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BODY SIZE AND GROWTH PATTERNS OF *MICROTUS PENNSYLVANICUS* (ORD.) IN CHESAPEAKE, VIRGINIA

by

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B.S. May 2004, Virginia Tech

A Thesis Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
Requirement for the Degree of

MASTER OF SCIENCE

BIOLOGY

OLD DOMINION UNIVERSITY
May 2010

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ABSTRACT

BODY SIZE AND GROWTH PATTERNS OF *MICROTUS PENNSYLVANICUS* (ORD.) IN CHESAPEAKE, VIRGINIA

Sara E. Bell
Old Dominion University, 2010
Director: Dr. Robert K. Rose

From Dec 2002-Feb 2008, a capture-mark-release study was conducted on 2 Chesapeake, Virginia populations of meadow voles (*Microtus pennsylvanicus*). The study sites were effectively 1 ha grids in oldfields. Two modified live Fitch-type traps were placed at 12.5 m intervals on grids that were trapped for 3 days each month. In northern North America, voles have distinct breeding cohorts (spring and autumn), experience autumn and winter weight loss, demonstrate both delayed growth and sexual maturation in autumn-born young, have lifespans less than 15 weeks, and average about 35-50 g as adults. Chesapeake voles bred year-round, experienced no seasonal weight loss, autumn-born young exhibited no delayed growth or sexual maturation, lived over 20 weeks, and nearly 20% weighed over 70 g. The longest-lived vole was an 80-week-old male. The heaviest voles were over 90 g and present in late autumn and winter at both sites. Body growth dynamics were different between grids, with voles from 1 grid having lower mean masses (≈52 g) and growth rates (≈1.5g/month), but longer lifespans (≈26 weeks). Voles from the other grid had higher mean masses (≈54 g) and growth rates (≈3g/month), but shorter lifespans (≈21 weeks).

ACKNOWLEDGMENTS

I thank my committee members, Dr. A. Scott Bellows and Dr. Deborah A. Waller for all of their help, support, and time, and Dr. Robert K. Rose, my advisor and committee chair, for heading the field work, being patient, and assisting me with putting together my final thesis. I also thank Dr. Lisa Horth and Dr. Kerry Kilburn for their suggestions throughout my revision process.

I have used ‘we’ rather than ‘I’ when referring to trapping efforts and trapping results because the field work was a cooperative effort among several students and Dr. Rose. Jay Kiser, a fellow graduate student, also assisted in the trapping efforts.

Additionally, I thank my parents, Brett and Rachel Bell, and my brother, Samuel Bell, for their encouragement and support through the years of data collection, analysis, and thesis writing. Finally, I dedicate this thesis to the memory of my other brother, Zachary Tyler Bell.

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CHAPTER I

INTRODUCTION

One reason rodents pique the interest of many scientists is because they are numerous, but rarely seen. The layperson may know rodents are present only due to the presence of scat, damaged food packaging, or destruction of plants. Most rodents, including voles, are *r*-selected species: they grow, mature, and reproduce quickly, and are short-lived. Most rodent species weigh less than 500 g; the largest is the 50 kg capybara (*Hydrochaeris hydrochaeris*) of South America. In North America the largest, the American beaver (*Castor canadensis*), weighs up to 30 kg.

In general, large body mass within a species of mammal is more adaptive than low body mass because those with a higher body mass are often heartier, more viable, and longer-lived than those with lower body mass. The adaptive value of large body size was recognized more than a century ago as Bergmann's Rule (Bergmann 1847), which states that within a species, the body mass increases with latitude and colder climate. The explanation relates to surface-to-volume ratios, and energy conservation in northern latitudes and energy radiation in southern latitudes. Many species of small mammals seem to not 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.

Mammalian body growth dynamics are of interest when one considers the phenomenon of body size of insular animals. The island rule, particularly apparent in

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The journal model for this thesis is the Journal of Mammalogy.

mammals, involves the miniaturization of large mammals and the gigantism of small mammals on islands. A classic example of miniaturization is the extinct Cyprus dwarf elephant (*Elephas [Palaeoloxodon] cypriotes)* from the Republic of Cyprus (≈35°10’N latitude) and an example of gigantism on islands is the 1 kg solenodon *(Solenodon* spp.), a muskrat-sized shrew from Cuba (≈22°00’N latitude) and Hispaniola (≈19°00’N latitude). By contrast, on mainland North America, the largest of nearly 50 shrew species is the 20 g *Blarina brevicauda* (northern short-tailed shrew).

Foster (1964), who surveyed 69 mammal species on islands, found dwarfism to be characteristic of lagomorphs, carnivores, and artiodactyls inhabiting islands. Later, Heaney (1978) examined the body sizes of a squirrel from islands of differing sizes in the Indonesian and Malaysian archipelagos and peninsular Thailand. *Callosciurus prevosti* (tri-colored squirrel, 198-274 mm long) is small on islands with small and large areas (10 km^2 and 10^7 km^2, respectively), but largest on medium-sized islands (10^4 km^2). Heaney (1978) explained 3 major factors affecting the size of *C. prevosti* in relation to island area. Food limitation is the largest influence on size on the smallest islands (Heaney 1978) because when food resources are limited, small body size is adaptive. As the island size increases, predation plays a more important role, making the largest squirrels less susceptible to all predators (Heaney 1978). Finally, competition with other species of squirrels drives the size of tri-colored squirrels down on large islands (Heaney 1978).

Besides variation on islands, populations of a species often vary in size or other morphological features depending on factors such as geographic location. This variation sometimes forms the basis for placing geographic populations into named subspecies. With the widest distribution of any North American rodent, *Microtus pennsylvanicus* has

26 subspecies based on pelage and size differences (MacDonald et al. 1998). The range of *M. pennsylvanicus* extends from central Alaska to the eastern coast of Canada and south from northern New Mexico to northern Georgia. The subspecies in eastern Virginia, *M. pennsylvanicus nigrans,* is the darkest (Hall 1981), and as the following analysis reveals, also the largest.

Four traits related to body size have been documented in meadow vole populations: high body mass during increasing and peaking populations (Krebs et al. 1969; Mihok et al. 1985), autumn and winter weight loss (Barbehenn 1955; Brown 1973; Iverson and Turner 1974; Unangst and Wunder 2003), suspended growth in autumn-born young (Barbehenn 1955; Brown 1973), and suspended sexual maturation in autumn-born young (Barbehenn 1955). The observed population density phase-related changes in average mass is called the Chitty effect (Chitty 1960). The advantage to remaining small for autumn-born young and for adult voles to lose body mass in autumn may be related to conserving energy by achieving the minimum body mass required to survive winter (Boonstra 2004). Loss of body mass in adults is not the result of decreased food sources, because mass loss begins while herbaceous plants and seeds are still plentiful. The energy costs of breeding may also drive young voles (<30 g) to suppress sexual maturation until spring.

Prior studies on meadow voles have been conducted in Pinawa, Canada (≈50°10’N latitude—Innes and Millar 1979; Iverson and Turner 1974; Mihok et al. 1985); northern Minnesota (≈47°50’N latitude—Brown 1973); Ithaca, New York (≈42°40’N latitude—Barbehenn 1955); southeastern Colorado (≈39°00’N latitude—Unangst and Wunder 2003); Charlottesville, Virginia (≈38°00’N latitude—Rose and

Dueser 1980); and southern Indiana (≈38°00'N latitude—Krebs et al. 1969). The vole populations in Chesapeake, Virginia (≈36°70'N latitude) are the southern-most whose size and growth have been studied. Chesapeake is near the mid-Atlantic coast and has hot summers and mild winters with monthly temperatures in July averaging 25.8°C and January averaging 4.2°C. These mild winters may cause less selection pressure for smaller mass.

GROWTH

In a 2-year study conducted near Ithaca, New York, Barbehenn (1955) reported growth rates in juvenile voles to be double those of adults; juveniles gained 0.4 g/day and adults 0.2 g/day. Campbell and Dobson (1992) reported growth rates of about 0.8 g/day during the first month of life, and about 0.3 g/day beyond 30 days. These were laboratory-born voles from wild-caught parents (Campbell and Dobson 1992). In the laboratory, they found that *M. pennsylvanicus* continued to add mass beyond the average lifespan of wild voles (Campbell and Dobson 1992). Krebs et al. (1969) calculated growth rates in their 2-year study of southern Indiana populations as ranging from about -0.5 g/day in November to 2.0 g/day in February. In 1977, Innes and Millar (1979) studied growth rates of young voles born in captivity from wild-caught parents captured in Pinawa, Canada. These voles gained up to 1 g/day during their first 30 days of life (Innes and Millar 1979). Innes and Millar (1979) compared values from previous studies and found a latitudinal trend, with meadow voles in the southern range gaining weight more rapidly.

Several studies have examined mass and growth dynamics during different phases of population cycles. Krebs et al. (1969) examined demographic changes in 4 *M.*

pennsylvanicus populations from June 1965 to August 1967 in southern Indiana. Their control grid had 120 voles/ha during peak population density (March 1966) and 20 voles/ha during the lowest population density (June 1967). Faster growth rates were documented during increase and peak phases (≈0.5 g/day) in contrast to the decline phase (≈0.2 g/day—Krebs et al. 1969). During the population peak, 24 voles (≈40%) weighing more than 46 g were present, but during the decline phase, only 1 vole (≈7%) weighed over 46 grams (Krebs et al. 1969). Winter breeding occurred only during the increase phase. Summer breeding during the peak phase ended about 1 month earlier than in all other phases (Krebs et al. 1969).

Mihok et al. (1985) examined body growth dynamics, including body composition, using 10 years of data collected in Pinawa, Manitoba. The mean percent body protein composition during the increase phase was 65% in 1969 and was 68% during peak density in 1970 (Mihok et al. 1985). The mean percent fat composition in 1969 was 10% and 28% in 1970 (Mihok et al. 1985). This study documented high growth rates and body masses during periods of increasing and peaking population densities, and lower growth rates during declining populations.

Campbell and Dobson (1992) used meadow voles born in a laboratory to wild-caught parents from Michigan to document mass and skeletal growth patterns in males and females. Using X-rays at regular intervals, they measured the lengths of the skull, zygoma, humerus, femur, and pelvis; this enabled them to identify typical growth patterns and growth characteristics. By 70 days old, males were significantly heavier than females, averaging about 40 g while females weighed about 33 g (Campbell and Dobson 1992). Though females usually out-live males (Krebs et al. 1969; Rose and Dueser 1980), they do not typically weigh more (Campbell and Dobson 1992). Males were significantly larger in all postcranial bone measurements by age 50 days, but skull measurements never differed significantly from females (Campbell and Dobson 1992).

SEASONAL MASS LOSS

Well-documented in meadow voles, autumn and winter mass loss is likely a survival strategy for the colder months when food is scarce. Smaller animals have lower energy requirements. Barbehenn (1955) reported that adult males in northern New York lost about 25% of their August mass by November. In north-central Minnesota, Brown (1973) reported meadow voles in a 3-year study reached peak body mass in early August. Few meadow voles achieved masses over 40 g and most dropped to about 30 g during the winter (Brown 1973). Iverson and Turner (1974), who trapped voles year-round for 2 years near Pinawa, Manitoba, reported that meadow voles lost mass between August and February. The average adult female went from 49 g, which includes pregnant individuals, to 27 g and adult males from 41g to 29 g (45% and 29% body mass loss, respectively—Iverson and Turner 1974). They captured no voles with masses over 35 g between December and March (Iverson and Turner 1974).

Unangst and Wunder (2003) studied meadow voles from southeastern Colorado and documented a positive correlation between latitude and reduction in fat-free mass. They compared winter mass loss to values reported on northern red-backed voles (*Clethrionomys rutilis*) in Alaska (65°00'N—Sealander 1966), meadow and Gapper's red-backed voles (*Myodes gapperi*) in Pinawa, Manitoba (Iverson and Turner 1974; Anderson and Rauch 1984), and prairie voles in Colorado (39°00'N—Voltura 1997) and found percent mass loss in winter decreased in lower latitudes (Unangst and Wunder 2003). In all of the above studies, voles began losing mass while food was still plentiful.

SUSPENDED GROWTH

For late summer/autumn-born voles in northern populations, growth is suppressed and these animals overwinter at low body masses, quickly gaining mass in late winter/early spring before or as they breed (Barbehenn 1955; Brown 1973). Suspended growth in autumn-born young may also be a survival strategy. If young remain small until spring, their energy requirements will be lower during the winter months. By contrast, young born in spring grow rapidly and enter the breeding population almost immediately (Barbehenn 1955; Brown 1973).

Barbehenn (1955) documented that males of all ages either lost mass or failed to gain mass during the autumn. Brown (1973) found that meadow voles demonstrated nearly zero growth in both mass and linear measurements throughout the winter in Minnesota. Growth resumed in March, supporting the notion that maturation and reproduction were delayed over winter (Brown 1973).

SUSPENDED SEXUAL MATURATION

Suspended sexual maturation in autumn-born young may also be a survival strategy. To avoid higher energy requirements during the winter months, young may postpone sexual maturation to eliminate the high energy costs of pregnancy and lactation. Barbehenn (1955) stated that males born after June did not become sexually mature in the year of their birth; however, the onset of puberty in females was not delayed and many spring-born females had litters in the same year. Rose and Dueser (1980) necropsied about 25 meadow voles each month for 2 years from near their trapping grids and found no evidence of delayed maturation in autumn-born voles in Charlottesville, Virginia.

LIFESPANS

A study by Morrison et al. (1977) examined longevity of *M. pennsylvanicus* in a laboratory population, using voles from central Alaska. Only the laboratory-born offspring were used for analysis. This study established potential maximum lifespans for meadow voles and documented that laboratory-raised voles continued growing in both length and mass beyond the typical lifespan of voles living in the wild. The males lived longer than females in the lab, with males living up to 68 weeks and females up to 56 weeks (Morrison et al. 1977).

Krebs et al. (1969) noted decreased life expectancies for both sexes during population declines in southern Indiana. Males lived about 11 weeks during increasing and peaking population phases, but about 6 weeks during declining phases. Females lived about 19 weeks during increasing and peaking population phases but only about 7 weeks during declining phases (Krebs et al. 1969). Their study also suggested a positive relationship between longevity and body mass represented by sigmoidal growth curves of individual voles (Krebs et al. 1969).

Rose and Dueser (1980) studied the lifespan of 6 *M. pennsylvanicus* grid populations near Charlottesville, Virginia, for 3.5 years and found that males lived about 23 weeks and females lived 25 weeks. Females lived significantly longer than males on 2 of their 6 trapping grids (Rose and Dueser 1980). Though not significant, females lived longer than males on 3 of the other grids and males outlived females on 1 grid (Rose and Dueser 1980).

OBJECTIVES

The *r*-selected characteristics make *M. pennsylvanicus* a model species for studying growth rates and population trends over many generations in a short time span. The 2 Chesapeake meadow vole populations that were the focus of this study are in the southern range of the species, unmanipulated, easily accessible, and provided an excellent opportunity to observe size and growth dynamics of wild voles.

I researched body size, growth rates, sexual maturation rates, and lifespans in 2 populations to determine how these characteristics compared to those from more northerly locations. I hypothesized that due to mild winters, these meadow voles would continue to gain mass throughout the year, achieve higher masses and perhaps live longer than meadow voles from more northerly locations, and that autumn-born voles would grow and reach sexual maturity at rates similar to young born in other seasons.

CHAPTER II

MATERIALS AND METHODS

STUDY AREAS

Our study sites were 2 oldfields in Chesapeake, Virginia (37°50'N, 76°20'W, 3 m elevation), 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 in effect these are isolated populations. The Su and Stephens sites are former agriculture fields, last used for farming in 2000 and 2003, respectively, and have begun secondary succession. Several small mammal species were present at both sites, including *Reithrodontomys humulis* (eastern harvest mouse), *Oryzomys palustris* (marsh rice rat), *Sigmodon hispidus* (hispid cotton rat), *Blarina brevicauda* (northern short-tailed shrew), *Blarina carolinensis* (southern short-tailed shrew), *Cryptotis parva* (least shrew), *Mus musculus* (house mouse), and *M. pennsylvanicus.*

Undeveloped mixed-wood forest surrounds the Su site. When the study grid was established in December 2002, herbaceous plants such as *Schizachyrium scoparium* (little bluestem), *Solidago spp.* (goldenrod), and *Aster* spp. (asters) dominated the field. Volunteer seedlings of *Pinus taeda* (loblolly pine) grew rapidly by 2005, and made the site increasingly unsuitable for herbivorous and omnivorous rodents. When trapping was initiated at the Stephens tract in October 2005, little bluestem, goldenrod, asters, and large patches of *Scirpus cyperinus* (wool grass) dominated the low-lying areas. *Liquidambar styraciflua* (sweet gum) and *Acer rubrum* (red maple) have increased since trapping began, but at low enough densities to still support oldfield rodent species.

TRAPPING

Each study area had an 8 x 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 is 1 ha. We conducted trapping on the Su grid monthly from December 2002 through March 2005 (28 months). The first vole was captured in January 2003. Trapping on the Stephens grid began in October 2005 and continues to the present, but my sampling ended in February 2008 (29 months).

We trapped animals during a 3-day period each month in modified Fitch-type live traps (Rose 1994). Permits required by the Virginia Department of Game and Inland Fisheries are listed in Appendix A. Consent from the Institutional Animal Care and Use Committee (IACUC) is in Appendix B. These 2 approvals cover trapping, handling, marking, collection, and necropsy of animals. We baited the traps with a combination of sunflower seeds and mixed birdseed. During the colder months, we added polyfill to each trap to provide the animals with insulation. At the start of each trapping period, we set the traps before sunset, checked them the following morning, and re-baited the traps for the next trapping day. During the warmer months (typically April through October), we locked traps open in the mornings and reset them in the late afternoon. This prevented heat-related mortality of trapped animals. On the last day of trapping, we locked the traps in the "open" position.

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

In September 2005 and June 2007, we reduced the trapping session to 2 days due to extreme trap disturbance by predators on the Stephens grid. To prevent too much time elapsing between the normal monthly sessions, we conducted 2 trapping sessions on the Stephens grid in August 2007.

We set live traps about 150 m north of the Stephens grid to collect meadow voles for necropsy, specifically to obtain weights, linear measurements, and sexual conditions for adult voles. This trapping began in December 2006 and additional trapping was conducted in March 2007, July 2007, and November 2007. We locked the traps in the "open" position while not in use. We brought adult ($\geq$30 g) meadow voles to the laboratory at Old Dominion University and weighed, recorded the sexual condition of, and euthanized the voles. Young voles (<30 g) and species other than meadow voles were released at the point of capture. Adult voles were immediately euthanized in the laboratory by carbon dioxide asphyxiation, their linear (total length, tail length, hindfoot length, and ear length) and weight measurements taken, and then voles were frozen until necropsy at a later time. One person did all of the measurements to minimize measurement error.

At necropsy, reproductive information collected from males was: testes size (mm), testes weight (mg), seminal vesicles size (mm), seminal vesicles weight (mg), degree of epididymal convolution, and fat index. Reproductive information collected from females was: embryos per horn, embryo size (mm), uterine weight (mg), uterine condition, placental scars per horn, uterine diameter (mm), corpora lutea per ovary, corpora lutea diameter (mm), ovary size (mm), degree of mammary development, and fat index. Tissue samples were taken and preserved in solution for later DNA analysis, and the carcass was preserved as skull and skeleton. Numbered specimens (including skin, tissue, skull and skeleton) and the related sheet of reproductive information for each later were donated to the Field Museum of Natural History.

Research on meadow voles followed American Society of Mammalogists guidelines (Gannon et al. 2007) for studies in field and lab.

STATISTICAL ANALYSIS

For all statistical analyses, young voles are defined as <30 g and adult voles as ≥30 g. Winter was considered December-February, spring was March-May, summer was June-August, and autumn was September-November. I performed all statistical analyses using SPSS 16.0 (SPSS 2007).

Basic population demographics

Because embryos add substantial mass to females, I excluded pregnant females when calculating monthly and grand mean masses for adult males and females on both grids. Scrotal males were included, because enlarged testes constitute only about 3% of adult male body mass. I determined the minimum number of voles alive (MNA) during each month of trapping at both Chesapeake sites by using the standard MNA calculation (Krebs 1966). Because the effective trapping area is 1 ha, the MNA provided population density estimates throughout the study. Chi-square analysis was used to determine if sex ratios were different than 1:1. The number of individuals captured divided by the MNA produced monthly trappability estimates for each sex and population (Krebs and Boonstra 1984). The first and last months of trapping were omitted from the trappability calculation to minimize skewing.

Linear measurements and mass from the necropsy data were averaged and 2-sample *t*-tests were used to determine the degree of sexual dimorphism for measured traits. Mass for pregnant females was calculated by subtracting the mass of the embryos from her overall mass. A linear regression analysis was used to determine the relationship between body length measurements and mass of necropsied animals.

Body mass variation

Because Krebs et al. (1969) and Mihok et al. (1985) found voles to be heavier during increasing and peaking populations, I used a linear regression analysis to determine if adult mass was related to the population density. I did 4 2-sample *t*-tests, 1 for each sex and grid, comparing the adult masses from the 3 consecutive months of peak density to the adult masses in all other months. Four 2-sample *t*-tests, 1 for each sex and grid, compared the adult masses from the 3 consecutive months of lowest density to the adult masses in all other months. Because autumn 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), 2-sample *t*-tests were used to compare autumn masses to the masses in all other seasons combined for adults of each sex and grid to determine if significant differences existed. Two-sample *t*-tests were used to compare mean masses during population density highs and lows for each grid. Visibly pregnant females were excluded from these analyses. All of the above-mentioned *t*-tests violate the assumption of independence because the same individuals were sometimes in both groups being compared; however, these methods have been used by Krebs et al. (1969) and Mihok et al. (1985). I did a second set of *t*-tests using only mass data obtained at first capture, which does not violate assumptions of independence. Results from this series of tests are reported in the Results section, but because no other studies used these methods, no previous results exist for me to compare them in the Discussion. The first series of tests provides a better comparison to previous studies.

Growth

I calculated monthly adult growth rates by using changes in body mass of an individual from its first capture in 1 trapping period to its first capture in a later month. The change in mass was divided by the number of days between these captures and multiplied by 30 to compute growth rates per month. Again, pregnancy causes extreme mass fluctuations and visibly pregnant females were excluded.

I excluded synonomized voles from analysis of growth patterns because of the uncertainty associated with the procedure of synonymizing tag numbers. Voles captured in only 1 month were also excluded from the analysis of growth patterns because at least 2 months of measurements are required to detect mass changes in an animal. A Model I 2-factor ANOVA was used to determine significant differences among months at each study site. The 4 ANOVAs evaluated both sexes on both grids and I ran a Ryan-Einot-Gabriel-Welsch F (REGWF) post-hoc test on data yielding significant ANOVA results. Two-tailed *t*-tests were used to determine if growth rates were higher during peak population densities for each sex and grid.

A linear regression analysis using the MNA and mean growth rates of each sex was performed to determine if a relationship existed between population density and growth rates. I analyzed only the Stephens grid voles for this association because, with its larger sample sizes, it provided the best chance to see a relationship.

Breeding seasons

The breeding season for *Microtus pennsylvanicus* in Chesapeake was determined using the necropsy data and then compared with the monthly capture-mark-release data. The presence of embryos in females and of convoluted epididymides in males were the internal indicators of active breeding. Of the 3 recorded external features for females on the grids, at least 2 of the following were required for a female to be deemed as actively breeding: open pubic symphysis, medium or large nipples, or perforate vagina. Males were considered actively breeding if they had descended testes. Breeding seasons are defined as those months when $\geq$50% of males and $\geq$30% of females are in reproductive condition (McCravy and Rose 1992).

Suspended growth and sexual maturation

To determine if autumn-born individuals suspended body growth over the winter, I examined young autumn-born voles captured in more than 1 month. For this study, autumn was 1 September-30 November. After recording whether each individual reached adult mass by the following month, a contingency table analysis (1-tailed Fisher's exact test) was used to determine if males and females differed significantly in early body growth rates. A 2-tailed *t*-test was used to compare the second month masses of autumn-born voles to those born in all other seasons. This revealed if young voles grew at similar rates without regard to season of birth.

To determine if autumn-born individuals delay sexual maturation through the winter, I examined data from all young voles captured in 2 or more months. An independent multi-factor ANOVA determined if significant differences existed in rates of sexual maturation between males and females and between voles born in autumn vs. other seasons. The maturation rate was calculated as the number of months that elapsed until a previously caught young vole was sexually mature. If the testes were descended into the scrotum, I considered the male sexually mature. Of the 3 recorded external features for females, at least 2 of the following were required for sexual maturity: open or slightly open pubic symphysis, medium or large nipples, or perforate vagina (McCravy and Rose 1992). Data from only the Stephens grid were used for analysis of maturation rate because at the Su tract only 1 young female and no males were later recaptured as sexually mature adults.

Lifespans

I calculated lifespan in weeks by the methods of Rose and Dueser (1980). Synonomized voles and those voles captured within the 3 months before the conclusion of the study were excluded. A 2-factor ANOVA compared males and females at each grid. One-sample *t*-tests compared the mean lifespan of each sex on each grid to the weighted averages from the study of Rose and Dueser (1980).

CHAPTER III

RESULTS

BASIC POPULATION DEMOGRAPHICS

On the Su grid, we captured 84 male and 65 female meadow voles, compared to 342 males and 381 females on the Stephens grid. Chi-square analysis revealed the sex ratios were the same on both grids (Su: $\chi^2 = 2.423$, $P = 0.12$; Stephens: $\chi^2 = 2.104$, $P = 0.15$). Of the 149 and 723 voles tagged on the Su and Stephens grids, respectively, 14 (9%) and 89 (13%) were juveniles or subadults at first capture. On the Su grid, 39 males (46%) and 37 females (57%) were captured only once and are considered transients. We captured 175 males (51%) and 167 females (44%) from the Stephens grid 1 time only. Overall, 50% of males and 46% of females are considered transients.

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 (Fig. 1). Overall trappability of this population was 49% (*SE* = 5.5) for males and 57% (*SE* = 6.7) for females. Predator disturbance caused lower trappability during several months of this study on both grids. The highest density on the Su grid resulted from population increases through autumn and winter in 2004.

By contrast, the density of voles on the Stephens grid was lowest in June 2007 ($n = 22$/ha) and highest in August 2006 with 223/ha (Fig. 2). The trappability of this population was 63% (*SE* = 4.1) for males and 65% (*SE* = 4.3) for females. This population increased during the first winter and through the summer and then declined through the following summer.

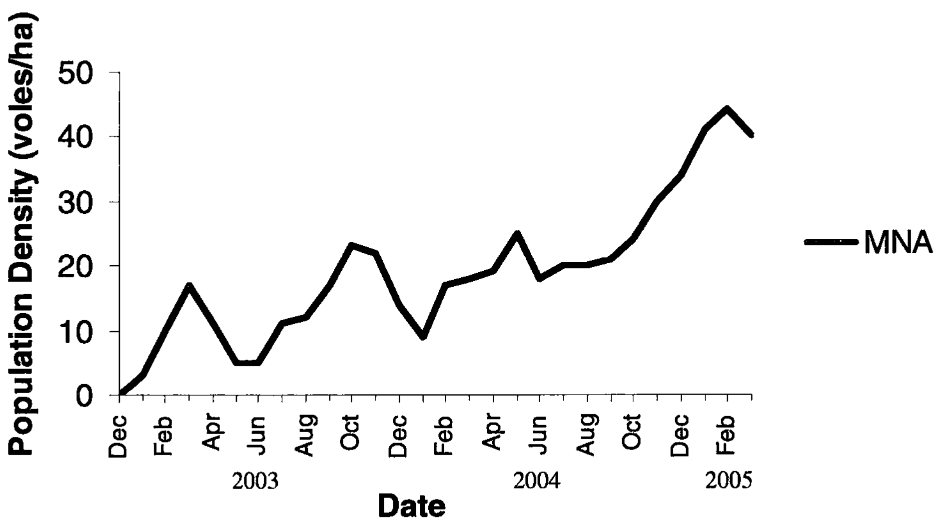

Fig. 1.—Population density changes in *M. pennsylvanicus* from December 2002-March 2005 on the Su grid.

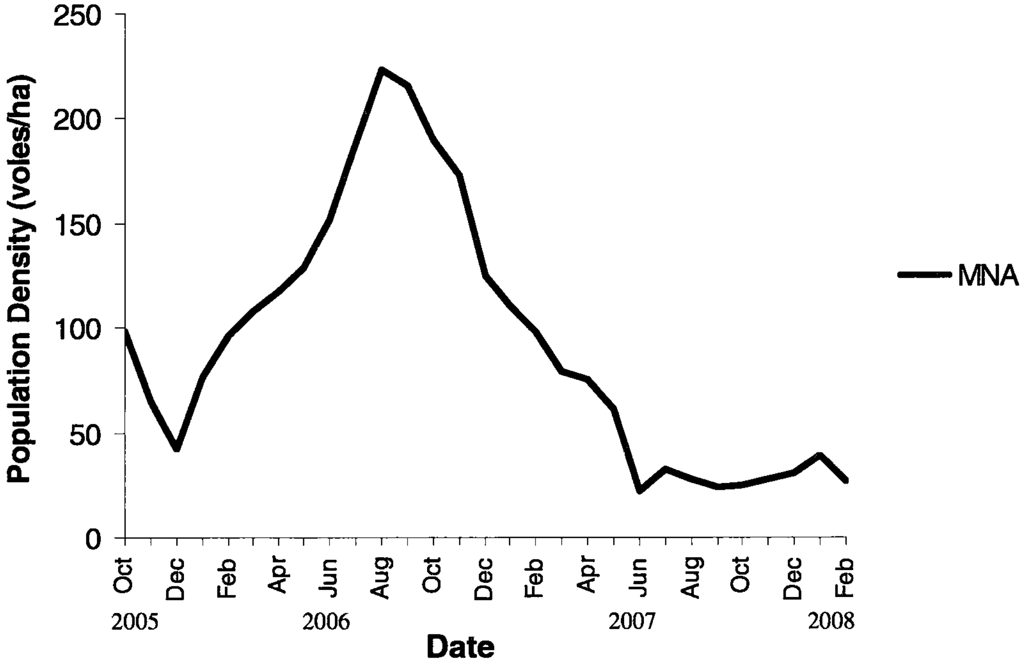

Fig. 2.—Population density changes of *M. pennsylvanicus* from October 2005-February 2008 on the Stephens grid.

Sample sizes for males and females on the Su grid ranged from 0 to 15 per month. Monthly mean mass for males was usually higher than for females (Fig. 3), with grand means of 59 g (range: 30-94 g, *SE* = 1.5) and 51 g (range: 30-70 g, *SE* = 1.1) for males and females (pregnant females excluded), respectively. A 2-tailed *t*-test indicated a significant difference in mass between males and females ($t = 4.334$, *d.f.* = 124, $P < 0.001$). All statistical test results are listed in Appendix C.

Monthly sample sizes on the Stephens grid ranged from 2 to 84 for each sex. Monthly mean mass for males was usually higher than females (Fig. 4), with grand means of 56 g (range 30-89 g, *SE* = 0.4) and 48 g (range: 30-75 g, *SE* = 0.3) for males and females, respectively. A 2-tailed *t*-test indicated a significant difference in mass between males and females ($t = 14.432$, *d.f.* = 1539, 16, $P < 0.001$).

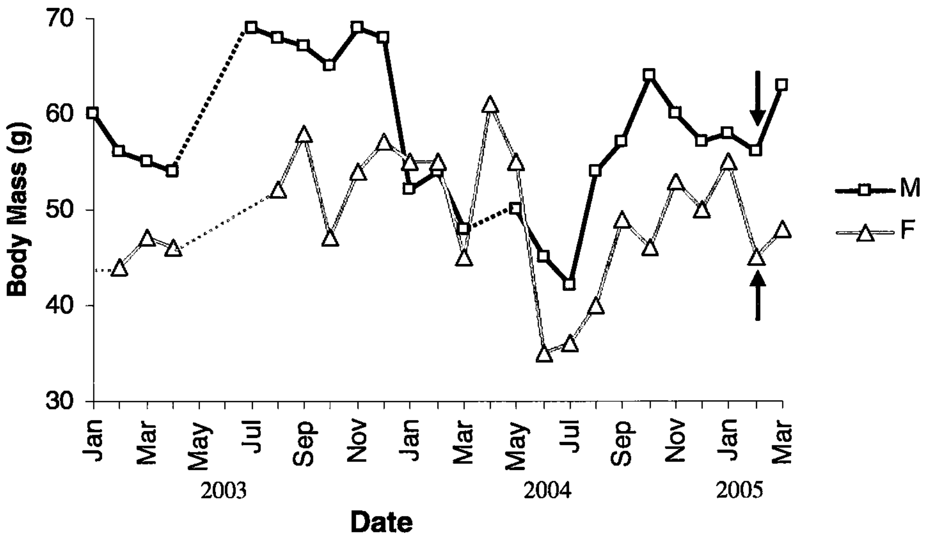

FIG. 3.—Monthly mean masses of adult males and females on the Su grid, excluding pregnant females. Dashed lines indicate no voles were trapped during those months. Arrows indicate when the population density peaked.

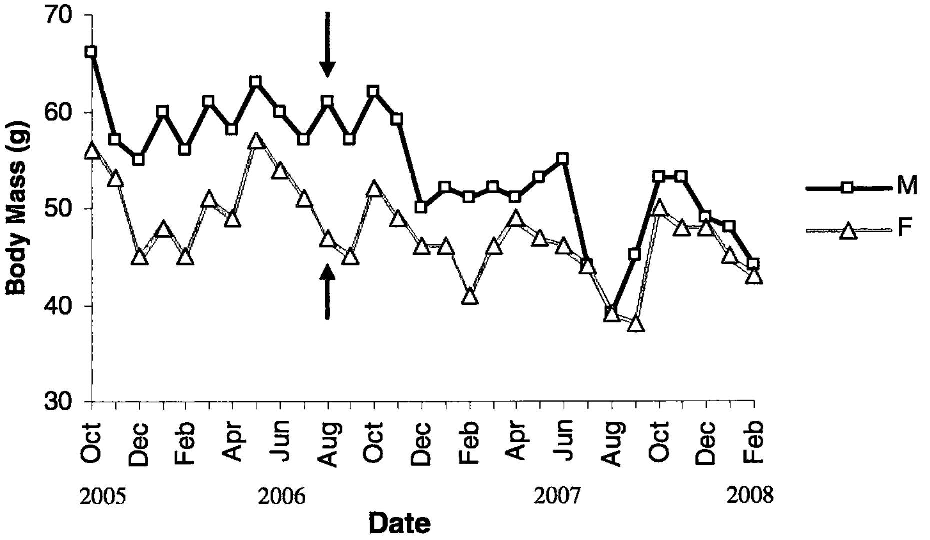

FIG. 4.—Monthly mean masses of adult males and females on the Stephens grid, excluding visibly pregnant females. Arrows indicate when the population density peaked.

I used necropsy data to calculate mean values for linear measurements and mass (Table 1). Two-tailed *t*-tests for each measurement established no significant difference in linear measurements and mass between the sexes, although the range of values was often higher for males than for females. Unlike live voles on the Stephens grid, the necropsied animals collected in 4 months were not sexually dimorphic in mass (Table 1).

A linear regression analysis showed a significant positive relationship between mass and body length of necropsied animals (Fig. 5—males: $R^2 = 0.732$, $t = 9.351$, $d.f. = 33$, $P < 0.001$; females: $R^2 = 0.721$, $t = 9.514$, $d.f. = 36$, $P < 0.001$).

TABLE 1.—Linear measurements (mm), mass (g), and significance values of the comparison for adult males (N = 34) and females (N = 37) trapped near the Stephens grid. Pregnant females were included with the mass of embryos subtracted.

Measurement	Male (*SE*)	Male range	Female (*SE*)	Female range	*P*
total length	182 (1.9)	163-204	181 (2.1)	153-198	0.649
body length	130 (1.4)	114-143	129 (1.4)	113-140	0.720
tail length	52 (0.8)	38-63	52 (0.9)	40-50	0.617
hindfoot length	23 (0.1)	21-25	23 (0.2)	21-24	0.945
ear length	13 (0.1)	12-15	13 (0.1)	11-14	0.237
mass	47 (1.5)	32-63	47 (1.5)	30-67	0.839

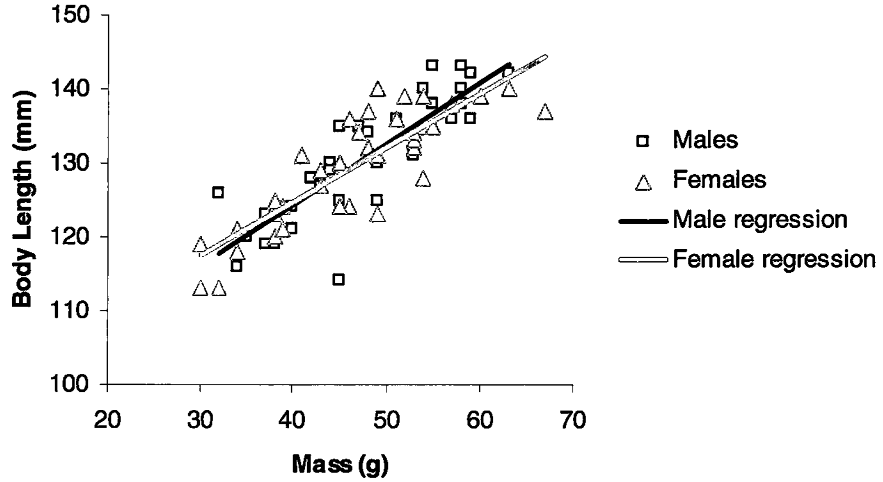

FIG. 5.—Body length (mm) against mass (g) for all adult voles from the necropsy samples.

BODY MASS VARIATION

Mean mass during the highest density on the Su grid (January-March 2005) was 58 g (n = 26, *SE* = 2.8) for males and 48 g (n = 24, *SE* = 1.9) for females. Two-tailed *t*-tests used to compare the mean mass of each sex during the peak population to the mean mass during all other months yielded non-significant results (males: *t* = 0.399, *d.f.* = 129, *P* = 0.691; females: *t* = -0.956, *d.f.* = 85, *P* = 0.625). Two-tailed *t*-tests used to compare the mean mass during the population low (January-March 2003) to the mean mass during all other months for each sex yielded non-significant results for males and females on the Su grid (males: *t* = 0.338, *d.f.* = 121, *P* = 0.736; females: *t* = 0.852, *d.f.* = 82, *P* = 0.399). During the population low, males and females weighed 54 g (n = 7, *SE* = 2.6) and 46 g (n = 3, *SE* = 3.5). With males 8% lighter and females 10% lighter than the grand mean mass, combining the sexes gives an estimate of ≈9% lower mass during the period of low population density. Mean masses between the 3-month periods of high and low population densities for each sex were not significantly different (males: *t* = 0.299, *d.f.* = 23, *P* = 0.767; females: *t* = 0.362, *d.f.* = 24, *P* = 0.721).

When only mass at first capture was used for analysis on the Su grid, males and females had a grand mean of 52 g (n = 69, *SE* = 1.6) and 46 g (n = 44, *SE* = 1.3), respectively. Males were not significantly different in mass during the 3-month period of the population peak (*t* = 0. 471, *d.f.* = 67, *P* = 0.639) nor low (*t* = 0.443, *d.f.* = 67, *P* = 0.659) when compared to other phases. Females were not significantly different in mass during the population peak (*t* = 0.682, *d.f.* = 42, *P* = 0.499) and only 1 female had an initial capture during the population low, so a *t*-test could not be run.

During the population peak on the Stephens grid from July-September 2006, males weighed 58 g (n = 73, *SE* = 0.9) and females weighed 47 g n = 68, *SE* = 0.7). Two-tailed *t*-tests comparing the mean mass of each sex during the peak population to the mean mass during all other months yielded significant results for males, but not for females (males: *t* = 2.339, *d.f.* = 812, *P* = 0.020; females: *t* = -1.722, *d.f.* = 303, *P* =

0.086). Two-tailed *t*-tests comparing the mean mass during the population low (August-October 2007) to the mean mass during all other months yielded significant results for males and females (males: $t = 5.408$, *d.f.* = 810, $P < 0.001$; females: $t = 3.647$, *d.f.* = 958, $P < 0.001$). During the population low, males and females weighed 44 g (n = 11, *SE* = 1.8) and 44 g (n = 8, *SE* = 1.9). With males 21% lighter and females 8% lighter than the grand mean mass, combining the sexes gives an estimate of ≈15% lower mass during the period of low population density. Mean masses between the high and low population densities were significantly different for males and females (males: $t = 5.769$, *d.f.* = 211, $P < 0.001$; females: $t = 2.505$, *d.f.* = 251, $P = 0.013$).

When only mass at first capture was used for analysis on the Stephens grid, males and females had grand means of 52 g (n = 286, *SE* = 0.8) and 46 g (n = 261, *SE* = 0.7), respectively. Males were not significantly heavier in mass during the population peak ($t = 0.453$, *d.f.* = 284, $P = 0.651$), but were significantly lighter (45 g, *SE* = 3.2) during the low ($t = 2.086$, *d.f.* = 284, $P = 0.038$) when compared to other phases. Females were significantly lighter during the peak (42 g, *SE* = 1.1) and low (38 g, *SE* = 2.6) population densities when compared to all other phases (peak: $t = 3.172$, *d.f.* = 259, $P = 0.002$; low: $t = 2.236$, *d.f.* = 259, $P = 0.026$).

There were periods on each grid with very large voles (≥70 g). On the Su grid, the heaviest vole was a 94 g scrotal male caught in December 2003. The heaviest female captured was 75 g and pregnant in December 2004. The heaviest non-pregnant female was 70 g in December 2003. We captured 14 males (17%) and 4 females (6%) ≥70 g on the Su grid throughout the study. Two of these large females were not pregnant. October-December 2003 was notable because we captured 5 males weighing 70-94 g and 3 (2 not pregnant) females ≥70 g, or 44% of our heavy animals in this short period. The heaviest vole on the Stephens grid was a 93 g pregnant female captured in October 2005. The heaviest male was scrotal and 89 g in March 2006 and the heaviest non-pregnant female was 75 g in October 2006. Sixty-four males (19%) were captured at ≥70 g on the Stephens grid, 23 (36%) of which were captured between September and November 2006. Forty-six females (12%) attained masses ≥70 g on the Stephens grid and 10 were not pregnant.

A linear regression analysis (Fig. 6) showed a significant relationship between population density and mean mass for males and females (males: $R^2 = 0.276$, $t = 4.622$, *d.f.* = 28, $P < 0.001$; females: $R^2 = 0.155$, $t = 2.229$, *d.f.* = 28, $P = 0.034$).

Two-sample *t*-tests comparing autumn masses to all other seasons yielded significant results for males and females on both grids (Table 2). All were significantly heavier in autumn.

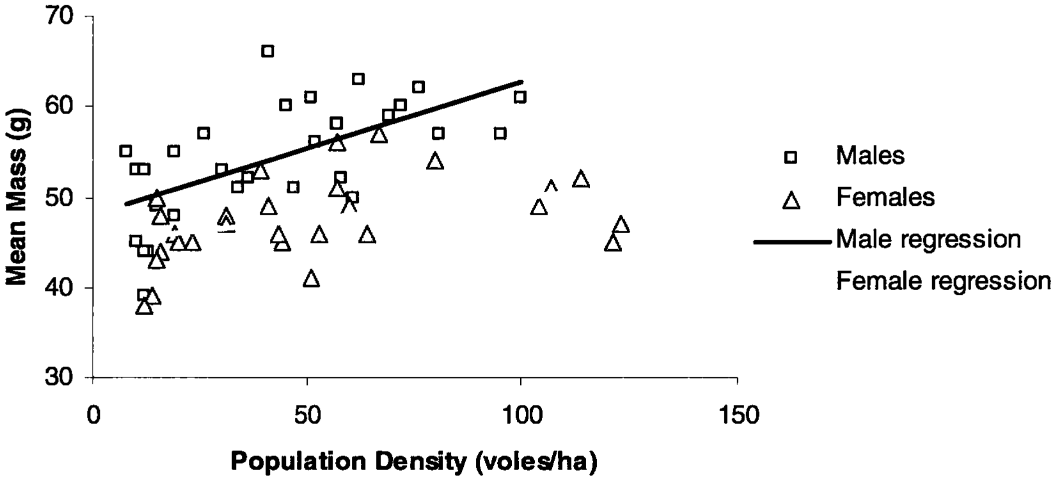

FIG. 6.—Mean mass of adult males and females of the Stephens tract plotted against the population density of each sex from October 2005-February 2008. Each point represents one month and the regression lines indicate the relationship.

TABLE 2.—Mean masses in autumn versus all other seasons for non-pregnant adults on each grid.

Grid	Sex	*t*	*df*	*P*	Autumn mass (g) (*SE*)	Other season mass (g) *(SE)*
Su	M	5.470	106	< 0.001	65 (1.6)	53 (1.5)
Su	F	2.610	47	0.012	52 (1.4)	47 (1.2)
Stephens	M	4.339	808	<0.001	59 (0.8)	55 (0.5)
Stephens	F	2.176	812	0.030	49 (0.6)	47 (0.4)

GROWTH

Voles at the threshold of adulthood (30 g) likely have higher growth rates than voles at 60 g, for instance. 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.

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. 7). The females had positive growth rates except during the months of August and November, 2003 and January, 2004 (Fig. 7). ANOVAs that compared growth rates for the males and females on the Su grid detected no significant difference among months (males: $F = 0.787$, *d.f.* = 22, 45, $P = 0.723$; females: $F = 1.190$, *d.f.* = 15, 16, $P = 0.366$).

The grand means for growth in males and females on the Su grid were +3.9 g/month ($SE = 0.6$) and +2.0 g/month ($SE = 0.9$), respectively, but this difference was non-significant ($t = 1.781$, *d.f.* = 97, $P = 0.078$). Two-tailed *t*-tests comparing the monthly mean growth rate of each sex during the January-March 2005 population peak to

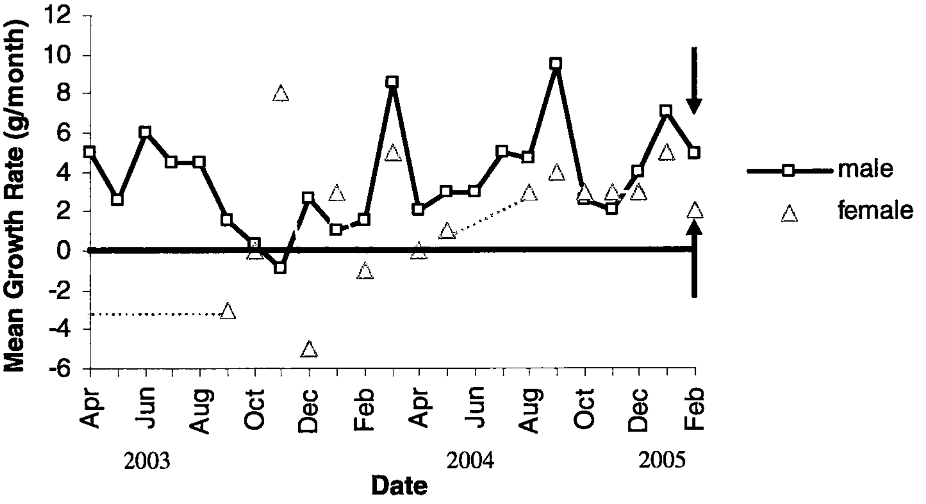

FIG. 7.—Mean growth rate (g/month) on the Su grid between April 2003 and February 2005. Dashed lines represent months for which female growth rates could not be calculated. Arrows indicate month of peak population density.

the mean growth rate during all other months yielded non-significant results for both sexes (males: $t = -1.483$, *d.f.* = 66, $P = 0.143$; females: $t = -0.872$, *d.f.* = 29, $P = 0.390$). Males gained an average of 5.8 g/month (*SE* = 1.79) during the peak months and 3.5 g/month (*SE* = 0.59) during all other months. Females gained an average of 3.4 g (*SE* = 1.60) during the peak months and 1.6 g (*SE* = 1.09) during all other months.

We had repeat captures of 138 males and 132 females on the Stephens grid. Monthly growth rates for males and females on the Stephens grid were erratic, but generally positive (Fig. 8); however, both sexes had negative growth rates in November 2005, December 2006, July, August, and November 2007, and February 2008. Females also had negative growth rates in August and September 2006 and in February and June 2007.

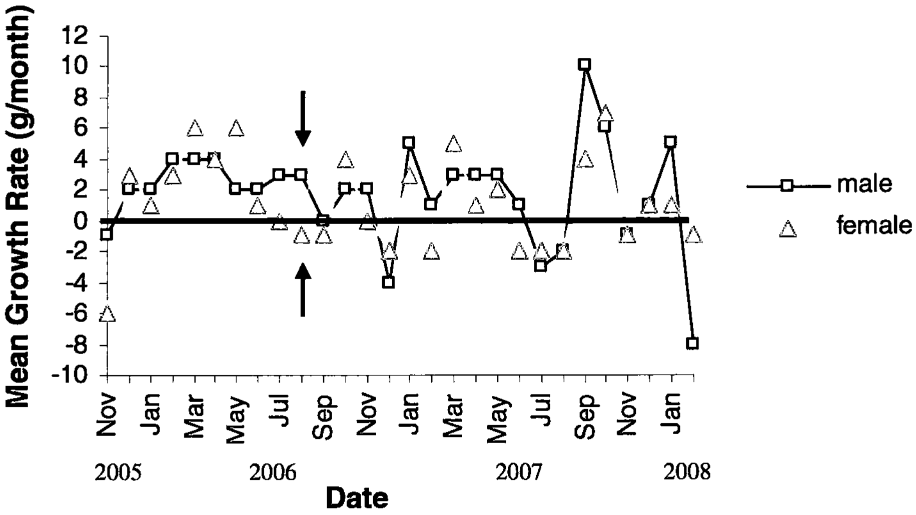

FIG. 8.—Mean growth rate (g/month) on the Stephens grid between November 2005 and February 2008. Arrows indicate month of peak population density.

The ANOVAs detected significant differences in growth rates among months for both sexes on the Stephens grid (males: $F = 2.300$, *d.f.* = 27, 416, $P < 0.001$; females: $F = 4.428$, *d.f.* = 27, 440, $P < 0.001$). The REGWF tests did not reveal a seasonal relationship to mass changes, so I did a linear regression analysis for both sexes to see if growth rates correlated with population density (Fig. 9). I found no significant relationships between mean growth and population density (males: $R^2 = 0.001$, $t = 0.170$, *d.f.* = 27, $P = 0.866$; females: $R^2 = 0.010$, $t = -0.518$, *d.f.* = 27, $P = 0.609$). The grand means for monthly growth rates in males and females were 2.0 g ($SE = 0.2$) and 1.1 g ($SE = 0.3$), respectively, and were significantly different ($t = 2.489$, *d.f.* = 1021, $P = 0.013$). Two-tailed *t*-tests comparing the mean growth rates of each sex during the peak population (July-September 2006) to the mean growth rates during all other months yielded no significant difference in growth rates for both sexes (males: $t = 0.710$, *d.f.* = 526, $P =$

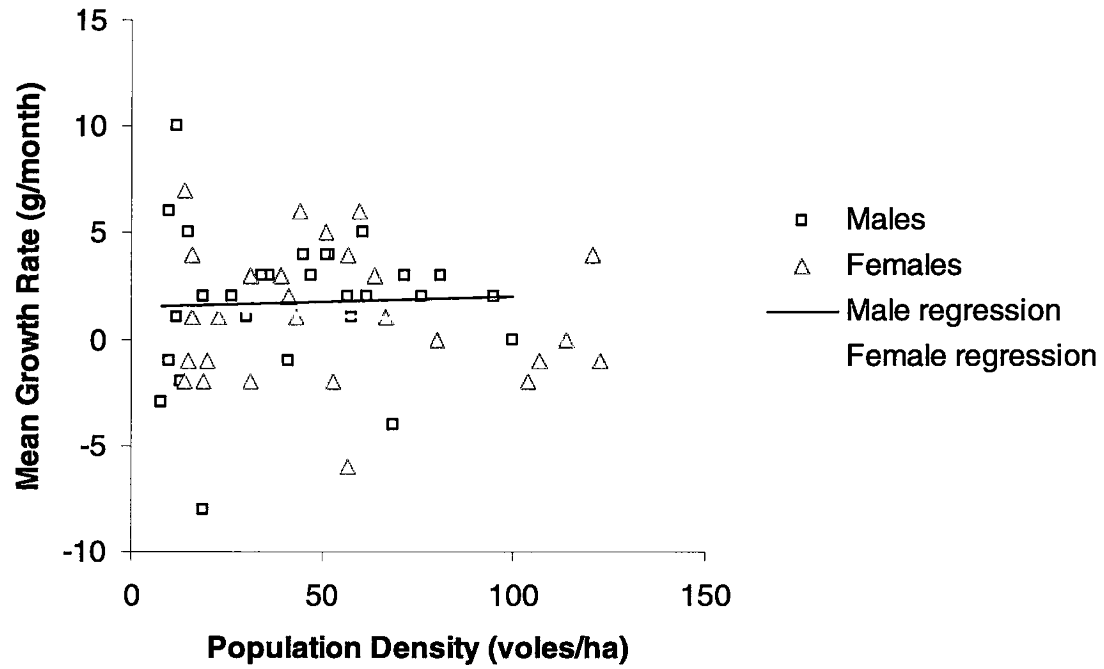

FIG. 9.—Mean growth rates (g/month) plotted against population density for voles on the Stephens grid between November 2005 and February 2008. Each point represents one month.

0.478; females: *t* = -1.178, *d.f.* = 283, *P* = 0.240). Males gained an average of 1.7 g (*SE* = 0.45) during the peak months of July-September 2006 and gained 2.1 g (*SE* = 0.27) during all other months. Females lost an average of 0.6 g (*SE* = 0.43) during the peak months and gained 1.3 g (*SE* = 0.32) during all other months.

BREEDING SEASONS

I evaluated the necropsy data to determine breeding seasons for the Stephens voles (Table 3). Year-round breeding occurred, but in summer 2007, when population density was low, we captured no females and were unable to confirm breeding. Females had 3 to 7 embryos, with an average of 5 and a mode of 4. Following the definition of McCravy and Rose (1992), I defined the breeding season as September-November and

March-May for this necropsy population, but we also observed some breeding in winter, with 2 of 19 females having litters.

Using the majority criterion for females and testes position for males, the capture-mark-release data also defined the breeding seasons. According to external indicators, the level of breeding in the Stephens population stayed above the minimum thresholds of $\geq$30% for females and $\geq$50 for males for most of the study period, indicative of year-round breeding (Fig. 10). However, the winter of 2005-2006 and summer and autumn of 2007 had at least 1 month when external breeding indicators were below critical levels.

Based on my measurements, when compared to the necropsy data, the majority criteria for external breeding signs overestimate the actual percent of actively breeding females by about 42% (*SD* = 23, omitting summer 2007 data), but are reliable indicators of breeding for males. Male necropsy data are 8% higher than the external data (*SD* = 9, omitting summer 2007). The low sample size of necropsied animals could also make the results less reliable.

TABLE 3.—Necropsy results about reproductive condition. Voles were from near the Stephens grid. Body length = total length – tail length.

Season	Sex	n	# in reproductive condition	% in reproductive condition	Mean mass (g)	Mean body length (cm)
Winter 2006	M	10	5	50	44	127
	F	19	2	11	46	128
Spring 2007	M	14	12	86	48	130
	F	12	6	50	44	127
Summer 2007	M	2	0	0	38	127
	F	0	0	.	.	.
Autumn 2007	M	8	8	100	51	134
	F	8	5	63	51	135

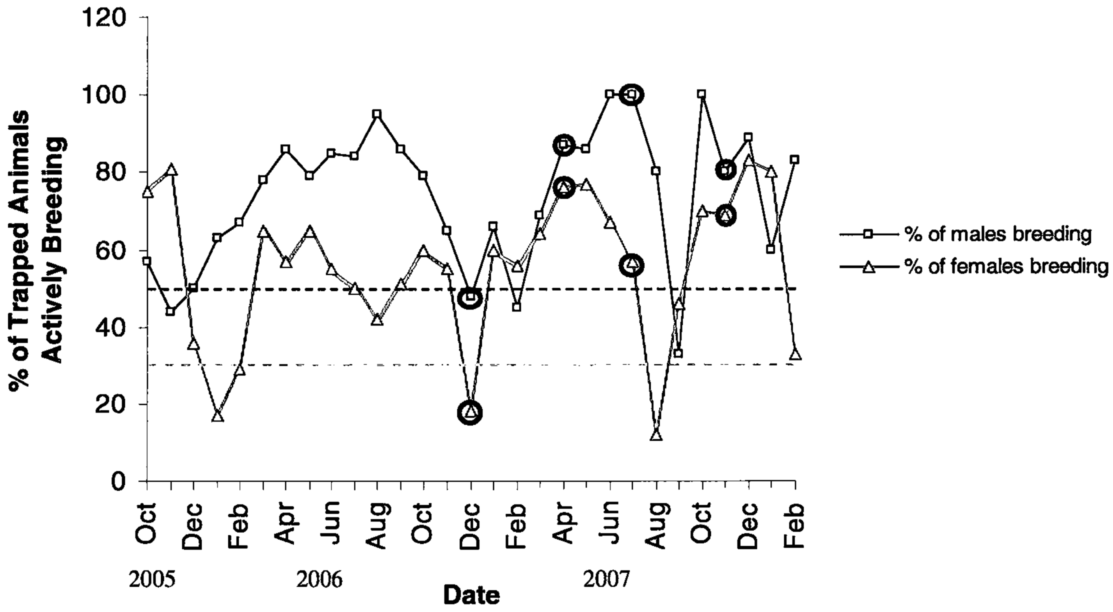

FIG. 10.—Percent of the trapped adult population having external indicators of active breeding on the Stephens grid between October 2005 and February 2008. Each point represents 1 month. The dashed lines mark the critical percent breeding values of 30% for females and 50% males, used to determine active breeding months. Bold dark circles indicate months for which corresponding necropsy data are available.

SUSPENDED GROWTH

At first capture on the Su grid, young males and females averaged 15 g (*SE* = 4.5, n = 3) and 20 g (*SE* = 2.6, n = 11), respectively. Young males and females on the Stephens grid averaged 22 g (*SE* = 0.7, n = 44) and 24 g (*SE* = 0.8, n = 45) at first capture.

A 1-tailed Fisher's exact non-parametric test, used to determine if males and females differed significantly in the proportion of young reaching adult mass by the following month, yielded no significant difference (Su: *P* = 0.60, Stephens: *P* = 0.21).

Males and females were therefore grouped together at each site to increase the sample sizes of young voles. Due to high growth rates in young voles (Barbehenn 1955; Campbell and Dobson 1992; Innes and Millar 1979), we expected them to attain adult mass (30 g) within a month. We captured 3 young males and 11 young females on the Su grid; however, only 1 male and 5 females were captured again, making the calculation of growth rates tenuous. On the Stephens grid, we caught 44 young males and 45 young females, but only 5 of these males and 16 females were caught in later months.

Two-tailed *t*-tests were used to determine if autumn-born voles suspended growth when compared to the young born in all other seasons. On the Su grid, only 1 vole was caught in the autumn, so the power of the test is weak. By month 2, the autumn-born vole of the Su grid had reached 46 g and the voles born in other seasons averaged 36 g (Table 3). The *t*-test that compared the second month masses of the autumn-born to voles born in other seasons was non-significant ($t = 0.876$, *d.f.* = 4, $P = 0.430$). The 1 vole captured in the autumn on the Su grid was not recaptured beyond her second month of life.

By month 2, the autumn-born young of the Stephens grid had reached a mean mass of 31 g and the young born in other seasons were 34 g (Table 4). The *t*-test found no

TABLE 4.—Mean mass for the second month of life of young born on the Su and Stephens grids in autumn and all other seasons. Autumn is September-November.

Site	Season of birth	n	Mean mass (g)	*SE*
Su	autumn	1	46	.
Su	winter, spring, summer	5	36	4.6
Stephens	autumn	10	31	1.5
Stephens	winter, spring, summer	11	34	1.1

significant differences ($t = -1.661$, *d.f.* = 19, $P = 0.113$), confirming that autumn-born voles do not suspend body growth or grow more slowly than young of other seasons.

SUSPENDED SEXUAL MATURATION

Because of the low numbers of captured young on the Su grid, only data from the Stephens grid were evaluated to determine if autumn-born voles suspend sexual maturation. Of the 16 young females caught in more than 1 month, only 5 were retrapped showing external signs of sexual maturation. Of the 6 young males caught in more than 1 month, 3 were trapped later as scrotal males. Young took 1-3 months to mature (Table 5); however, the ANOVA showed the maturity rate difference between sexes was non-significant (Table 6). Season also had no significant effect on the rate of sexual maturation for either sex (Table 6).

TABLE 5.—Mean months until sexual maturation for male and female young on the Stephens grid grouped by season of birth. Autumn is September-November.

Sex	Season	Mean months to sexual maturation	Range (months)	n
Male	Autumn	1.33	1-2	3
	Spring, summer, winter	.	.	0
Female	Autumn	1.67	1-2	3
	Spring, summer, winter	2.50	2-3	2

TABLE 6.—ANOVA results displaying significance values for months voles took to reach sexual maturity. Seasons were 1) autumn and 2) all other seasons combined.

Source	Type III sum of squares	*df*	Mean square	*F*	*P*
Sex	0.167	1	0.167	0.455	0.530
Season	0.833	1	0.833	2.273	0.192

LIFESPANS

On the Su grid, the average lifespan was 24 weeks (n = 20, *SE* = 1.9) for males and 19 weeks (n = 12, *SE* = 2.0) for females. Four individuals lived 41 weeks, which was the longest lifespan on the Su grid. Voles from the Su grid showed a tendency to continuously gain body mass throughout their lifespans (Fig. 11).

At the Stephens site, the average lifespan was 25 weeks (n = 97, *SE* = 0.9) for males and 27 weeks (n = 109, *SE* = 1.1) for females. Male #1746 lived a minimum of 80 weeks, which was the longest on Stephens grid. I selected 4 long-lived adults from the Stephens grid and graphed their growth trajectories. The expected sigmoidal growth curve was not exhibited on the Stephens tract and sporadic gains and losses in mass were apparent for both sexes (Fig. 12). This pattern was also seen in monthly growth rates.

The results from the 2-factor ANOVA comparing lifespans of males and females from each grid were significant for the grid ($F = 4.495$, *d.f.* = 1, 234, $P = 0.035$) and non-significant for sex ($F = 0.401$, *d.f.* = 1, 234, $P = 0.527$). The REGWF post-hoc test done on the crossed factors of sex and grid revealed that females from the Su grid lived significantly shorter lives than the females from the Stephens grid ($F = 0.259$, *d.f.* = 3, 234, $P = 0.050$).

When compared to lifespans documented by Rose and Dueser (23 weeks for males and 25 weeks for females—1980) in Charlottesville, females from the Su grid had significantly shorter lives ($t = 3.035$, *d.f.* = 11, $P = 0.011$). Lifespans of Su grid males and Stephens grid males and females were similar when compared to the Charlottesville values (Su males: $t = 0.423$, *d.f.* = 19, $P = 0.677$; Stephens males: $t = 1.707$, *d.f.* = 96, $P = 0.091$; Stephens females: $t = 1.567$, *d.f.* = 108, $P = 0.120$).

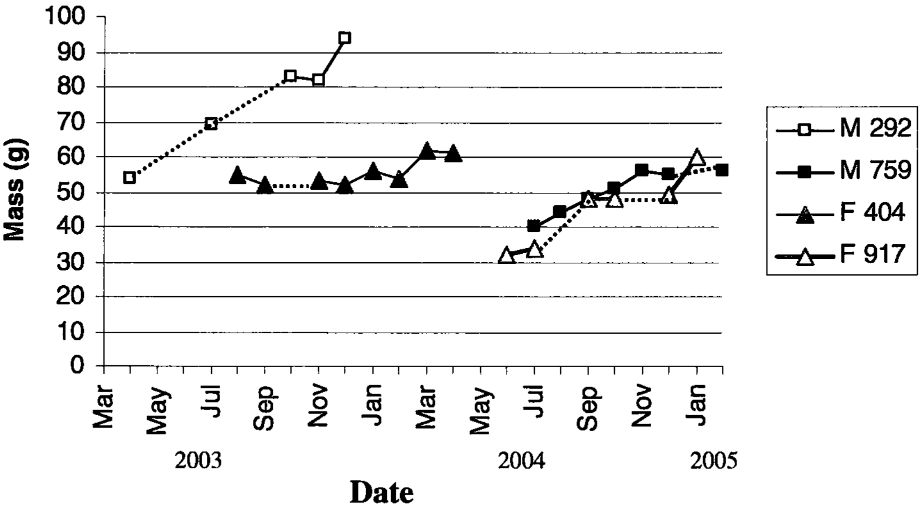

FIG. 11.—Growth trajectories of selected long-lived individuals from the Su grid. Dashed lines represent intervals between actual captures. Each point represents an actual month of capture.

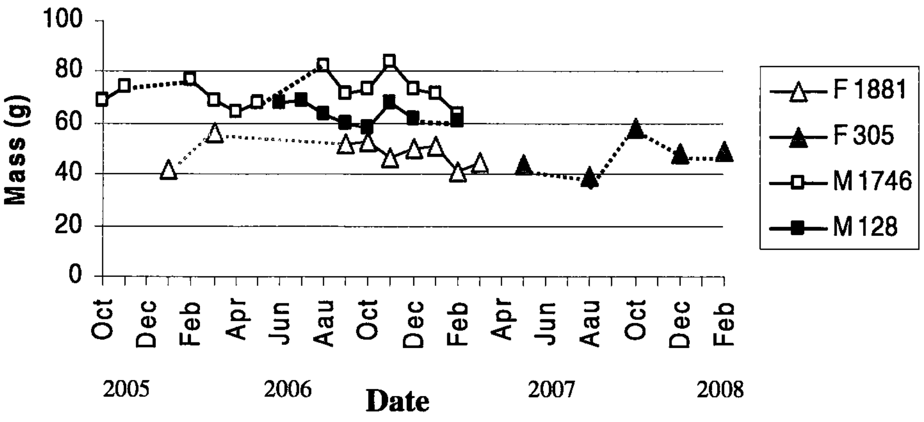

FIG. 12.—Growth trajectories of selected long-lived individuals from Stephens tract. Dashed lines represent intervals between captures. Each point represents an actual month of capture.

Table 7 summarizes mass and growth rate patterns among seasons, and lifespans, for both grid populations.

TABLE 7. Means of mass and growth rates grouped seasonally by sex and grid. Lifespan is given for the entire study period.

	Su		Stephens	
Seasonal measurement	M	F	M	F
Winter				
mean mass (g)	58	53	51	45
mean growth rate (g/month)	4	1	1	1
Spring				
mean mass (g)	56	50	56	50
mean growth rate (g/month)	5	2	3	4
Summer				
mean mass (g)	57	44	50	46
mean growth rate (g/month)	5	2	1	-1
Autumn				
mean mass (g)	64	51	55	47
mean growth rate (g/month)	5	2	3	2
mean lifespan throughout study (weeks)	24	19	25	27

CHAPTER IV

DISCUSSION

Population studies of *Microtus pennsylvanicus* on sites undergoing secondary succession present unique challenges because meadow voles inhabit oldfields. The progression of fields into young forests causes habitat loss for voles. It is difficult to know whether to attribute population fluctuations to habitat losses or normal annual changes in population. With desirable habitat present for a short period, we find problems such as truncated lifespans due to emigration and shrinking usable habitat that can only support low density populations. This results in low sample sizes, making analysis unreliable. This describes the situation at the Su grid, where population declines occurred in all rodent species and no meadow voles were captured after summer 2005.

BASIC POPULATION DEMOGRAPHICS

Both Chesapeake populations had large fluctuations in population density throughout the study. The Su grid voles steadily grew in numbers despite population density dips about every six months (Fig. 1). The Stephens tract provided a unique opportunity to see a population climb, peak, and then decline (Fig. 2). *Microtus pennsylvanicus* in Chesapeake may indeed experience population density cycles; however, this study does not span enough time to confirm this. A population low may explain the low density beyond July 2007 on the Stephens grid, but the highest density on the Su grid was when loblolly pines began dominating the site, which is counterintuitive because habitat was becoming less suitable.

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 Charlottesville, Virginia. The highest density recorded on the Su tract was only 44 voles/ha and this density was, in part, the result of a population increase through autumn and winter. The initial oldfield habitats at both sites were similar, but vole population densities were extremely different as habitat succession proceeded. The population density high and low 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 plenty of suitable vole habitat beyond our grids, so we undoubtedly had high numbers of individuals moving in and out of our grids. This is evident by the high proportions (50% for males, 46% for females) of voles captured during only 1 month. We would expect population density to be higher during the breeding seasons; however, mortality rates for young are also high (Krebs et al. 1969). Since only about 6% of young captured on either grid were later recaught, high gross mortality (= death + emigration) rates for juveniles and subadults are apparent.

Iskjaer et al. (1989) determined that mass and linear measurements were highly correlated in their study of small mammals, including *M. pennsylvanicus* trapped near Baltimore, Maryland. The necropsy data from near the Stephens grid support this observation (Fig. 5). Voles from the Su and Stephens grids were sexually dimorphic in mass, but our necropsy sample, trapped from an area adjacent to the Stephens site, was not. When I compared the mean mass of the voles from the necropsy site to voles trapped in the same months from the Stephens site, the necropsied animals consistently had lower masses, except in November 2007 when the Stephens site voles also had low masses. The sample sizes for the necropsy groups were smaller than those from the Stephens grid, which may contribute to the difference between the Stephens and necropsy grid sample groups.

BODY MASS VARIATION

I found males and females were significantly lighter (≈15%) on the Stephens grid during the period of low population density. Mean masses of males and females converged at this time. The population low at this site was in summer (2007), a time of year when voles in northern populations tend to be large (Barbehenn 1955, Brown 1973). Males and females on the Su grid were lighter (≈9%, but non-significantly) during the population low, which occurred in winter 2003. Winter is a period when lower masses are expected, particularly with numerous studies finding low winter masses and mass loss (Barbehenn 1955; Brown 1973; Iverson and Turner 1974; and Unangst and Wunder 2003).

I found a significant positive relationship between mass and population density on the Stephens grid for both males and females (Fig. 6). The significant regression is more likely due to both sexes being smaller during the period of low population density than to being larger during the peak density. This is because both sexes on the Stephens grid were significantly lighter during the population low (≈15%), but only males were significantly heavier during the population peak (4%). Though statistically significant, males being only 4% heavier during the peak (58 g compared to 56 g) was below the 20-50% predicted by Krebs and Myers (1974).

Data supplied by Dr. Chris Conroy (pers. comm.), the mammal curator at the Museum of Vertebrate Zoology, University of California, Berkeley, confirmed that only 1 meadow vole out of the 50 in his collection, which had specimens from Virginia north to Canada, was over 70 g. This large vole was a female from Accomack County, Virginia. Burt and Grossenheider (1998) and Whitaker and Hamilton (1998) list 70 g as the highest expected mass for *M. pennsylvanicus* in the field; however, nearly 20% of males at both sites were over the maximum expected value. The 3-month time periods when extra-large (≥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. This is contrary to findings by Krebs et al. (1969), who found *M. pennsylvanicus* to be smallest during population decline phases.

At the population level, voles on the Su grid had steady growth rates during the period of extra-large voles, but males decreased in mean mass while females increased. A "population sink" effect at this time is evident with males, because steady growth rates, declining population density, and decreased mean mass indicate that lighter animals entered the population and continued growing, while heavier ones either died or emigrated. On the Stephens grid, voles experienced decreased growth rates and lower masses than the months surrounding the 3-month period of extra-large voles. These large voles likely out-competed others, causing the more massive voles to flourish at the cost of growth-deficiencies in their peers. Lidicker and Ostfeld (1991), who examined 13 years of data for California meadow voles from Brooks Island, California, found that 71% of extra-large voles were present during the spring (Lidicker and Ostfeld 1991), whereas the majority of our extra-large meadow voles were present in the autumn and early winter. Importantly, the large voles were observed on our grids in autumn, when meadow voles from more northerly locations are losing mass.

Boonstra and Krebs (1979), evaluating data from studies of meadow voles in southern Indiana, found evidence of a survival advantage for large voles during rapidly increasing populations. They also found that being large was a survival disadvantage during high population density (Boonstra and Krebs 1979). This latter finding may help explain why we found many large voles during periods of population decline. Why such large voles were predominantly present on our grids during the cool seasons is unknown.

Voles in this study were significantly larger in autumn compared to all other seasons (Table 2). Perhaps these voles are strategically adding mass in preparation for winter and the associated food scarcity. The abundance of massive voles during October-December 2003 (Su) and September-November 2006 (Stephens) supports this theory. This mass-gaining strategy is opposite of that seen in more northern populations, where voles are losing mass, even when food is still abundant, as if to prepare for winter. Barbehenn (1955) and Iverson and Turner (1974) reported autumn weight loss of 25% and 45%, respectively, in meadow voles from Ithaca, New York and Pinawa, Canada.

GROWTH

R-selected species 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 lifespans (Campbell and Dobson 1992, Iskajaer 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 Chesapeake is that they are continuously adding body mass, demonstrating an indeterminate growth pattern in contrast to the determinate growth associated with most *r*-selected species.

On the Su site, males demonstrated positive growth rates in all but 1 month and females in all but 3, which supports the likelihood of indeterminate growth. After evaluating the growth trajectories of individual voles (Figs. 11 and 12), a sigmoidal growth pattern is evident on the Su grid, but not on the Stephens grid. The continuous growth of voles at the Su site supports the finding by Campbell and Dobson (1992), who described *M. pennsylvanicus* as continuously adding mass throughout its lifespan in the laboratory.

The growth patterns of populations studied by Krebs et al. (1969) and Mihok et al. (1985), who found higher body masses and growth rates in increasing and peaking populations, did not hold true for the voles from the Su grid. These voles were neither significantly heavier nor growing significantly faster during the period of population increase or peak (Figs. 3 and 7). In fact, monthly growth rates were almost always positive on the Su grid (fig. 7), but erratic on the Stephens grid (Fig. 8) and irrespective of density.

As a population, voles on the Stephens tract had erratic growth rates, and when growth rates of long-lived individuals were examined, the same pattern was evident. Few voles demonstrated sigmoidal growth patterns (Fig. 12). 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 are seemingly related to low population density. Although summer is a period of lush growth and high biomass of herbaceous vegetation, the principle foods of *M. pennsylvanicus*, high temperatures may prevent voles from diurnal foraging, resulting in mass loss. Other studies have found the highest growth rates during periods of increasing density and at population peaks, but there are 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).

Voles at the Stephens site also demonstrated lower growth rates for males and females during the population peak of July-September 2006 than during all other months (Fig. 8). Females had negative growth rates during the peak, which was unexpected. Two voles with growth trajectories I examined lost mass during the 3 months of the population peak. These results are contrary to findings by Krebs et al. (1969) and Mihok et al. (1985). One explanation for this mass loss is that high population density resulted in diminished food supplies, and therefore, mass loss.

Overall growth rates on the Stephens grid were significantly higher for males than for females. Although not significant on the Su grid, possibly due to small samples sizes, growth rates were also higher for males than females. An interesting fact is that voles on the Su grid were often heavier and had higher growth rates than voles on the Stephens grid (Table 7). Paradoxically, lifespans at the Su site were shorter for both sexes in comparison to lifespans at the Stephens site (Table 7). One explanation for this paradox is that faster growth and becoming larger results in a shortened lifespan. Though these populations were nearly adjacent, they were using 2 different life strategies. Su voles compromised longer lifespans for larger mass and faster growth, which possibly allowed for more qualitative reproduction efforts such as more successful pregnancies and larger litters. Stephens voles compromised larger mass and faster growth for longer lifespans, which allowed for more quantitative reproductive efforts, or simply more time to mate.

Extreme autumn and winter weight loss, such as the 25% reported near Ithaca, New York (Barbehenn 1955) and 45% near Pinawa, Manitoba, Canada (Iverson and Turner 1974), did not happen in either of the Chesapeake populations. In fact, winter masses were comparable to or heavier than those of summer voles (Table 7) and autumn masses were significantly heavier than all other seasons combined.

Chesapeake meadow voles seemed to have had indeterminate growth, and with long lifespans, these may be the heaviest masses ever recorded for the species. Growth rates on the Su tract were almost always positive, which supports my hypothesis that Chesapeake meadow voles grow asymptotically, continuing to add mass and length throughout their lifespans.

BREEDING SEASONS

In meadow voles, 2 cohorts generally are recognized: autumn-born young that survive the winter and breed once or twice, and spring- or summer-born young that breed the same year of their birth, but few survive the winter (Barbehenn 1955; Brown 1973). Barbehenn (1955) found no evidence of late winter breeding in New York and Krebs et al. (1969) detected some winter breeding in southern Indiana. The presence of pups in traps and young voles in traps during all seasons indicate that *M. pennsylvanicus* bred year-round on both grids in Chesapeake, Virginia. In most months voles had external indicators of breeding above critical levels on the Stephens grid (Fig. 10). Though winter had the lowest amount of breeding, dips below the critical levels were not consistent across years. The most active breeding seasons for these voles are in spring, summer, and autumn.

SUSPENDED GROWTH

As hypothesized, autumn-born voles from neither site demonstrated suspended growth, which contradicts findings by Barbehenn (1955) and Brown (1973), and supports the study of Rose and Dueser (1980). Because the Su grid data set had only 1 autumn-born juvenile qualifying for growth analysis, I examined autumnal growth patterns with the Stephens data. Although the mean mass was slightly lower for the second month of life for autumn-born young when compared to the second month of young born in all other seasons, this mass difference was not significant. Autumn-born young grow at rates comparable to young born in other seasons.

SUSPENDED SEXUAL MATURATION

I found no delay in sexual maturation of autumn-born young from the Stephens site. This supports findings by Rose and Dueser (1980) and is contrary to findings of Barbehenn (1955). Barbehenn (1955) also reported that females of *Microtus* species may begin breeding at age 3 to 4 weeks and males at age 5 to 6 weeks. The external sexual features indicated that females at the Stephens grid took longer to become sexually mature than males, which was an unexpected result (Table 5). Because so few young were ever recaptured after sexual maturity, it is important to note that we had a very small sample size available for analysis.

LIFESPANS

On the Su grid, 4 voles lived 41 weeks, compared to the longest lived vole on the Stephens grid, a male living at least 80 weeks. This male outlived the longest living vole in the Charlottesville study (Rose and Dueser 1980) by 15 weeks. Females from the Su site had statistically shorter lives than those from Charlottesville, which I am unable to explain. Because these females reached such large body masses, they must have higher growth rates than the Charlottesville voles. Males from the Su and Stephens grids and females from the Stephens grid did not live significantly longer than voles from the Charlottesville study. These voles from Chesapeake had much longer lifespans than the Indiana voles of Krebs et al. (1969): ≈11 weeks for males and ≈14 weeks for females.

Morrison et al. (1977) examined longevity of *M. pennsylvanicus* in a laboratory population, using voles from central Alaska. The males lived longer than females, with males living up to 68 weeks and females up to 56 weeks (Morrison et al. 1977), indicating their potential maximum lifespans. Morrison et al. (1977) also noted that laboratory-raised voles continued growing in length and added mass beyond the typical lifespan of voles living in the field. Their finding that males lived longer is contradictory to the findings of Krebs et al (1969), Rose and Dueser (1980), and this study, so it is likely that mortality rates are higher for males in nature.

Lifespans on the Stephens grid were longer than those on the Su grid (Table 7) and females from the Stephens grid lived statically longer on than females from the Su grid. Females typically outlive males (Krebs et al. 1969, Rose and Dueser 1980), but on the Su grid, males lived longer than females by about 5 weeks.

CHAPTER V

CONCLUSIONS

As a result of this study, I conclude that Chesapeake meadow voles were larger than those reported in other studies. It was unexpected that nearly 20% of all males reached masses $\geq$70 g. Body size was positively related to population density, but growth rate was unrelated to population density and season. Autumn-born Chesapeake meadow voles had similar rates of both growth and sexual maturation as those born in other seasons. These voles lived longer than voles in northern latitudes, but had similar lifespans to those in Charlottesville, Virginia. The idea that the average vole in this study maintained or continually gained mass in all months and seasons was not supported by voles on the Stephens grid, but individuals from the Su grid fit this indeterminate growth profile.

Of unresolved interest was the finding that females on the Su tract lived shorter lives than males. This, paired with the stark contrast in body growth dynamics between voles of the Su and Stephens sites, made for an unusual population study of 2 nearly adjacent populations of *Microtus pennsylvanicus*.

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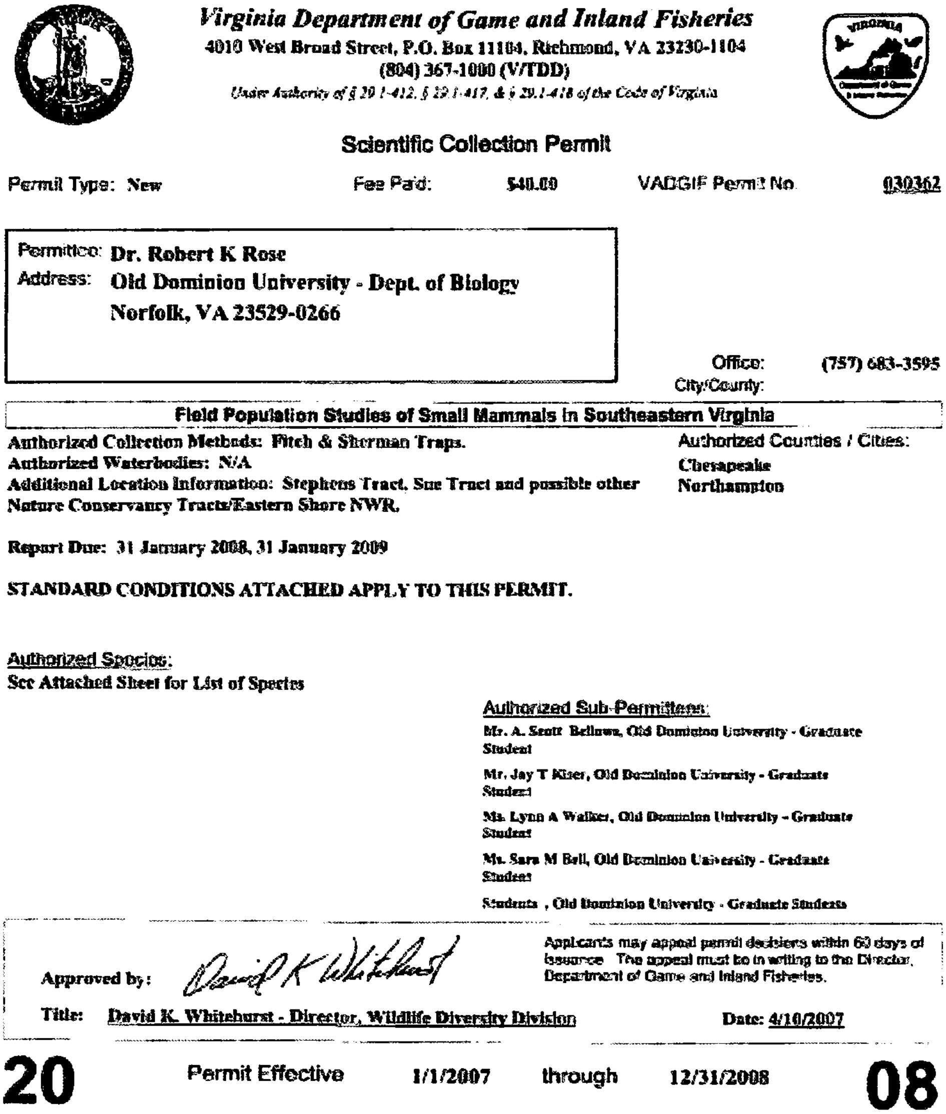
APPENDIX A

STATE PERMITS



Virginia Department of Game and Inland Fisheries
4010 West Broad Street, P.O. Box 11104, Richmond, VA 23230-1104
(804) 367-1000 (V/TDD)
Under Authority of § 29.1-412, § 29.1-417, & § 29.1-418 of the Code of Virginia

Scientific Collection Permit

Permit Type: **New** Fee Paid: **$40.00** VADGIF Permit No. **030362**

Permittee: **Dr. Robert K Rose**
Address: **Old Dominion University - Dept. of Biology**
Norfolk, VA 23529-0266

Office: **(757) 683-3595**
City/County:

Field Population Studies of Small Mammals in Southeastern Virginia

Authorized Collection Methods: Fitch & Sherman Traps.
Authorized Waterbodies: N/A
Additional Location Information: Stephens Tract, Sue Tract and possible other Nature Conservancy Tracts/Eastern Shore NWR.

Authorized Counties / Cities:
Chesapeake
Northampton

Report Due: 31 January 2008, 31 January 2009

STANDARD CONDITIONS ATTACHED APPLY TO THIS PERMIT.

Authorized Species:
See Attached Sheet for List of Species

Authorized Sub-Permittees:

Mr. A. Scott Bellows, Old Dominion University - Graduate Student

Mr. Jay T Kiser, Old Dominion University - Graduate Student

Ms. Lynn A Walker, Old Dominion University - Graduate Student

Ms. Sara M Bell, Old Dominion University - Graduate Student

Students , Old Dominion University - Graduate Students

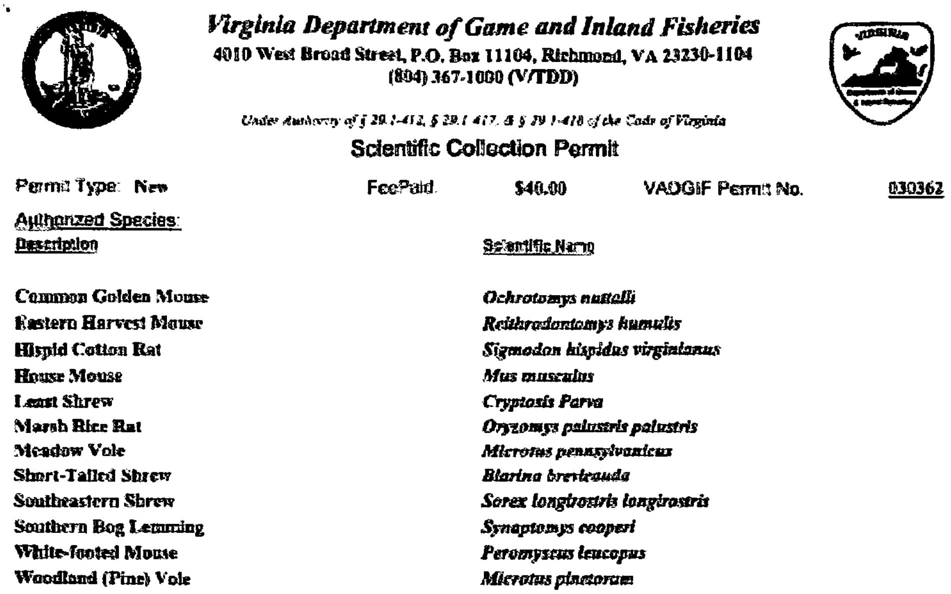
Approved by: David K Whitehurst

Applicants may appeal permit decisions within 60 days of issuance. The appeal must be in writing to the Director, Department of Game and Inland Fisheries.

Title: David K. Whitehurst - Director, Wildlife Diversity Division **Date: 4/10/2007**

20 Permit Effective **1/1/2007** through **12/31/2008** **08**

APPENDIX A CONTINUED



Virginia Department of Game and Inland Fisheries
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(804) 367-1000 (V/TDD)

Under Authority of § 29.1-412, § 29.1-417, & § 29.1-418 of the Code of Virginia

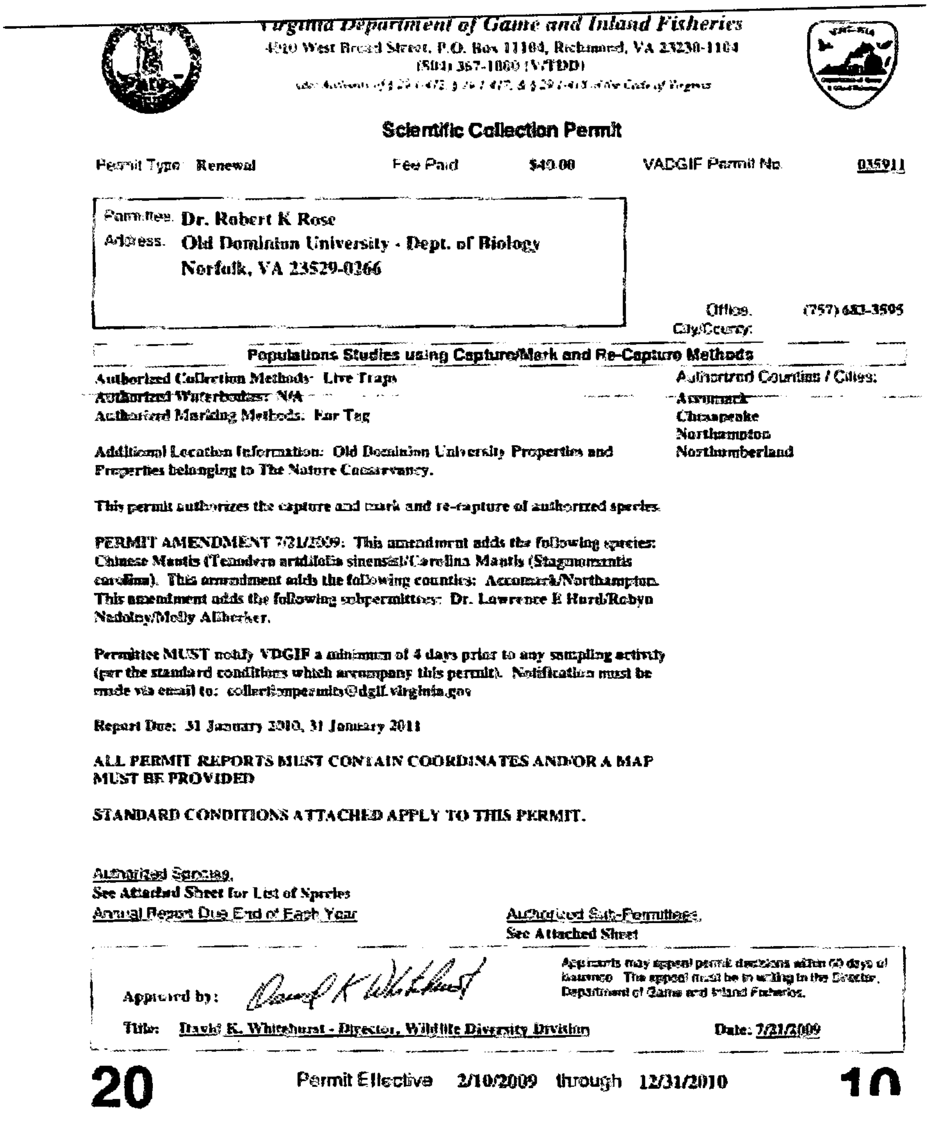
Scientific Collection Permit

Permit Type: **New** FeePaid **$40.00** VADGIF Permit No. **030362**

Authorized Species:

Description	Scientific Name
Common Golden Mouse	*Ochrotomys nuttalli*
Eastern Harvest Mouse	*Reithrodontomys humulis*
Hispid Cotton Rat	*Sigmodon hispidus virginianus*
House Mouse	*Mus musculus*
Least Shrew	*Cryptosis Parva*
Marsh Rice Rat	*Oryzomys palustris palustris*
Meadow Vole	*Microtus pennsylvanicus*
Short-Tailed Shrew	*Blarina brevicauda*
Southeastern Shrew	*Sorex longirostris longirostris*
Southern Bog Lemming	*Synaptomys cooperi*
White-footed Mouse	*Peromyscus leucopus*
Woodland (Pine) Vole	*Microtus pinetorum*

APPENDIX A CONTINUED



Virginia Department of Game and Inland Fisheries

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(804) 367-1000 (V/TDD)
Under Authority of § 29.1-412, § 29.1-417, & § 29.1-418 of the Code of Virginia

Scientific Collection Permit

Permit Type **Renewal** Fee Paid **$40.00** VADGIF Permit No. **035911**

Permittee: **Dr. Robert K Rose**
Address: **Old Dominion University - Dept. of Biology**
Norfolk, VA 23529-0266

Office: **(757) 683-3595**
City/County:

Populations Studies using Capture/Mark and Re-Capture Methods

Authorized Collection Methods: Live Traps
Authorized Waterbodies: N/A
Authorized Marking Methods: Ear Tag

Authorized Counties / Cities:
Accomack
Chesapeake
Northampton
Northumberland

Additional Location Information: Old Dominion University Properties and Properties belonging to The Nature Conservancy.

This permit authorizes the capture and mark and re-capture of authorized species.

PERMIT AMENDMENT 7/21/2009: This amendment adds the following species: Chinese Mantis (Tenodera aridifolia sinensis)/Carolina Mantis (Stagmomantis carolina). This amendment adds the following counties: Accomack/Northampton. This amendment adds the following subpermittees: Dr. Lawrence E Hurd/Robyn Nadolny/Molly Allbecker.

Permittee MUST notify VDGIF a minimum of 4 days prior to any sampling activity (per the standard conditions which accompany this permit). Notification must be made via email to: collectionpermits@dgif.virginia.gov

Report Due: 31 January 2010, 31 January 2011

ALL PERMIT REPORTS MUST CONTAIN COORDINATES AND/OR A MAP MUST BE PROVIDED

STANDARD CONDITIONS ATTACHED APPLY TO THIS PERMIT.

Authorized Species:
See Attached Sheet for List of Species
Annual Report Due End of Each Year

Authorized Sub-Permittees:
See Attached Sheet

Approved by: David K Whitehurst

Applicants may appeal permit decisions within 60 days of issuance. The appeal must be in writing to the Director, Department of Game and Inland Fisheries.

Title: David K. Whitehurst - Director, Wildlife Diversity Division **Date: 7/21/2009**

20 Permit Effective **2/10/2009** through **12/31/2010** **10**

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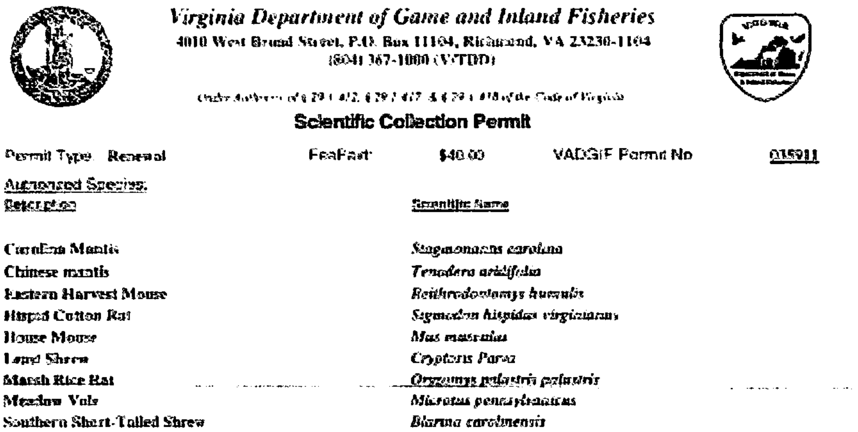

Virginia Department of Game and Inland Fisheries

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Under Authority of § 29.1-412, § 29.1-417 & § 29.1-418 of the Code of Virginia

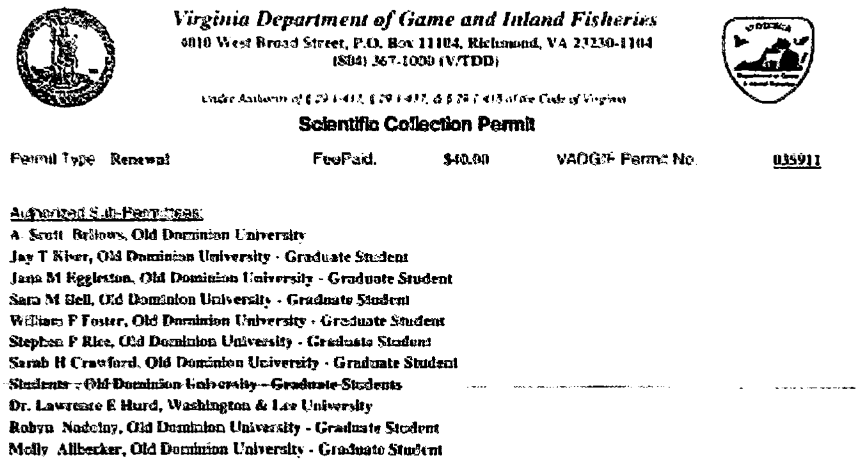
Scientific Collection Permit

Permit Type **Renewal** Fee Paid **$40.00** VADGIF Permit No **035911**

Authorized Species:

Description	Scientific Name
Carolina Mantis	***Stagmomantis carolina***
Chinese mantis	***Tenodera aridifolia***
Eastern Harvest Mouse	***Reithrodontomys humulis***
Hispid Cotton Rat	***Sigmodon hispidus virginianus***
House Mouse	***Mus musculus***
Least Shrew	***Cryptotis Parva***
Marsh Rice Rat	***Oryzomys palustris palustris***
Meadow Vole	***Microtus pennsylvanicus***
Southern Short-Tailed Shrew	***Blarina carolinensis***

APPENDIX A CONTINUED



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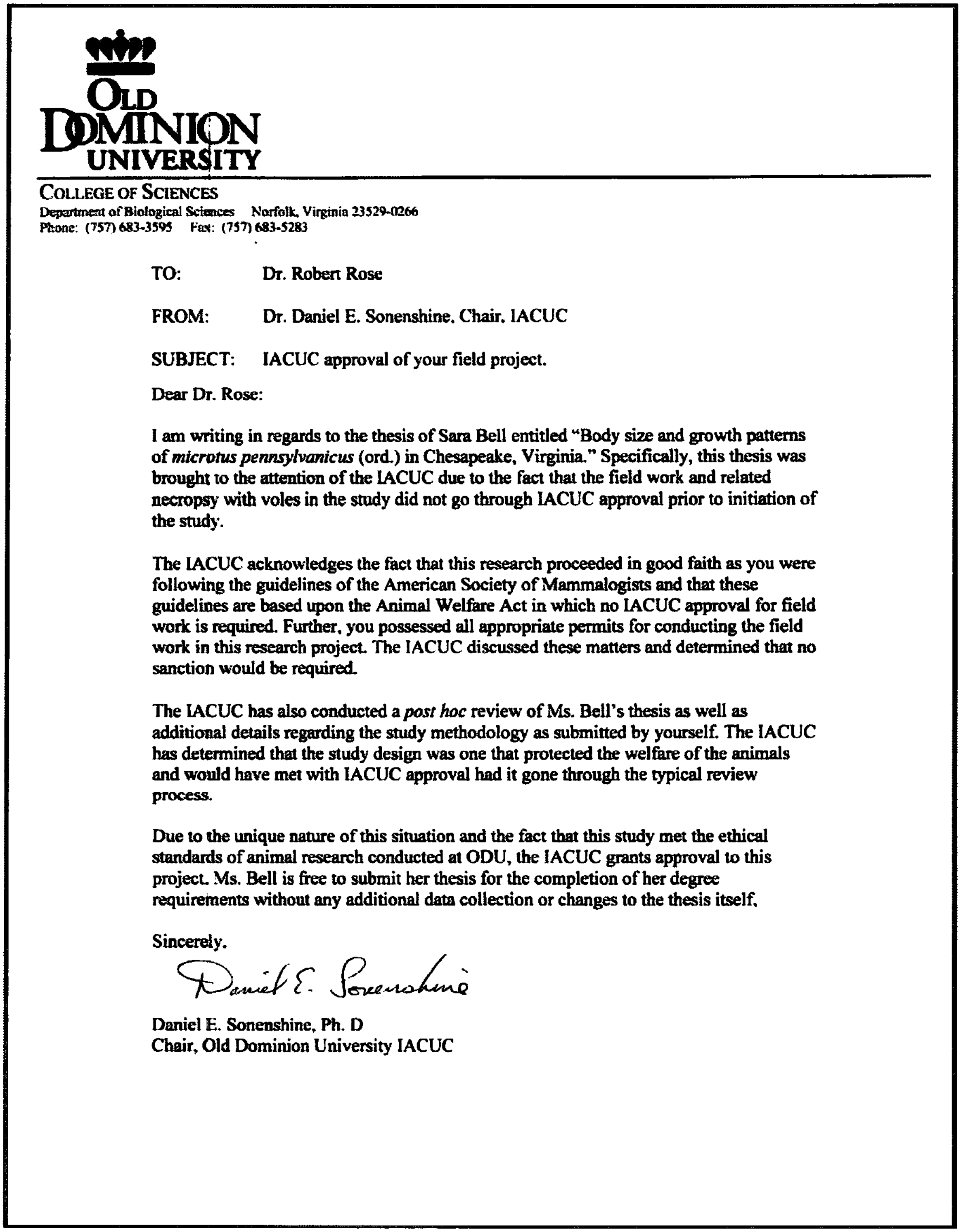
Scientific Collection Permit

Permit Type **Renewal** FeePaid. **$40.00** VADGIF Permit No. **035911**

Authorized Sub-Permittees:
A. Scott Bellows, Old Dominion University
Jay T Kiser, Old Dominion University - Graduate Student
Jana M Eggleston, Old Dominion University - Graduate Student
Sara M Bell, Old Dominion University - Graduate Student
William F Foster, Old Dominion University - Graduate Student
Stephen P Rice, Old Dominion University - Graduate Student
Sarah H Crawford, Old Dominion University - Graduate Student
~~**Students - Old Dominion University - Graduate Students**~~
Dr. Lawrence E Hurd, Washington & Lee University
Robyn Nadolny, Old Dominion University - Graduate Student
Molly Allbecker, Old Dominion University - Graduate Student

APPENDIX B



OLD
DOMINION
UNIVERSITY
COLLEGE OF SCIENCES
Department of Biological Sciences Norfolk, Virginia 23529-0266
Phone: (757) 683-3595 Fax: (757) 683-5283

TO: Dr. Robert Rose

FROM: Dr. Daniel E. Sonenshine, Chair, IACUC

SUBJECT: IACUC approval of your field project.

Dear Dr. Rose:

I am writing in regards to the thesis of Sara Bell entitled "Body size and growth patterns of *microtus pennsylvanicus* (ord.) in Chesapeake, Virginia." Specifically, this thesis was brought to the attention of the IACUC due to the fact that the field work and related necropsy with voles in the study did not go through IACUC approval prior to initiation of the study.

The IACUC acknowledges the fact that this research proceeded in good faith as you were following the guidelines of the American Society of Mammalogists and that these guidelines are based upon the Animal Welfare Act in which no IACUC approval for field work is required. Further, you possessed all appropriate permits for conducting the field work in this research project. The IACUC discussed these matters and determined that no sanction would be required.

The IACUC has also conducted a *post hoc* review of Ms. Bell's thesis as well as additional details regarding the study methodology as submitted by yourself. The IACUC has determined that the study design was one that protected the welfare of the animals and would have met with IACUC approval had it gone through the typical review process.

Due to the unique nature of this situation and the fact that this study met the ethical standards of animal research conducted at ODU, the IACUC grants approval to this project. Ms. Bell is free to submit her thesis for the completion of her degree requirements without any additional data collection or changes to the thesis itself.

Sincerely,

Daniel E. Sonenshine

Daniel E. Sonenshine, Ph. D
Chair, Old Dominion University IACUC

APPENDIX C

SUMMARY OF STATISTICAL TESTS

Su grid

H_0	Statistic	*df*	*P*
Sex ratios equal	$\chi^2 = 2.423$	1	0.120
Male and female mean mass equal	$t = 4.334$	124	<0.001
Male mean mass equal during population density peak and all other phases	$t = 0.399$	129	0.691
Female mean mass equal during population density peak and all other phases	$t = -0.956$	85	0.625
Male mean mass at first capture equal during population density peak and all other phases	$t = 0.471$	67	0.639
Female mean mass at first capture equal during population density peak and all other phases	$t = 0.682$	42	0.499
Male mean mass equal during population density low and all other phases	$t = 0.338$	121	0.736
Female mean mass equal during population density low and all other phases	$t = 0.852$	85	0.399
Male mean mass at first capture equal during population density low and all other phases	$t = 0.443$	67	0.659
Male mean mass equal during autumn and all other seasons	$t = 5.470$	106	<0.001
Female mean mass equal during autumn and all other seasons	$t = 2.610$	47	0.012
Male mean mass equal during periods of low and high population density	$t = 0.299$	23	0.767
Female mean mass equal during periods of low and high population density	$t = 0.362$	24	0.721
Males have equal growth rates in all months	$F = 0.787$	22, 45	0.723
Females have equal growth rates in all months	$F = 1.190$	15, 16	0.366
Males and females have equal growth rates	$t = 1.781$	97	0.078
Males have equal growth rates during population density peak and all other density phases	$t = -1.483$	66	0.143
Females have equal growth rates during population density peak and all other density phases	$t = -0.872$	29	0.390
Mean mass in second month of life is equal for young born in autumn and all other seasons	$t = 0.876$	4	0.430
Lifespans of males and females are equal at both the Su and Stephens grids	$F = 4.495$	1, 234	0.035
Males have equal lifespans to voles in Charlottesville	$t = 0.423$	19	0.677
Females have equal lifespans to voles in Charlottesville	$t = 3.035$	11	0.011

APPENDIX C CONTINUED

Stephens grid

H_0	Statistic	*df*	*P*
Sex ratios equal	$\chi^2 = 2.104$	1	0.150
Male and female mean mass equal	$t = 14.432$	1539	<0.001
Male mean mass unrelated to population density	$R^2 = 0.276$; $t = 4.622$	28	<0.001
Female mean mass unrelated to population density	$R^2 = 0.155$; $t = 2.229$	28	0.034
Male mean mass equal during population density peak and all other phases	$t = 2.339$	812	0.020
Female mean mass equal during population density peak and all other phases	$t = -1.722$	303	0.086
Male mean mass at first capture equal during population density peak and all other phases	$t = 0.453$	284	0.651
Female mean mass at first capture equal during population density peak and all other phases	$t = 3.172$	259	0.002
Male mean mass equal during population density low and all other phases	$t = 5.408$	810	<0.001
Female mean mass equal during population density low and all other phases	$t = 3.647$	958	<0.001
Male mean mass at first capture equal during population density low and all other phases	$t = 2.086$	284	0.038
Female mean mass at first capture equal during population density low and all other phases	$t = 2.236$	259	0.026
Male mean mass equal during autumn and all other seasons	$t = 4.339$	808	<0.001
Female mean mass equal during autumn and all other seasons	$t = 2.176$	812	0.030
Male mean mass equal during periods of low and high population density	$t = 5.769$	211	<0.001
Female mean mass equal during periods of low and high population density	$t = 2.505$	251	0.013
Males have equal growth rates in all months	$F = 2.300$	27, 416	<0.001
Females have equal growth rates in all months	$F = 4.428$	27, 440	<0.001
Males and females have equal growth rates	$t = 2.489$	1021	0.013
Males have equal growth rates during population density peak and all other density phases	$t = 710$	526	0.478
Females have equal growth rates during population density peak and all other density phases	$t = -1.178$	283	0.240
Male population density unrelated to male mean growth rate	$R^2 = 0.001$; $t = 0.170$	27	0.866
Female population density unrelated to female mean growth rate	$R^2 = 0.010$; $t = -0.518$	27	0.609
Mean mass in second month of life is equal for young born in autumn and all other seasons	$t = -1.661$	19	0.113
Males and females reach sexual maturity at equal rates	$F = 455$	1	0.530

APPENDIX C CONTINUED

H_o	Statistic	*df*	*P*
Autumn-born young and young born in all other seasons reach sexual maturity at equal rates	$F = 2.273$	1	0.192
Lifespans of males and females are equal at both the Su and Stephens grids	$F = 4.495$	1, 234	0.035
Males have equal lifespans to voles in Charlottesville	$t = 1.707$	96	0.091
Females have equal lifespans to voles in Charlottesville	$t = 1.567$	108	0.120
Necropsy grid			
Male and female mean mass equal	$t = 0.205$	69	0.839
Male and female total length equal	$t = 0.457$	69	0.649
Male and female body length equal	$t = 0.360$	69	0.720
Male and female tail length equal	$t = 0.502$	69	0.617
Male and female hindfoot length equal	$t = 0.069$	69	0.945
Male and female ear length equal	$t = 1.192$	69	0.237
Male mass unrelated to body length	$R^2 = 0.732$; $t = 9.351$	33	<0.001
Female mass unrelated to body length	$R^2 = 0.721$; $t = 9.514$	36	<0.001

VITA

Sara E. Bell

EDUCATION: B.S. Wildlife Science, Biology minor, Virginia Tech, Blacksburg, VA, 2004

M.S. Biology, Old Dominion University, Norfolk, VA, 2010

EXPERIENCE: Natural Resources Specialist, Naval Facilities Engineering Command MidLant, Norfolk, VA, September 2008-Present.

Laboratory Assistant, Environmental Services and Consulting, Blacksburg, VA, February 2002-April 2004

Research Assistant, Conservation Management Institute, Blacksburg, VA, January-May 2003

Research Assistant, Dr. Jim Berkson, College of Natural Resources, VA Tech, Blacksburg, VA, September 2002-May 2003

Environmental Educator, Cincinnati Nature Center, Milford, OH, May-June 2002

MEMBERSHIPS: National Military Fish and Wildlife Association, 2008-Present

Alpha Zeta, Agriculture and Natural Resources Honor Fraternity, 2002-Present

Xi Sigma Pi, National Forestry Honor Society, 2002-Present

The Wildlife Society, Virginia Tech, 2001-2004

State Representative for Virginia Tech's chapter of The Wildlife Society, 2002