduction

Patterns of population dynamics of a species may differ among localities or habitat types, or may depend on interactions with other species, especially near the limits of a species' geographic range, where environmental conditions often are near the limits of tolerance (e.g., Arnason and Grant 1976, Remington 1968). Therefore, it is important to understand the demography of species throughout their ranges. The geographic ranges of *Microtus pennsylvanicus* (Ord), the meadow vole, and *Oryzomys palustris* (Harlan), the marsh rice rat, overlap in the northeastern US. Both species occur in salt marshes in coastal Virginia, but they rarely have been studied where they co-occur.

The geographic distribution of *M. pennsylvanicus* extends throughout Canada and most of the northern and eastern regions of the United States (Hall 1981). The population ecology of this species has been studied extensively (e.g., Adler and Wilson 1989, Birney et al. 1976, Boonstra and Rodd 1983, Jones 1990, Peles and Barrett 1996, Tamarin 1977, Tamarin 1985 and references therein). However, relatively little work has focused on *M. pennsylvanicus* in salt marshes (Getz 1966, Harris 1953). *O. palustris*, on the other hand, is the most northerly member of a primarily tropical genus and is common in the southeastern US. Studies of the population ecology of *O. palustris* have concentrated in habitats along the Gulf Coast (Kruczek 2004, Negus et al. 1961, Smith and Vrieze 1979, Wolfe 1985). Only Harris (1953) conducted a relatively long-term (> 1 year) study of the ecology of these two species in salt marshes (in Maryland), and he presented no detailed data on their population dynamics. No published data exist on population dynamics of northern populations of *O. palustris*.

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Because Virginia is near the limits of the geographic ranges of both species, local populations could be expected to face hardships related to seasonality. *M. pennsylvanicus* does not thermoregulate well at high temperatures; the upper lethal limit for the species is between 34 and 39 °C (Wiegert 1961). Thus, the long hot summers typical of southeastern Virginia may cause *M. pennsylvanicus* to reduce activity and, consequently, reproductive output, and may decrease survivorship. In contrast, *O. palustris* faces winters in Virginia that can be severe, with precipitation followed by several days of freezing temperatures (Porter and Spitler 1996). *O. palustris* could be expected to undergo reductions in density during winter. Winter conditions may be particularly stressful in a tidal marsh environment for a species that, like *O. palustris*, spends a great deal of time swimming (Esher et al. 1978, Forsy and Dueser 1993).

The goal of this study was to examine population dynamics of *M. pennsylvanicus* and *O. palustris* near the limits of their geographic ranges. In addition, we study coastal wetlands, a habitat where environmental conditions are not ideal for either species, but to which *O. palustris* may be better adapted than *M. pennsylvanicus*.

Methods

Trapping grids were located in two tidal marsh sites on the eastern coast of the Delmarva Peninsula, near the towns of Oyster and Townsend, Northampton County, VA. Both sites contained extensive patches of salt marsh grass, *Spartina alterniflora* Loisel, salt meadow hay, *S. patens* Muhl., black needlerush, *Juncus roemerianus* Scheele, and saltbush, *Baccharis halimifolia* L., and were bordered on the landward side by common reed, *Phragmites australis* (Cav.) Trin. Compared to the Townsend site, the Oyster site was more sparsely vegetated (determined by point-frequency sampling; Sowell 1995), closer to forested patches and human habitations, and less uniform in elevation. In addition, the grid at Oyster flooded less evenly than did that at Townsend.

The grid at Townsend covered 1.3 ha of effective area and contained 130 trap stations located at 10-m intervals (13 rows, 10 columns). The grid at Oyster, constrained by geography of the study site, effectively covered 0.75 ha and contained 75 stations, also at 10-m intervals (maximum 7 rows, 14 columns). Each trapping station consisted of a single Fitch live trap (Rose 1994) fastened to a Styrofoam float and tethered to a wooden stake by 1 m of monofilament fishing line. Floating platforms were necessary to avoid submergence of traps during high tides. Traps were baited with commercial birdseed mix supplemented with sunflower seeds.

Traps were run for 2–3 nights monthly from May 1995 to March 1997 at both sites. Trapping extended into April 1997 at the Townsend site. Captured animals were individually marked by ear tagging or toe clipping. Species, weight, sex, point of capture, and reproductive status based on external indicators were recorded. Males were considered to be in breeding

condition if testes were descended, and females were considered in breeding condition if the vagina was perforate or if obvious pregnancy or lactation was detected. Animals were released at the point of capture.

Jolly-Seber estimates of density were calculated using the program JOLLY (Pollock et al. 1990) for all monthly trapping periods; Jolly-Seber estimates cannot be calculated for the first and last sampling periods. Irregularities were removed from the time series using a 3-point moving average (Chatfield 1989). Mean residence times (i.e., the number of months between the first and last capture of an animal, inclusive) of resident *O. palustris* and *M. pennsylvanicus* were compared within sites using two-sample *t*-tests. Residents were defined as individuals captured in more than 1 month.

Mean body mass was compared between sexes, between sites, and among seasons (summer = June–August; autumn = September–November; winter = December–February; spring = March–May) for each species using a three-way analysis of variance (ANOVA). For individuals captured multiple times, body mass was estimated as mean mass within each season. Obviously pregnant females were excluded from these estimates. Prior to analysis, body mass estimates of *M. pennsylvanicus* were \log_{10} -transformed to eliminate violation of the assumption of equality of error variances (Sokal and Rohlf 1995). Spearman's rank correlation coefficient was calculated for population densities between species within sites and between sites for each species, and Chi-square goodness-of-fit tests were used to test sex ratios of each species at each site for departures from unity. A series of G-tests (Sokal and Rohlf 1995) was used to evaluate the hypothesis that the proportion of individuals breeding was contingent upon season for males and females of each species. The G-tests could be used only for the population at Townsend, however, as small sample sizes at Oyster resulted in many small (≤ 3) expected values, potentially introducing serious bias (Sokal and Rohlf 1995).

Results

At Oyster, we made 347 captures of 226 individuals of 6 species, compared to 1601 captures of 796 animals of 5 species at Townsend (Table 1).

Table 1. Summary of small mammals trapped at two tidal marshes in Northampton County, VA, from June 1995 to April 1997, indicating the number of individuals, total number of captures, and average number of captures per individual for each species. Individuals that escaped before being tagged are excluded.

| Species | Oyster site | | | Townsend site | | |
|--|-------------|----------|-------------|---------------|----------|-------------|
| | Individuals | Captures | Cap. / ind. | Individuals | Captures | Cap. / ind. |
| <i>Microtus pennsylvanicus</i> | 88 | 148 | 1.7 | 359 | 828 | 2.3 |
| <i>Oryzomys palustris</i> | 63 | 102 | 1.6 | 390 | 722 | 1.9 |
| <i>Peromyscus leucopus</i> (Rafinesque) | 30 | 49 | 1.6 | 5 | 5 | 1.0 |
| <i>Mus musculus</i> L. | 38 | 41 | 1.1 | 26 | 29 | 1.2 |
| <i>Blarina brevicauda</i> (Say) | 6 | 6 | 1.0 | 16 | 17 | 1.1 |
| <i>Scalopus aquaticus</i> (L.) | 1 | 1 | 1.0 | 0 | 0 | – |

O. palustris and *M. pennsylvanicus* were the most common small mammals captured at both sites.

Population densities of *O. palustris* and *M. pennsylvanicus* at Oyster (Fig. 1a) were negatively correlated ($r_s = -0.46$, $P = 0.04$). Density of *O. palustris* peaked at 15 individuals/ha during the winter of 1995 and was lowest (3 individuals/ha) during the spring of 1996. Highest density of *M. pennsylvanicus* (40 individuals/ha) was in late spring–early summer and was lowest in late autumn. In contrast, population densities of the two species at Townsend were positively correlated ($r_s = 0.66$, $P < 0.001$), with highs (*O. palustris*: 87 individuals/ha; *M. pennsylvanicus*: 68 individuals/ha) during autumn and lows (*O. palustris*: 8 individuals/ha; *M. pennsylvanicus*: 26 individuals/ha) during winter (Fig. 1b).

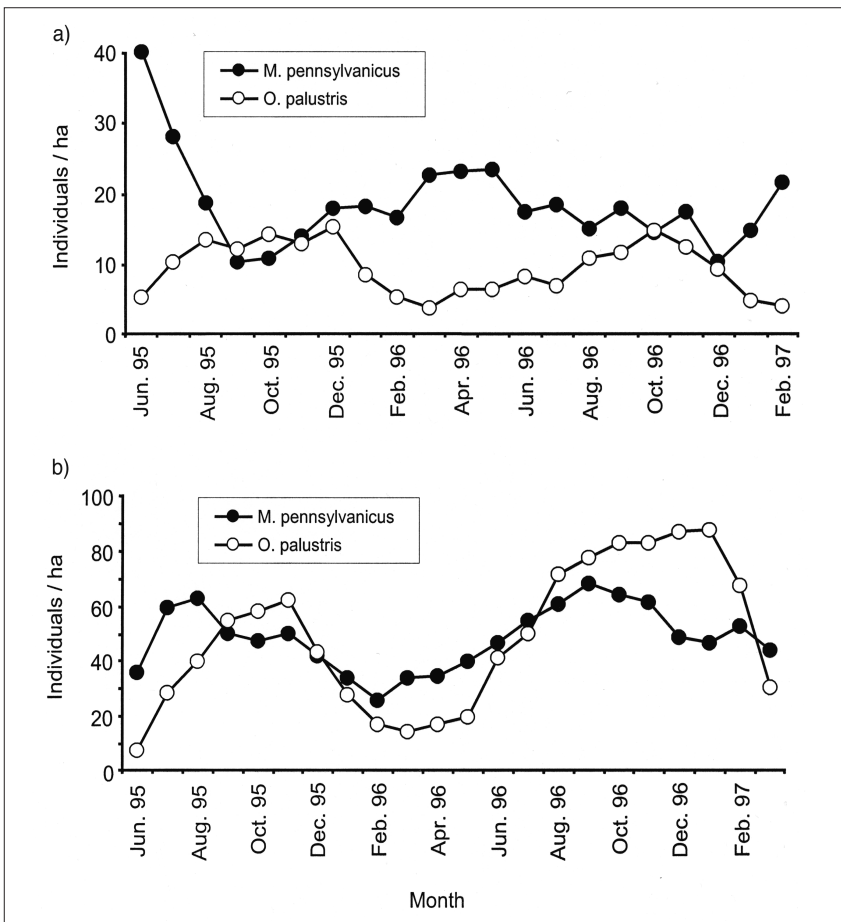


Figure 1. Three-point running mean of monthly Jolly-Seber estimates of population density (Individuals/ha) of *Oryzomys palustris* (open circles) and *Microtus pennsylvanicus* (filled circles) at (a) Oyster, and (b) Townsend, Northampton County, VA. X axes are of different lengths because trapping extended one month longer at Townsend than at Oyster.

Densities of both species were higher at Townsend than at Oyster. Density of *O. palustris* averaged 9.3 ± 0.8 (SE) individuals/ha and never exceeded 15 individuals/ha at Oyster, whereas densities averaged 48.2 ± 5.6 individuals/ha at Townsend. Similarly, densities of *M. pennsylvanicus* averaged 48.0 ± 11.4 individuals/ha at Townsend, but only 18.5 ± 1.5 at Oyster. Population densities were not correlated between sites for either *O. palustris* ($r_s = 0.39$, $P = 0.09$) or *M. pennsylvanicus* ($r_s = -0.23$, $P = 0.32$).

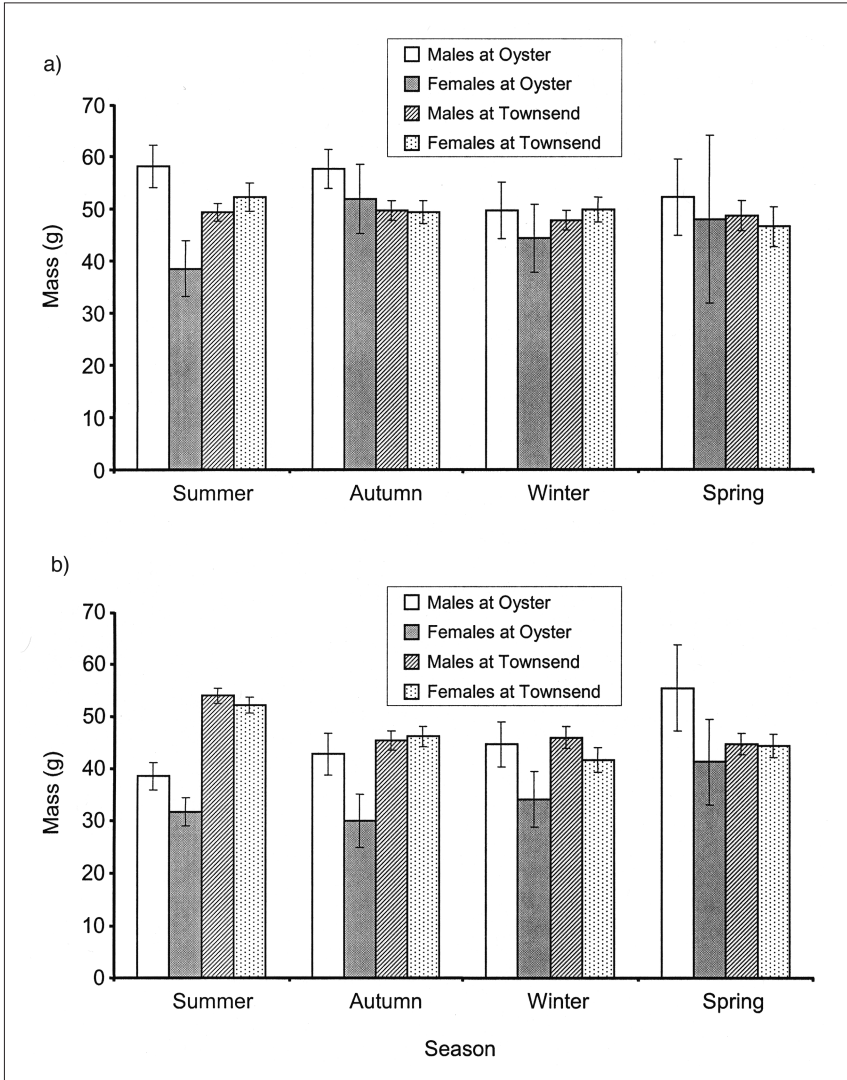


Figure 2. Mean body mass of (a) *Oryzomys palustris* and (b) *Microtus pennsylvanicus* at Oyster and Townsend, Northampton County, VA, in summer (June–August), autumn (September–November), winter (December–February), and spring (March–May). Error bars represent one standard error around the mean.

Mean residence time did not differ between the two species at Oyster (*O. palustris*: 3.78 ± 0.6 months, *M. pennsylvanicus*: 4.50 ± 0.7 months; $t = 0.76$, $df = 41$, $P = 0.45$) or at Townsend (*O. palustris*: 4.40 ± 0.3 months, *M. pennsylvanicus*: 4.64 ± 0.3 months; $t = 0.60$, $df = 300$, $P = 0.55$). Maximum residency of *O. palustris* was 12 months at the Oyster site and 18 months at Townsend. *M. pennsylvanicus* exhibited maximum residence times of 12 months at Oyster and 21 months at Townsend.

Mean body mass of *O. palustris* did not differ between sexes, sites, or among seasons (Fig. 2a; $F = 1.11$, $df = 15$, 486, $P = 0.34$). For *M. pennsylvanicus*, differences in body mass were evident (Fig. 2b; Table 2). There was a site x season interaction ($F = 5.41$, $df = 3$, 549, $P = 0.001$), with individuals at Townsend being heavier than those at Oyster in summer and autumn, but not in winter or spring. In addition, there was a significant site x sex interaction ($F = 8.20$, $df = 1$, 549, $P = 0.004$); females were larger at Townsend than at Oyster, but males did not differ in mass between sites. Irrespective of the interaction terms, males were larger than females and individuals at Townsend were larger than those at Oyster (Table 2).

The sex ratio of *O. palustris* was male-biased at Townsend (214 males, 148 females; $\chi^2 = 12.03$, $df = 1$, $P < 0.001$), but not at Oyster (38 males and 23 females; $\chi^2 = 3.69$, $df = 1$, $0.05 < P < 0.10$). The sex ratio of *M. pennsylvanicus* was not significantly different from 1:1 at either site (Oyster: 47 males, 39 females; $\chi^2 = 0.74$, $df = 1$, $0.1 < P < 0.5$; Townsend: 179 males, 163 females; $\chi^2 = 0.75$, $df = 1$, $0.1 < P < 0.5$).

Breeding condition of male *O. palustris* at Townsend was contingent on season ($G = 93.76$, $df = 7$, $P < 0.001$), with the largest proportion of individuals breeding in summer and the lowest proportion of individuals breeding in winter (Table 3). Females displayed qualitatively the same pattern (Table 3), but the variation among seasons was not statistically significant ($G = 8.6$, $df = 7$, $P = 0.28$). Sample sizes at Oyster were small in most seasons for both sexes (Table 4), but 18 of 19 males and 15 of 16 females captured during summers were in breeding condition.

Reproductive status of both male ($G = 32.25$, $df = 7$, $P < 0.001$) and female ($G = 114.1$, $df = 7$, $P < 0.001$) *M. pennsylvanicus* at Townsend was also contingent on season (Table 3). Breeding of females was depressed in

Table 2. Results of Analysis of Variance on \log_{10} body mass of *Microtus pennsylvanicus*.

| Source of variance | Df | F | P |
|---------------------|-----|-------|--------|
| Model | 15 | 6.58 | <0.001 |
| Season | 3 | 1.51 | 0.212 |
| Sex | 1 | 11.39 | 0.001 |
| Site | 1 | 12.11 | 0.001 |
| Season x sex | 3 | 0.21 | 0.889 |
| Season x site | 3 | 5.41 | 0.001 |
| Sex x site | 1 | 8.20 | 0.004 |
| Season x sex x site | 3 | 0.86 | 0.459 |
| Error | 549 | | |
| Total | 564 | | |

summer, and females remained reproductively active through the winter; males were least reproductively active in the summer of 1995 and the winter of 1996–1997. Sample sizes of both males and females at Oyster were small

Table 3. Number and proportion of individuals in breeding condition (males: descended testes; females: perforate vagina, obvious pregnancy or lactation) at Townsend.

| Species Season | Males | | | Females | | |
|--------------------------|----------|------------------|------------|----------|------------------|------------|
| | Breeding | Non- breeding | Proportion | Breeding | Non- breeding | Proportion |
| <i>O. palustris</i> | | | | | | |
| Summer 95 | 65 | 7 | 0.90 | 38 | 5 | 0.88 |
| Autumn 95 | 36 | 18 | 0.67 | 44 | 17 | 0.72 |
| Winter 95–96 | 17 | 9 | 0.65 | 22 | 10 | 0.69 |
| Spring 96 | 13 | 3 | 0.81 | 10 | 2 | 0.83 |
| Summer 96 | 58 | 5 | 0.92 | 23 | 4 | 0.85 |
| Autumn 96 | 50 | 10 | 0.83 | 31 | 9 | 0.78 |
| Winter 96–97 | 24 | 53 | 0.31 | 31 | 14 | 0.69 |
| Spring 97 | 31 | 7 | 0.82 | 17 | 6 | 0.74 |
| <i>M. pennsylvanicus</i> | | | | | | |
| Summer 95 | 57 | 41 | 0.58 | 16 | 59 | 0.21 |
| Autumn 95 | 31 | 4 | 0.89 | 35 | 4 | 0.90 |
| Winter 95–96 | 16 | 5 | 0.76 | 20 | 1 | 0.95 |
| Spring 96 | 18 | 3 | 0.86 | 34 | 4 | 0.89 |
| Summer 96 | 67 | 16 | 0.81 | 45 | 34 | 0.57 |
| Autumn 96 | 40 | 9 | 0.82 | 45 | 34 | 0.57 |
| Winter 96–97 | 31 | 21 | 0.60 | 39 | 11 | 0.78 |
| Spring 97 | 45 | 6 | 0.88 | 34 | 5 | 0.87 |

Table 4. Number and proportion of individuals in breeding condition (males: descended testes; females: perforate vagina, obvious pregnancy or lactation) at Oyster.

| Species Season | Males | | | Females | | |
|--------------------------|----------|------------------|------------|----------|------------------|------------|
| | Breeding | Non- breeding | Proportion | Breeding | Non- breeding | Proportion |
| <i>O. palustris</i> | | | | | | |
| Summer 95 | 15 | 1 | 0.94 | 13 | 1 | 0.93 |
| Autumn 95 | 12 | 3 | 0.80 | 4 | 2 | 0.67 |
| Winter 95–96 | 3 | 5 | 0.38 | 6 | 0 | 1.00 |
| Spring 96 | 1 | 2 | 0.33 | 1 | 2 | 0.33 |
| Summer 96 | 3 | 0 | 1.00 | 2 | 0 | 1.00 |
| Autumn 96 | 7 | 2 | 0.78 | 5 | 1 | 0.83 |
| Winter 96–97 | 5 | 1 | 0.83 | 1 | 2 | 0.33 |
| Spring 97 | 1 | 1 | 0.50 | 1 | 0 | 1.00 |
| <i>M. pennsylvanicus</i> | | | | | | |
| Summer 95 | 12 | 16 | 0.43 | 6 | 31 | 0.16 |
| Autumn 95 | 9 | 1 | 0.90 | 6 | 2 | 0.75 |
| Winter 95–96 | 7 | 1 | 0.88 | 2 | 2 | 0.50 |
| Spring 96 | 3 | 1 | 0.75 | 0 | 1 | 0.00 |
| Summer 96 | 8 | 3 | 0.73 | 6 | 2 | 0.75 |
| Autumn 96 | 8 | 2 | 0.80 | 2 | 2 | 0.50 |
| Winter 96–97 | 0 | 8 | 0.00 | 0 | 3 | 0.00 |
| Spring 97 | 1 | 0 | 1.00 | 2 | 0 | 1.00 |

in most seasons, but breeding clearly was depressed in the summer of 1995, when only 18 of 65 individuals were in reproductive condition.

Discussion

Population densities of both species were considerably higher at Townsend than at Oyster. Densities of *O. palustris* at Townsend, in fact, exceeded 80 individuals/ha in late 1996 and early 1997. Only Smith and Vrieze (1979) report greater population densities (up to 200 individuals/ha on small seasonal islands in the Florida Everglades where animals become concentrated on the islands to escape widespread flooding during the wet season). In contrast, densities of *M. pennsylvanicus* were low relative to many other studies; densities of hundreds of individuals/ha are common for this species (Taitt and Krebs 1985).

Nevertheless, direct comparisons of densities to previous studies may be of limited value, because most report densities based on enumeration estimators (e.g., Minimum Number Known Alive). Such estimates are more conservative than Jolly-Seber estimates and are inappropriate for interspecific comparisons because capture probabilities differ among species (Nichols 1986). For the same reason, they are probably of little value in comparing densities of a single species among habitat types or geographic areas.

Patterns of population dynamics, on the other hand, may be more comparable among studies. Population dynamics of *O. palustris* in Virginia were similar to those elsewhere in the range of the species. Populations from Florida (Smith and Vrieze 1979, Wolfe 1982) and Texas (Kruckek 2004) tend to be most dense in summer or early autumn, with winter declines. An island population in Louisiana behaved similarly, except during a mild winter (Negus et al. 1961) when the population continued to grow.

Populations of *M. pennsylvanicus* may exhibit either annual fluctuations (usually with lowest densities following winter), multi-annual cycles, or both (Taitt and Krebs 1985). Dynamics at Townsend were consistent with annual fluctuations. At Oyster, the pattern was opposite, with no great decline in density over winter. Instead, density plummeted in the summer of 1995, during the first few months of this study. Two explanations are possible. First, some characteristic of the Oyster grid may differ substantially from the Townsend grid, producing different patterns of population dynamics. Alternatively, the summer population crash, along with the relatively small magnitude of population fluctuations over the remainder of the study, may indicate the end of a multi-year population cycle. In an oldfield in Manitoba, for example, a population of *M. pennsylvanicus* remained at low population densities for approximately 2 yrs following such a cycle (Mihok 1984). Unfortunately, this possibility is difficult to explore without a longer-term data set.

The marked difference in population dynamics of *M. pennsylvanicus* between sites was unexpected. This finding and the much greater density of both species at Townsend probably indicated that this site contained better

habitat for both species. This conclusion also was supported by the finding that no *M. pennsylvanicus* survived for > 1 yr at Oyster, whereas several individuals did so at Townsend (including one that remained on the grid for 21 months). Additionally, body mass of female *M. pennsylvanicus* was greater at Townsend than at Oyster.

These results may have stemmed from differences in vegetation between the sites. Vegetation at Townsend was taller (mean vegetation height 60–80 cm, depending on season) than at Oyster (mean vegetation height 30–40 cm; Sowell 1995). In addition, successful trap sites (i.e., those where animals were captured) at Townsend were covered with denser vegetation (93–99% herbaceous cover, on average, depending on season) than were successful trap sites at Oyster (79–96% herbaceous cover, on average, depending on season), and a greater proportion of trap sites at Oyster were in open marsh with virtually no vegetation (Sowell 1995). This difference probably was of particular importance to *M. pennsylvanicus*, which was captured on both sites at trap stations with denser vegetation than those at which *O. palustris* was captured, and was less likely to be captured at trap stations in open areas of the marshes (Sowell 1995). Increased cover reduced aggression and mortality in crowded laboratory populations of *M. pennsylvanicus* (Warnock 1965). Density of *M. pennsylvanicus* also was higher in areas with greater grass cover in Massachusetts (Adler and Wilson 1989) and midwestern prairies (Birney et al. 1976), and density, recruitment, survivorship, and body mass of females in Ohio were lower in areas where grass cover was reduced (Peles and Barrett 1996). Therefore, lower vegetative cover at Oyster likely was responsible for the low density and low female body masses that we observed for *M. pennsylvanicus* at that site. The unexpected pattern of population fluctuations at Oyster may result at least in part from increased interspecific pressure from competitors or predators in the absence of dense vegetative cover.

The pattern of reproductive activity for *O. palustris*, like its population dynamics, was similar to that of other populations. Throughout its range, *O. palustris* is reproductively most active in summer and least so in winter (e.g., Edmonds and Stetson 1993, Harris 1953, Kruchek 2004, Smith and Vrieze 1979, Wolfe 1985). Some studies report that breeding ceased altogether during winter (Brimley 1923, Dreelin 1997, Edmonds and Stetson 1993, Harris 1953), whereas others suggest that breeding may continue through the winter (Hice and Schmidly 1999, Kruchek 2004, Wolfe 1985), at least when weather conditions are sufficiently mild (Negus et al. 1961). Ours is the first report of winter breeding in a northern population of *O. palustris*; proportions of individuals breeding were higher than in most previous studies, although the accuracy of external indicators of reproductive condition has been questioned (Dreelin 1997, McCravy and Rose 1992). As with a population in Texas (Kruchek 2004), seasonal variability in the proportion of individuals in breeding condition was greater for males than females.

The breeding season does not appear to be circumscribed for *M. pennsylvanicus*, as breeding through the winter has been observed in many parts of its geographic range (reviewed in Keller 1985), including populations near Virginia (North Carolina and Maryland; Brimley 1923 and Harris 1953, respectively). Our results suggest that breeding may be depressed instead during summer; reproductive activity of *M. pennsylvanicus* (especially females) declined during that season. It was unlikely that this resulted simply from an influx of prereproductive individuals, as only 17 voles weighing < 20 g were captured throughout the study, of which 6 were captured during December. This low capture rate for juveniles was mirrored by *O. palustris*, and probably results from high rates of dispersal. Neither species displayed great fidelity to the trapping sites (over half of the individuals of each species were captured only once). Additionally, in Texas, juveniles made up a greater proportion of the population in upland habitats, which may represent dispersal sinks, than in marshes (Kruchek 2004).

In summary, populations of *O. palustris* in Virginia marshes behaved similarly to those in other geographic regions. Population dynamics of *M. pennsylvanicus* were not consistent between sites; whether differences in habitat characteristics (e.g., vegetative cover) were responsible was unclear, but this seemed to be the most likely cause. Even though both species are near the margins of their geographic ranges, they reproduced during the entire year, albeit not with equal intensity throughout. For *M. pennsylvanicus*, this is unsurprising, but for *O. palustris*, no northerly population previously has been documented to breed through the winter. Further study is necessary to determine whether such winter breeding is typical of mid-Atlantic populations and the degree to which climatic conditions influence the length of the breeding season.

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