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## Unusually high body mass in Virginia meadow voles

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We used monthly capture–mark–recapture information to determine growth rates and life spans for 2 populations of meadow voles studied for 28 and 29 months in eastern Virginia in order to learn whether the exceptionally large body masses of some voles were due to rapid growth, long lives, or both. On 1 study grid, 64 males (19%) and 43 nonpregnant females (11%) were  $\geq 70$  g, with the largest male being 89 g. Mostly positive growth rates (averaging 1.1–3.9 g/month) were recorded, even in autumn and winter months, times when meadow voles are losing mass in northern populations, where most studies of body growth have been conducted. Periods of low mean body mass were associated with low population density more than high body mass was associated with high population density. Patterns of body mass dynamics were related more to season than to density in our populations. We concluded that the large body masses we observed in some voles were due more to long field lives than to unusually high rates of body growth.

Key words: body growth, life span, mass, meadow vole, *Microtus pennsylvanicus*, Virginia

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In general, large body mass within a species of mammal is believed to be more adaptive than small body mass because large size is often associated with physical vigor and survival. The adaptive value of large body size was recognized more than a century ago as Bergmann's rule, which states that within a species, body mass increases with latitude and colder climate. The explanation relates to surface-to-volume ratios, and energy conservation in the northern latitudes and energy radiation in the south. However, many species of small mammals seem not to follow Bergmann's rule, including meadow voles (*Microtus pennsylvanicus*—McNab 1971) and shrews (*Sorex* spp.—Ochocinska and Taylor 2003), in which the smallest subspecies are the most northerly.

With one of the widest distributions of any North American rodent, *M. pennsylvanicus* has 26 subspecies based on morphology, pelage, and size differences (MacDonald et al. 1998). The smallest subspecies is *M. p. drummondii* in northern Canada. The darkest subspecies is *M. p. nigrans* of eastern Virginia, and as the following analysis reveals, it is also the largest. Adult size typically ranges from 30 g (Dueser et al. 1981) to 60 g (L. Getz, University of Illinois pers. comm.).

The body mass of meadow voles has been studied in several North American populations, but almost exclusively in Canada or northern states. No previous study has examined the patterns of body size in populations in the southern range of *M. pennsylvanicus*, as we have done for 2 grid populations

in Chesapeake, Virginia (37°50'N, 76°20'W, 3-m elevation). We compared periods of extralarge voles ( $\geq 70$  g) in our southern populations with periods of heavier voles reported in northern populations. Our goal was to learn whether the frequently observed large body size of meadow voles in southeastern Virginia could be the result of high rates of body growth or long life spans, or both.

### MATERIALS AND METHODS

*Study area.*—Our study sites were 2 old fields in Chesapeake, Virginia, both owned by The Nature Conservancy. The Su tract is 11.5 ha and the Stephens tract is 60 ha. At their nearest points, the trapping grids are 1.8 km apart. Van Vleck (1969) calculated home ranges for *M. pennsylvanicus* to be 0.04–0.35 ha depending on sex and season, so our 2 grids are isolated populations. The Su and Stephens sites are former agriculture fields, last used for farming in 2000 and 2003, respectively, and are undergoing secondary succession. Other small mammal species present at both sites were, in order of decreasing abundance: *Sigmodon hispidus* (hispid cotton rat), *Reithrodontomys humulis* (eastern harvest mouse), *Oryzomys palustris* (marsh rice rat), *Mus musculus* (house mouse),



*Blarina brevicauda* and *B. carolinensis* (short-tailed shrews), and *Cryptotis parva* (least shrew).

Undeveloped mixed forest surrounds the Su site. When our study grid was established in December 2002, herbaceous plants such as *Schizachyrium scoparium* (little bluestem), *Solidago* spp. (goldenrods), and *Aster* spp. (asters) dominated the field. Volunteer seedlings of *Pinus taeda* (loblolly pine) grew rapidly and by 2005 made the site increasingly unsuitable for herbivorous and omnivorous rodents. When trapping was initiated at the Stephens grid in October 2005, little bluestem, goldenrod, and asters also dominated, with large patches of *Scirpus cyperinus* (wool grass) in the low-lying areas. *Liquidambar styraciflua* (sweet gum) and *Acer rubrum* (red maple) increased in number throughout our study period.

*Field studies.*—Each study area had an 8 × 8 grid, with trapping stations at 12.5-m intervals and 2 traps per station (128 traps total per grid). The effective trapping area of each grid was 1 ha. We conducted trapping on the Su grid monthly from December 2002 through March 2005 (28 months). The 1st vole was captured in January 2003. Trapping on the Stephens grid extended from October 2005 to February 2008 (29 months). We followed guidelines of the American Society of Mammalogists for the use of mammals in research (Sikes et al. 2011).

Using modified Fitch-type live traps (Rose 1994) baited with a combination of sunflower seeds and mixed birdseed, we trapped animals during a 3-day period each month. During the colder months, we added polyfill for insulation in each trap. At the start of each trapping period, we baited and set the traps before sunset and checked them early the next morning. During the warmer months (April–October), we locked traps open in the morning and reset them in the late afternoon to prevent heat-related mortality. On the last day of trapping, traps were locked open until the next trapping period.

We identified each captured animal to species, gave each new capture a uniquely numbered ear tag in the right ear, recorded its body mass and sexual condition, and released it at the point of capture. If a vole lost its ear tag, it was retagged and synonymized with its most likely match from previous months based on sex, grid location, and mass. Heavily pregnant females were identified by palpation. Because frequent recaptures contribute to loss of body mass (Barbehenn 1955; Iverson and Turner 1974), we did not reweigh voles with multiple captures during the same month. We weighed each animal to the nearest gram in the field using a Pesola spring scale (Pesola, Baar, Switzerland), the accuracy of which we verified in the laboratory using an electronic balance.

*Statistical analysis.*—For statistical analyses, young voles are defined as <30 g and adult voles as ≥30 g. We use 30 g as a cut-off mass because meadow voles in Virginia are typically sexually mature at ≥30 g (Dueser et al. 1981). Campbell and Dobson (1992) also determined that voles mature as a function of mass rather than age. We defined winter as December–February, spring as March–May, summer as June–August, and autumn as September–November. We performed all statistical analyses using SPSS 16.0 (SPSS Inc. 2007).

We determined the minimum number of voles alive during each month of trapping at both grids by using the standard

minimum number alive calculation (Krebs 1966). The number of individuals captured divided by the minimum number alive produced monthly trappability estimates for each sex and population (Krebs and Boonstra 1984). The 1st and last months of trapping were omitted from the trappability calculation to minimize skewing.

Pregnant females, young voles, and voles found dead in traps were excluded from calculations of adult monthly masses. Two-tailed *t*-tests compared masses of each sex on both grids and linear regression was used to determine if mass was related to population density. The peak-density period was defined as the 3 consecutive months of highest density, the low-density period was defined as the 3 consecutive months of lowest density, and the 3 consecutive months having the most extralarge voles (≥70 g) was defined as the extralarge period. Twelve 2-tailed *t*-tests, 1 for each sex and grid, compared separately the masses from the 3 months of peak density, the 3 months of low density, and the 3 months of extralarge voles to those of all other months. Because autumn and winter mass loss has been documented in the northern range of the meadow vole (Barbehenn 1955; Brown 1973; Iverson and Turner 1974; Unangst and Wunder 2003), an analysis of variance (ANOVA) was run for each sex and grid to determine if adult mass differed significantly among seasons.

We calculated monthly growth rates of adults by using changes in body mass of an individual from its 1st capture in 1 trapping period to its 1st capture in a later month. We emphasize that we calculated growth rates only for adults (≥30 g). This approach removes the confounding effects of the high growth rates associated with periods when young enter the population, and focuses more on the patterns of positive and negative growth and season. The change in mass was divided by the number of days between these captures and multiplied by 30 to compute growth rates per month. We excluded synonymized voles from analysis of growth patterns because of the relative uncertainty associated with the procedure of synonymizing tag numbers. Voles captured in only 1 month also were excluded from the analysis of growth patterns because at least 2 months of measurements are required to detect mass changes in an animal. A 1-factor ANOVA was used to determine significant differences among seasons at each study grid. The 4 ANOVAs evaluated both sexes on both grids and we ran a Ryan–Einot–Gabriel–Welsch *F* post hoc test on data yielding significant ANOVA results. A linear regression analysis using the minimum number alive values and mean growth rates of each sex was performed on the Stephens data to determine if a relationship existed between population density and growth rates. We analyzed only the voles of the Stephens grid for this association because, with its larger sample sizes, it provided the best chance to see a relationship.

We used 2-tailed *t*-tests to determine if growth rates were higher for each sex and grid during peak population densities and during the period of extralarge voles. We calculated life span in weeks for voles caught 3 or more times (Rose and Dueser 1980). Synonymized voles and those voles captured

within the 3 months before the conclusion of the study were excluded. Two-tailed *t*-tests for each sex and grid compared life spans of voles reaching the extralarge threshold ( $\geq 70$  g, including pregnant females) to life spans of voles that never reached extralarge mass. Pregnant females were included in life-span calculations because they often had long capture histories and changing body mass does not confound life span. We used 70 g as the extralarge threshold because L. Getz did not capture any meadow voles weighing more than 66 g during his 25 years of study in eastern Illinois.

## RESULTS

**Sample sizes and trappability.**—On the Su grid, we captured 84 male and 65 female meadow voles and their overall trappability was  $49\% \pm 5.5\%$  SE and  $57\% \pm 6.7\%$ , respectively. Monthly sample sizes for each sex ranged from 0 to 15. We captured 342 males and 381 females on the Stephens grid, where monthly sample sizes for each sex ranged from 2 to 84 and trappability was  $63\% \pm 4.1\%$  for males and  $65\% \pm 4.3\%$  for females. Predator disturbance caused lower trappability during some months on both grids.

On the Su grid, 39 males (46%) and 37 females (57%) were captured only during 1 month and are considered transients, compared to 175 male (51%) and 167 female (44%) transients from the Stephens grid. Overall, 50% of males and 46% of females are considered transients. Of the 872 tagged voles, 14 (Su: 9%) and 89 (Stephens: 13%) were young ( $<30$  g) at 1st capture.

**Population density.**—The density of *M. pennsylvanicus* on the Su grid was lowest early in the study and peaked in February 2005 with a density of 44 voles/ha after increases through autumn and winter (Fig. 1a). The highest density on the Su grid resulted from population increases through autumn and winter in 2004. The population density on the Su grid steadily grew in numbers despite dips about every 6 months.

By contrast, the density of voles on the Stephens grid was highest in August 2006 with 223 voles/ha and lowest in June 2007 ( $n = 22$  voles/ha; Fig. 1b). This population increased during the 1st winter and through the summer and then declined through the following year and remained moderate to low.

**Body mass variation.**—Monthly mean mass for adult voles on the Su grid was usually higher for males than for females (Fig. 2a), with grand means of  $57 \text{ g} \pm 1.2 \text{ SE}$  (range: 30–94 g) and  $51 \pm 0.1 \text{ g}$  (range: 30–70 g) for males and females, respectively. A 2-tailed *t*-test indicated a significant difference in mass between the sexes ( $t_{225} = 3.706$ ,  $P < 0.001$ ). We captured 14 males (17%) and 4 females (6%)  $\geq 70$  g on the Su grid, with the heaviest male being a 94-g scrotal male caught in December 2003. The heaviest nonpregnant females on the Su grid were both 70 g in November and December 2003. The October–December 2003 period was notable because we captured 5 males weighing 70–94 g and 2 nonpregnant females  $\geq 70$  g, or 39% of our heavy animals. A 2-tailed *t*-test revealed both sexes were significantly heavier during the extralarge period than all other months (males:  $t_{135} = 4.1311$ ,  $P < 0.001$ ; females:  $t_{88} = 2.638$ ,  $P = 0.010$ ). During the

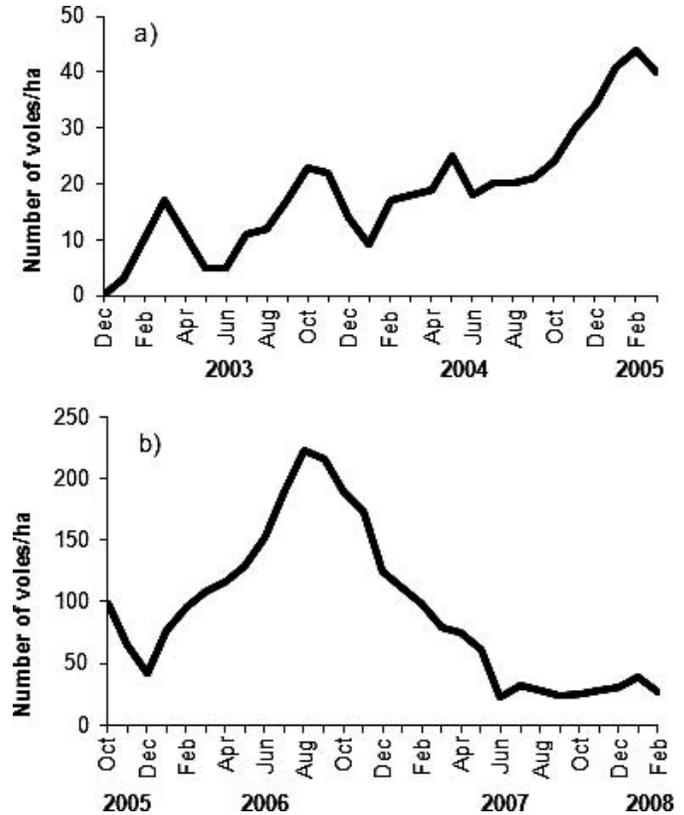


FIG. 1.—Population density changes in *Microtus pennsylvanicus* on the a) Su and b) Stephens grids.

period of extralarge voles, adult males and females averaged  $67 \text{ g} \pm 2.2$ , SE ( $n = 24$ ) and  $55 \pm 2.0 \text{ g}$  ( $n = 19$ ), respectively.

On the Stephens grid, monthly mean mass for males also was usually higher than for females (Fig. 2b), with grand means of  $56 \pm 0.4 \text{ g SE}$  (range: 30–89 g) and  $48 \pm 0.3 \text{ g}$  (range: 30–75 g). A 2-tailed *t*-test indicated a significant difference in mass between males and females ( $t_{1,539} = 14.432$ ,  $P < 0.001$ ). We captured 64 males (19%) and 43 females (11%)  $\geq 70$  g on the Stephens grid. The heaviest male was 89 g in March 2006 and the heaviest nonpregnant female was 75 g in October 2006. September–November 2006 was notable because we captured 23 males and 14 females  $\geq 70$ g, or 33% of our heavy animals in this 3-month period. Males were significantly heavier during the extralarge period than all other months ( $t_{801} = 3.668$ ,  $P < 0.001$ ), but females were not ( $t_{803} = 0.339$ ,  $P = 0.735$ ). During the period of extralarge voles, males and females averaged  $59 \pm 1.0 \text{ g}$  ( $n = 179$ ) and  $48 \pm 0.7 \text{ g}$  ( $n = 221$ ), respectively.

Mean mass during the period of highest density on the Su grid (January–March 2005) was  $59 \pm 2.3 \text{ g}$  ( $n = 37$ ) for males and  $49 \pm 1.3 \text{ g}$  ( $n = 32$ ) for females. Two-tailed *t*-tests used to compare the mass of each sex during the peak population to the mass during all other months yielded nonsignificant results (males:  $t_{135} = 1.272$ ,  $P = 0.206$ ; females:  $t_{88} = 1.206$ ,  $P = 0.231$ ).

During the population peak from July to September 2006 on the Stephens grid, males were significantly heavier than females ( $t_{1,606} = 14.392$ ,  $P < 0.001$ ). Males weighed  $58 \pm$

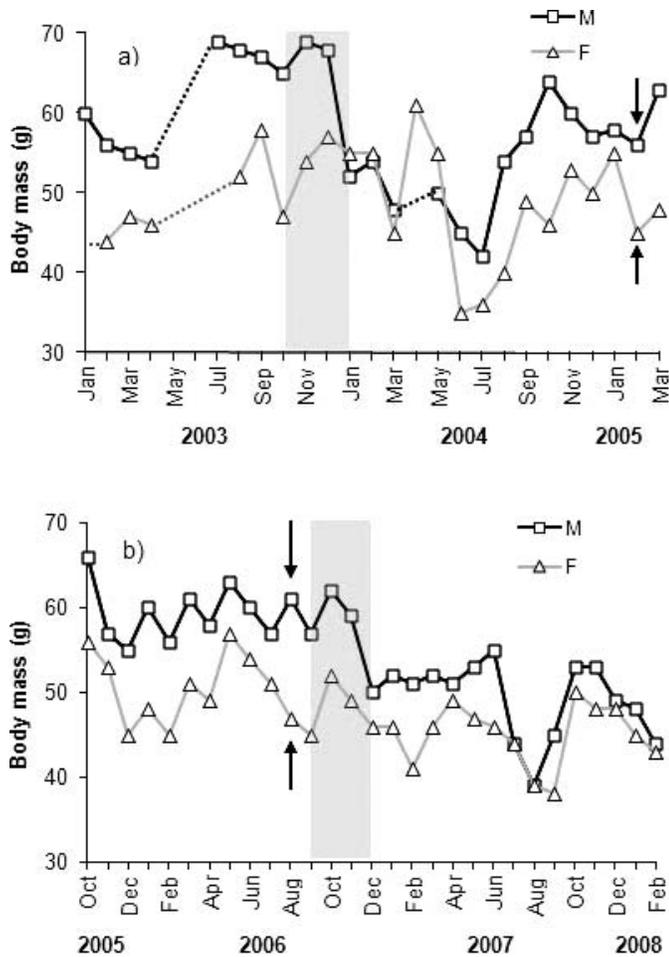


FIG. 2.—Monthly mean masses of adult male and female meadow voles (*Microtus pennsylvanicus*) on the a) Su and b) Stephens grids, excluding pregnant females. Dashed lines indicate no voles were trapped during those months. The shaded region marks the 3-month period of extralarge voles. Arrows indicate the middle month of the 3-month period of peak density.

0.9 g ( $n = 187$ ) and females weighed  $47 \pm 0.7$  g ( $n = 194$ ) then. Males were significantly heavier during the population peak than all other months ( $t_{801} = 2.483$ ,  $P = 0.013$ ), but females were not ( $t_{803} = -1.702$ ,  $P = 0.089$ ).

For the Stephens voles, we also compared mean masses during the 3 months of low density to those of all other months. Both sexes were significantly lighter during the population low (August–October 2007) when compared to the mass during all other months (males:  $t_{801} = 5.417$ ,  $P < 0.001$ ; females:  $t_{803} = 4.398$ ,  $P < 0.001$ ). During the population low, males and females weighed  $44 \pm 1.8$  g ( $n = 26$ ) and  $41 \pm 1.5$  g ( $n = 32$ ), with males 21% lighter and females 13% lighter than the grand mean mass. Mean masses between the high- and low-density periods were significantly different for both sexes (males:  $t_{211} = 5.769$ ,  $P < 0.001$ ; females:  $t_{224} = 3.265$ ,  $P = 0.001$ ), being lower in periods of low density.

Linear regression analyses between population density and monthly mean mass for each sex yielded nonsignificant results for the Su grid (males:  $R^2 = 0.016$ ,  $F_1 = 0.397$ ,  $P = 0.534$ ;

TABLE 1.—Analysis of variance and post hoc results comparing masses of meadow voles (*Microtus pennsylvanicus*) among seasons for each sex and grid. REGWF = Ryan–Einot–Gabriel–Welsch  $F$ -test, M = male, F = female.

Grid	Sex	$F$	$df.$	$P$	REGWF results
Su	M	10.145	3	<0.001	Autumn voles significantly heavier
Su	F	2.192	3	0.096	Not needed
Stephens	M	15.691	3	<0.001	Winter voles significantly lighter
Stephens	F	10.851	3	<0.001	Winter voles significantly lighter

females:  $R^2 = 0.014$ ,  $F_1 = 0.350$ ,  $P = 0.560$ ). The same analyses on the Stephens voles revealed a significant relationship for males ( $R^2 = 0.176$ ,  $F_1 = 4.913$ ,  $P = 0.037$ ), but not for females ( $R^2 = 0.042$ ,  $F_1 = 1.004$ ,  $P = 0.327$ ).

Analyses of variance comparing masses among seasons yielded significant results for males on both grids and for females on Stephens grid (Table 1). Males were significantly heavier in autumn than in other seasons on the Su grid and both sexes were lighter in winter on the Stephens grid.

**Body growth.**—Voles at the threshold of adulthood (30 g) likely have higher growth rates than voles at 60 g, because the high growth rates of mammals slow at sexual maturity. This is important because periods of high recruitment may result in skewed calculations of growth rates, with the false appearance that all voles are growing faster, when really just the “new” adult voles are growing more rapidly than older voles. We examined growth rates only of adults.

On the Su grid, we had repeat captures of 24 males and 10 females. No females were recaptured until September 2003. Monthly mean growth rates for males were positive in all months except October 2003 (Fig. 3a) and females had positive growth rates except during August and November 2003 and January 2004. ANOVAs of growth rates on the Su grid detected no significant difference among months (males:  $F_{22,45} = 0.787$ ,  $P = 0.723$ ; females:  $F_{15,16} = 1.190$ ,  $P = 0.366$ ).

The grand means for growth in males and females on the Su grid were  $+3.9$  g/month  $\pm 0.6$  SE and  $+2.0 \pm 0.9$  g/month, respectively, but this difference was nonsignificant ( $t_{97} = 1.781$ ,  $P = 0.078$ ). We used 2-tailed  $t$ -tests to compare growth rates of each sex during the January–March 2005 population peak to those of all other months (males:  $t_{65} = -1.483$ ,  $P = 0.143$ ; females:  $t_{30} = -0.872$ ,  $P = 0.390$ ). Adult males gained an average of  $5.8 \pm 1.79$  g/month during the peak months and  $3.5 \pm 0.59$  g/month during all other months, whereas adult females gained an average of  $3.4 \pm 1.60$  g/month during the peak months and  $1.6 \pm 1.09$  g/month during all other months.

Two-tailed  $t$ -tests comparing the monthly growth rate of each sex during the October–December 2003 period of extralarge voles to the monthly growth rate of all other months were nonsignificant for both sexes (males:  $t_{65} = 1.541$ ,  $P = 0.128$ ; females:  $t_{30} = 0.379$ ,  $P = 0.707$ ). Males

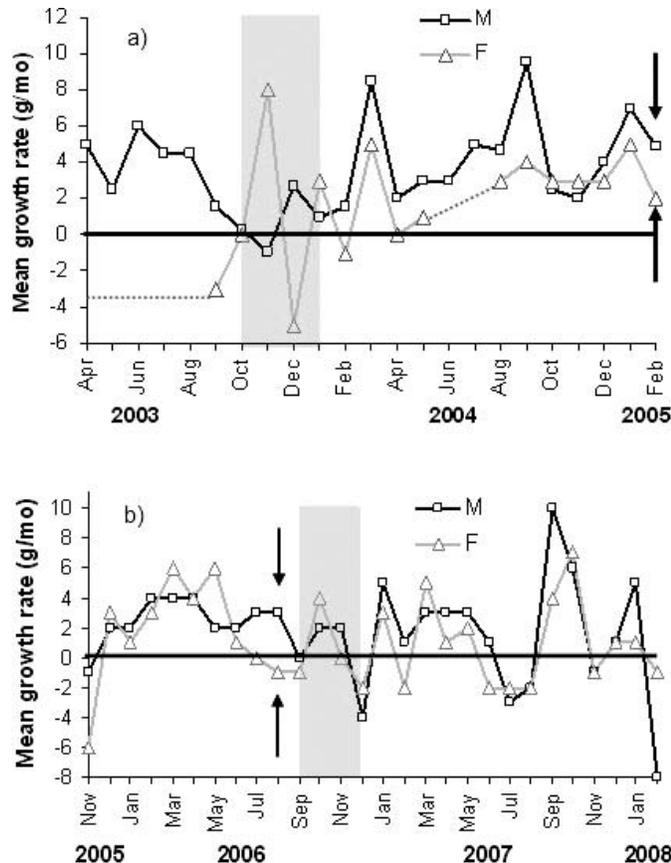


FIG. 3.—Monthly mean growth rates (g/month) of meadow voles (*Microtus pennsylvanicus*) for the a) Su and b) Stephens grids. Dashed lines represent months for which growth rates could not be calculated due to small sample size. The shaded regions indicate the 3 months of extralarge voles and the arrow is the middle month of the 3 months of highest density.

gained an average of  $2.2 \pm 1.56$  g/month during the period of extralarge voles and gained  $4.6 \pm 0.62$  g/month during all other months. Females gained  $1.5 \pm 2.35$  g/month during the period of extralarge voles and  $2.2 \pm 0.75$  g/month during all other months.

On the Stephens grid we had repeat captures of 138 males and 132 females to use in computing growth rates. Monthly growth rates of Stephens voles were erratic, but generally positive (Fig. 3b); however, both sexes had negative growth rates in November 2005; December 2006; July, August, and November 2007; and February 2008 and females also had additional negative growth rates in August and September 2006 and in February and June 2007.

The grand means for monthly growth rates in adult males and females were  $+2.0$  g  $\pm$  0.2 SE and  $+1.1 \pm 0.3$  g, respectively, and were significantly different ( $t_{1,021} = 2.489$ ,  $P = 0.013$ ). Two-tailed  $t$ -tests comparing the monthly growth rates of each sex during the peak population (July–September 2006) to the monthly growth rates during all other months yielded nonsignificant results for both sexes (males:  $t_{442} = 0.835$ ,  $P = 0.404$ ; females:  $t_{517} = 1.041$ ,  $P = 0.298$ ). Males gained an average of  $1.7 \pm 0.48$  g/month during the peak

months and  $2.2 \pm 0.32$  g/month during all other months, whereas females lost  $0.7 \pm 0.43$  g/month during the peak months and grew  $1.3 \pm 0.31$  g/month during all other months. ANOVAs detected significant differences in growth rates among months for both sexes on the Stephens grid (males:  $F_{27,416} = 2.300$ ,  $P < 0.001$ ; females:  $F_{27,440} = 4.428$ ,  $P < 0.001$ ). The Ryan–Einot–Gabriel–Welsch  $F$ -tests did not reveal a seasonal relationship in growth rates (although Table 1 results showed a significant relationship between mass and season) and the linear regression analysis comparing growth rates with population density revealed no significant relationships (males:  $R^2 = 0.001$ ,  $t_{27} = 0.170$ ,  $P = 0.866$ ; females:  $R^2 = 0.010$ ,  $t_{27} = -0.518$ ,  $P = 0.609$ ).

Two-tailed  $t$ -tests comparing the monthly growth rate of each sex during the September–November 2006 period of extralarge voles to that of all other months yielded significant results for males ( $t_{442} = 2.489$ ,  $P = 0.013$ ) but not for females ( $t_{517} = 0.133$ ,  $P = 0.895$ ). Males grew  $0.7 \pm 0.88$  g/month during the period of extralarge voles and  $2.4 \pm 0.26$  g/month during all other months. Females gained  $1.2 \pm 0.67$  g/month during the extralarge period and  $1.1 \pm 0.27$  g/month during all other months.

**Life span.**—The average life span was 28 weeks  $\pm$  3.1 SE ( $n = 11$ ) for Su males and 20  $\pm$  2.4 weeks ( $n = 10$ ) for females. Four individuals lived a minimum of 41 weeks, which was the longest life span observed on the Su grid. Males that reached the extralarge threshold ( $\geq 70$  g) lived significantly longer than those always  $< 70$  g ( $t_9 = 2.295$ ,  $P = 0.048$ ). The test could not be done on females because only 1 female  $\geq 70$  g was captured that met the criterion for life-span calculations (3 captures).

The average life span for the Stephens grid was 25  $\pm$  1.0 weeks ( $n = 94$ ) for males and 27  $\pm$  1.2 weeks ( $n = 96$ ) for females. One animal lived a minimum of 80 weeks as an adult. Voles that reached the extralarge threshold ( $\geq 70$  g) lived significantly longer than those always  $< 70$  g (males:  $t_{92} = 3.152$ ,  $P = 0.002$ ; females:  $t_{94} = 2.046$ ,  $P = 0.044$ ). Again, large voles had long life spans.

## DISCUSSION

**Sample sizes.**—With the heaviest males weighing 94 g and 89 g and grand means for adults of 57 g and 56 g (males) and 51 g and 48 g (females), the meadow voles in our populations were larger than those of earlier studies. Monthly growth rates were mostly positive and nearly twice as great for the Su population as for voles on the Stephens grid, where both sexes had negative growth rates during multiple months. Although the durations of the studies were similar (28 and 29 months), monthly sample sizes were much larger for the Stephens population, enabling more statistical comparisons and perhaps stronger conclusions.

**Population density.**—As is typical with meadow voles, both populations had large fluctuations in density throughout the study. The peak density on the Stephens tract, 223 voles/ha, was much higher than the 120 voles/ha of Krebs et al. (1969)

in southern Indiana and 136 voles/ha of Rose and Dueser (1980) in central Virginia. The highest density recorded on the Su tract was only 44 voles/ha and the result of a population increase through autumn and winter of 2004–2005, at a time when pine forest was overtaking old-field habitat. That spring and beyond, populations of all rodents declined and meadow voles were the 1st to disappear. The population peak occurred in winter on the Su grid and summer on the Stephens grid.

Immigration and emigration can have a large role in meadow vole populations (Dueser et al. 1981). Our study sites contained abundant suitable vole habitat beyond our grids, so numerous voles likely moved in and out of our grids during our field studies. This was evident by the high proportions (50% for males and 46% for females) of voles captured during only 1 month. Mortality rates for young are high (Krebs et al. 1969) and with only 6% of young tagged on either grid later recaptured, high gross mortality (= death + emigration) rates for juveniles and subadults were apparent on our grids.

*Body mass variation.*—Although we relied primarily on published reports of mass and growth, we searched the Arctos 2011 database (Arctos Database Museum) to learn that out of 3,427 meadow voles with reported masses, only 2 weighed more than 70 g. These were a 94-g pregnant female and a 76-g scrotal male, both snap-trapped in Lemhi County, Idaho, in summer 2010. Further, of 4,566 meadow voles (>12,000 captures) handled by L. Getz, University of Illinois, (pers. comm.) and his colleagues near Champaign, Illinois, none was  $\geq 70$  g; the largest 8 males were 63–66 g. In contrast, nearly 20% of males at our sites were  $\geq 70$  g.

The 3-month periods when extralarge ( $\geq 70$ -g) voles were captured on the Su and Stephens grids (October–December 2003 and September–November 2006, respectively) were both during population-decline phases (Fig. 2). This was especially true on the Stephens grid during the rapid decline after the August 2006 peak. Large size during a decline is contrary to findings by Krebs et al. (1969), who reported *M. pennsylvanicus* to be smallest during population-decline phases in Indiana. Importantly, we observed the large voles in autumn, the season when meadow voles from more northerly locations are losing mass (Barbehenn 1955; Brown 1973; Iverson and Turner 1974; Unangst and Wunder 2003). The 3-month periods of extralarge voles were characterized by significantly higher masses than combined other months across both sexes and grids, except for females from the Stephens grid.

On both grids, males were significantly heavier than females. On the Su grid, mass and population density were unrelated, but on the Stephens grid, a significant relationship was found only for males. Males were 4% heavier during high density and 21% lighter during the 3-month period of population low. On the Stephens grid, female voles were 13% (but not significantly) lighter during the population low.

Several studies have examined mass dynamics during different phases of vole population cycles, which often last 3–4 years in northern populations. For example, Chitty (1960) reports that *M. agrestis* (field vole) in the United Kingdom is 20–30% heavier in increasing and peak population densities;

Krebs et al. (1969) document the smallest meadow voles during population declines in Indiana; and Krebs and Myers (1974 [Indiana]) and Mihok et al. (1985 [Ontario, Canada]) report the largest meadow voles during peak population density. Burthe et al. (2010), who also studied field voles in the United Kingdom, document voles to be about 9% heavier during the population peak. They attribute this to voles living longer during the peak phase, and therefore having more time to add mass (Burthe et al. 2010). We agree with the idea that voles living longer have more time to add mass and the growth trajectories of selected long-lived and frequently trapped voles support this notion.

In our populations, seasonality had more of an effect on mass than did population density. Krebs et al. (1969) and Mihok et al. (1985) found meadow voles to be heavier during peaking populations, but except for males on the Stephens grid, where mass was positively related to population density, mass and population density for males were unrelated. It is important to note that the relationship between mass of males and population density was more influenced by significantly lighter mass (21%) during the 3-month period of population low, instead of the 4% heavier mass of the population peak.

In our study, adult voles were significantly heavier in autumn (Su: males) and lighter in winter (Stephens: both sexes) compared to all other seasons (Table 1). With a mean annual temperature of 15°C (59°F) and rare periods of snow cover or frozen ground, winter in eastern Virginia, although mild compared to conditions elsewhere in the range of the meadow vole, had depressive effects on body mass of the Stephens voles.

The abundance of extralarge voles during October–December 2003 (Su) and September–November 2006 (Stephens) supports that autumn voles are large. This mass-gaining strategy is the opposite of that seen in more northerly populations, where voles lose mass in autumn, even when food is still abundant, as if to prepare for winter. Extreme autumn and winter weight loss, such as the 25% reported near Ithaca, New York (Barbehenn 1955), and 45% mass loss near Pinawa, Manitoba, Canada (Iverson and Turner 1974), did not happen in either of our populations. Although the rates of mass loss in winter voles were minimal compared to those seen in northern populations, voles on the Stephens grid were significantly lighter during winter than in other seasons (Table 1).

*Body growth.*—Species that are *r*-selected typically exhibit determinate growth (Pianka 1970). Previous studies on *M. pennsylvanicus* concur that this species exhibits other *r*-selected characteristics, such as rapid growth, early maturity, large and numerous litters, and short life spans (Campbell and Dobson 1992; Iskjaer et al. 1989; Iverson and Turner 1974), but it is unclear if growth is determinate in *M. pennsylvanicus*. One reason *M. pennsylvanicus* attains such large masses in eastern Virginia is that monthly growth rates are usually positive. With mostly positive growth rates, voles on both grids seem to support the findings of Campbell and Dobson (1992) and Morrison et al. (1977), who describe *M. pennsylvanicus* as continuously adding mass throughout its life span in the laboratory. Our large voles were not adding

just mass but were adding length too; an 86.4-g male that drowned in a trap during an unexpected heavy rain on 12 December 2003 was 218 mm long.

Both sexes had lower growth rates during the periods of extralarge voles, but this relationship was significant only for Stephens males. Boonstra and Krebs (1979), who evaluated data from studies of meadow voles in southern Indiana, found evidence of a survival advantage for large voles during rapidly increasing populations. Our findings were different because the periods of extralarge voles were early in the decline phase on both grids (Fig. 3).

Males had higher growth rates than did females on both grids, but the difference was not significant on the Su grid, perhaps due to small sample sizes. Monthly growth rates on the Su grid were nearly twice as great for both sexes compared to those on the Stephens grid.

No relationship between population density and growth was seen in our study. Growth rates did not vary significantly among months on the Su grid, but did on the Stephens grid, although neither a seasonal nor population density relationship could be confirmed. Although the growth-rate fluctuations on the Stephens grid could not be attributed to population density or season, the negative growth rates seen in July and August 2007 for males and June–August 2007 for females seemingly are related to low population density. Despite summer being a period of lush growth and high biomass of herbaceous vegetation, the principal foods of *M. pennsylvanicus*, high temperatures may prevent voles from long periods of diurnal foraging, perhaps contributing to loss of mass then. Other studies have found the highest growth rates during periods of increasing density and at population peaks, but we found no reports of lowest growth rates and low mean mass at low density, only reports of low growth rates during the population decline (Krebs et al. 1969).

The monthly growth rates of our voles averaged 1.1–3.9 g, depending on grid and sex, and were lower than those reported in other studies, in which growth of young voles is included. Barbehenn (1955) reported summer growth rates of 6 g/month for a combined group of adult and subadult voles and Campbell and Dobson (1992), in their laboratory study, documented as much as 10 g/month of growth in adult voles up to 70 days old, but no seasonal variation in rates of body growth. The latter authors reported that growth slowed as voles aged, but was negative near the end of life only for females. Iverson and Turner (1974) reported extreme mass losses, of up to 61%, during the Manitoba winter. Barbehenn (1955) also reported that some individuals began losing mass in late summer through autumn. We did not observe the seasonal mass losses such as Iverson and Turner (1974) and Barbehenn (1955) did, but with our growth rates so much lower than those of Barbehenn (1955) and Campbell and Dobson (1992), the heavy masses we observed in eastern Virginia probably are due to longer lives coupled with moderate and mostly positive monthly growth rates.

*Life span.*—Meadow voles in eastern Virginia have similar life spans to those in central Virginia, where males lived about

23 weeks and females lived 25 weeks (Rose and Dueser 1980). Blair (1948) documented meadow voles living about 17 weeks in southern Michigan and Krebs et al. (1969) reported meadow voles living 6–19 weeks, varying with sex and population phase. No previous field study has examined life span and body mass together.

Extralarge voles from the Su grid and extralarge males from the Stephens grid lived significantly longer than other voles, which supports findings by Morrison et al. (1977), who documented that laboratory-raised voles continued growing in both length and mass beyond the typical life span of voles living in the wild. Further, Campbell and Dobson (1992) also described *M. pennsylvanicus* as continuously adding mass throughout its life span in the laboratory. Meadow voles from our populations seem to have indeterminate growth, and with long life spans, these may be the heaviest masses ever recorded for the species. Growth rates on both grids were almost always positive, which supports our belief that the unusually high body masses of *M. pennsylvanicus* in eastern Virginia are due primarily to longer life spans.

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