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An Examination of Seasonal Growth and Survivorship of *Sigmodon hispidus* in Southeastern Virginia

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AN EXAMINATION OF SEASONAL GROWTH AND SURVIVORSHIP OF *SIGMODON HISPIDUS* IN SOUTHEASTERN VIRGINIA

By

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ABSTRACT

AN EXAMINATION OF SEASONAL GROWTH AND SURVIVORSHIP OF *SIGMODON HISPIDUS* IN SOUTHEASTERN VIRGINIA

Heather Alyssa Green
Old Dominion University, 2006
Director: Dr. Robert K. Rose

A reexamination of specific population dynamic aspects of *Sigmodon hispidus,* the hispid cotton rat, is necessary in order to gain additional knowledge and perspective on this species in its northernmost distribution on the east coast of the United States. Previous studies of Virginia cotton rats were based on data from necropsies, which do not allow for the determination of certain population characteristics, such as density, growth, and survival. General population trends and rates of growth and survival in males and females throughout the seasons in Virginia will also provide a basis for comparison with populations of cotton rats in other parts of its range. A monthly mark-and-recapture study was conducted in an old field in Chesapeake, Virginia, between December 2002 and March 2005 to elucidate these aspects of the population, as well as to confirm previous reproductive patterns for this geographic region.

Annual population density in this study is similar to that observed in other northern populations of cotton rats. However, slight bimodal distributions also began to surface, which are more common in southern distributions of this species. Current patterns of reproduction were not significantly different from those previously reported in Virginia and were similar to patterns in northern portions of the species' range. Highest rates of growth were present in the summer, while winter exhibited the lowest rates of growth. Previous Virginia studies have suggested males have the ability to gain mass over the winter months. Although positive winter growth in males was observed in this study, nil or negative growth was just as common. Higher rates of survival were present in the spring and autumn, while lowest rates of survival were in summer and winter and were influenced by energetic and environmental stresses, as well as other intrinsic population factors. Newly collected winter data reveal that winter growth and survivorship in cotton rats are very similar to trends observed in Kansas populations located at the same latitude. The new information from this study helps to better understand why different geographic populations exhibit differences in body size and other population characteristics and the relevant forces of selection promoting these patterns.

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I would like to thank the Nature Conservancy for allowing us to conduct this research on their property. I would also thank the various weather centers, NOAA, SERCC, HPRCC and Dr. Bradley Bergstrom for their assistance in obtaining the weather data incorporated into this study. I would also like to thank Dr. Norman A. Slade, who provided his knowledge and expertise into certain aspects of my research.

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INTRODUCTION

Of the major terrestrial biomes of the world, those found in the temperate zones pose unique challenges to the animal species that inhabit them. These areas often experience warm summers and cold winters. Precipitation varies throughout the year and snow is common in the northern limits of the zone. Due to these seasonal changes in climate, animals must continuously respond and alter their energy budgets to survive. Non-hibernating mammals, with their large costs associated with homeothermy, have especially high energy requirements during the winter months.

During the warm seasons, most mammals can maintain their daily energy demands without a problem. Reproductive timing is strongly tied to the emerging vegetation, which for herbivorous mammals supports the high energy costs associated with pregnancy and lactation. Winter is by far the most difficult season for most mammals. Some escape winter through migration, while a few others hibernate.

However, these winter strategies are not options for most small mammals. They simply endure the effects of winter. Because of their small body size, they already have to constantly eat to fulfill their energy demands due to their high metabolic rates (Rose 1986). In addition, small mammals lose proportionately more heat than larger species due to their larger surface-to-volume ratios. To sustain these high energy demands, some small mammals cache food, but others simply consume more food and pay the costs of dealing with the colder temperatures (Smith and Reichman 1984). Most small mammals undergo a suspension of breeding and exhibit a regression of the gonads to reduce

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The model journal used in this thesis is the Journal of Mammalogy.

metabolic costs in winter. The total energetic costs incurred during the winter are greater than or equal to the costs during reproduction in the spring and summer, which would make reproduction in the winter energetically impossible for most species (Fournier et al. 1999).

Additionally, most small mammals will get a denser pelage during the pre-winter molt, thereby increasing the amount of insulation and reducing the amount of heat lost to the environment. A few small herbivorous mammals have the ability to increase the length of small intestine to extract more energy from nutrient-poor standing dead vegetation (Gross 1986). Some practice coprophagy, which is another way to extract more energy from food. Many small mammals build insulative nests to reduce heat loss during their inactive hours (Sealander 1952). There are some instances in which small mammals will engage in communal behavior, such as huddling within communal nests, which also clearly reduces heat loss for each individual (Sealander 1952). Often small mammals will become more diurnal in the winter than in the summer, which reduces or eliminates the need to be active during the night, the coldest period (Stokes et al. 2001).

Sigmodon hispidus, the hispid cotton rat, is a good example of a temperate-zone small mammal which is subject to these seasonal conditions. However, this originally Neotropical species is at even more of a disadvantage than its north temperate counterparts because it lacks some of the energy-saving adaptations of other small mammals. *S. hispidus* has been known to burrow or construct underground nests, but this behavior is not widespread or well-developed (Dawson and Lang 1973; Shump, Jr. 1978). Cotton rats do suspend breeding and regress their gonads in the winter. *S. hispidus* is not known to cache food, despite the fact that during the winter months their high-energy and high-quality foods disappear (Cameron and Spencer 1981). They are forced to eat poor quality foods, namely standing dead vegetation. Oftentimes, *S. hispidus* will have docked tails due to loss from frost bite, further evidence that winter is a difficult time for cotton rats.

Depending on the geographic location of populations of *S. hispidus*, the impact of winter may be more or less severe. For instance, the subspecies from Kansas and the subspecies in southeastern Virginia are located at the same latitude (37° N) in the United States, but the winters experienced in Virginia are much milder due to its maritime climate (Rose and Mitchell 1990; Campbell and Slade 1995; Eifler and Slade 1999). The effects of winter in Kansas populations of free-living cotton rats have been well documented (Slade et al. 1984; Sauer 1985; Slade and Iskjaer 1990; Campbell and Slade 1993; Eifler and Slade 1998; Eifler and Slade 1999) and include substantial loss of body mass and even localized extinctions in severe winters. However, the effects of winter on Virginia populations have been less well studied (Rose 1986; Rose and Mitchell 1990; Bergstrom and Rose 2004). An in-depth investigation of *S. hispidus* in southeastern Virginia will serve to further demonstrate how this species has adapted to survive at its most northerly location on the east coast and how it meets its seasonal energetic requirements, most importantly those associated with the winter months.

Sigmodon hispidus is a relatively short-lived and fast-growing species (Campbell and Slade 1995) in the family Muridae. *S. hispidus* has dark brown pelage with yellow near the tips, giving it its hispid qualities. Its underside is pale and slightly gray (Cameron and Spencer 1981). The distribution of *S. hispidus* extends from northern South America through Central America and Mexico into the midwestern and southeastern United States (Cameron and McClure 1988). The genus *Sigmodon* has its origins in the tropics and it began to spread northward during the late Pliocene era. During the last glaciation in North America, some *S. hispidus* were forced to take refuge in Florida and Mexico (Blair 1958; Baker 1969). After the retreat of the glaciers, cotton rats began to move northward into the Great Plains and eastern United States (Dalby and Lillevik 1969). Cameron and McClure (1988) suggest that the Pleistocene retreat could have had a significant impact on the two separate populations of *Sigmodon* that were isolated during this time. Variation in body size and litter size throughout their present geographic distribution may be the result of this major event.

Southeastern Virginia is the location of northernmost distribution of *S. hispidus* on the east coast of the United States. The presence of *S. hispidus* was first recorded in Virginia in 1940 (Patten 1941) and it has continued moving northward into central Virginia (Rose and Mitchell 1990), although its northward path is now blocked by the Chesapeake Bay and the large rivers running eastward into it. *S. hispidus* was thought to be distributed from Virginia Beach westward to locations north of Richmond and extending south and west into Halifax County (Rose and Mitchell 1990). However, since 2001, Dr. Jack A. Cranford, a mammalogist at Virginia Tech, has reported the species from Montgomery and Giles counties, near Blacksburg in western Virginia (pers. comm. to R. Rose).

The average body mass of cotton rats varies geographically (Cameron and McClure 1988). Adult *S. hispidus* weigh from 110 to 225 g in males and 100 to 200 g in females (Cameron and Spencer 1981). In general, there seems to be a trend for cotton rat subspecies from northern latitudes to be larger than those in the southern parts of their distribution. The Virginian subspecies ("virginianus") is one of the smallest, reaching 150 g for males and somewhat less for females (Cameron and McClure 1988). Therefore, the smaller size of the "virginianus" subspecies goes against the general body mass trends.

The largest of the 32 *Sigmodon* subspecies (Hall 1981), *S. h. texianus*, is concentrated in Kansas, Oklahoma, and northern Texas (Cameron and McClure 1988). Cameron et al. (1979) suggest that some of this geographic difference in body size may reflect higher fat accumulations in the northern populations. The Virginia subspecies, *S. h. virginianus*, exhibits small body size, which could result from having a shorter life span than its southern counterparts (Bergstrom and Rose 2004). Although *S. h. texianus* from Kansas and *S. h. virginianus* from southeastern Virginia are located at the same latitude (37° N) in the United States, they display different body masses. Rose and Mitchell (1990), using samples drawn from different locations throughout the year in eastern Virginia, noted that although *S. h. virginianus* males gained weight over the winter, female body mass remained relatively low and did not exhibit any substantial loss or gain during winter. Their results, however, were based on collections of monthly samples for necropsy and not from following the rates of growth of tagged individuals in a mark-release-recapture study, as I have done.

In general, small mammals are at a disadvantage because of their high metabolic demands and larger surface areas from which heat is lost more rapidly than in larger mammals (Rose 1986). In order to compensate for their small size, *S. hispidus* consumes a mixed diet of both monocots, dicots and some arthropod foods, presumably to maximize energy intake and enhance intake of required nutrients (Randolph and

Cameron 2001). A typical cotton rat diet includes green stems of monocots, such as little bluestem grass, gulf cordgrass or eastern gamagrass (Randolph and Cameron 2001), plus lesser amounts of dicots and insects (Kincaid and Cameron 1985). The varying levels of protein content in plants of different geographic locations may significantly influence growth in *S. hispidus* (Cameron and McClure 1988). In western Kansas, where the year-round diet has been examined, Fleharty and Olson (1969) observed cotton rats eating insects and other animal material when available.

In addition to the dietary requirements necessary to support their high metabolic energy needs, some cotton rats may draw on their limited fat reserves over the winter and in times of food scarcity (Fleharty and Choate 1973; Bergstrom and Rose 2004). Heavier cotton rats have the ability to store more fat and energy in muscle mass, and these heavier individuals may have the advantage over smaller animals during times of low food availability and the high energy demands of winter (Campbell and Slade 1993). Others, however, speculate that smaller size in cotton rats may be advantageous because less absolute energy is required to sustain an 80 g animal than a 120 g animal. The chances of survival of these smaller animals potentially increase during the winter, as a result of a reduction in their metabolic needs when food resources are already limited and are of poorer nutrient quality then compared to other seasons (Eifler and Slade 1998).

Food availability may also influence population density, which itself may affect overall body size and growth rates. Doonan and Slade (1995) observed increases in population density in food-supplemented populations in eastern Kansas, which indicates that food may be a limiting resource to individuals and thus affects rates of population growth. High-density populations have the potential to constrain body size, especially in the face of increased densities of competitors that reduce access to food (Doonan and Slade 1995).

Cotton rats in some northern locations, particularly in Virginia, have the ability to gain mass over the winter months (Rose and Mitchell 1990). Rose and Mitchell (1990) also observed that newly recruited male cotton rats of small size grow steadily throughout the winter. In contrast, some wintering adult cotton rats that were relatively large in size have demonstrated weight loss instead of weight gain in eastern Kansas (Campbell and Slade 1993). However, there is a general tendency for cotton rats in Kansas to converge towards an intermediate size by the end of winter, which can result by weight gain in smaller animals and weight loss in larger animals (Slade et al. 1984). In eastern Kansas, cotton rats of all age classes must reach a certain mass (ca. 80 g) before the onset of winter in order to survive (Sauer 1985).

Seasonally low temperatures of northern localities, such as those observed in Virginia and Kansas, may constrain the breeding seasons of *S. hispidus*. Unlike the cotton rats in Georgia, which have the ability to breed all year long, *S. h. virginianus* females are reproductively inactive from November through February (Rose and Mitchell 1990; Bergstrom and Rose 2004). The cessation of breeding in the winter is also observed in Kansas populations of *S. hispidus* (McClenaghan and Gaines 1978). In comparison to females, males have a longer period of reproductive activity. They are capable of breeding one month earlier than females in the spring and one month later than females in the fall (Rose and Mitchell 1990; Bergstrom and Rose 2004). Because males do not experience the energetic constraints of pregnancy and lactation, they can more easily afford to stay reproductively active longer than females and still have a good chance of surviving over the winter.

Females are not quite at their maximal reproductive potential in March and October, the first and last months of the breeding season in eastern Virginia (Rose 1986; Rose and Mitchell 1990; Bergstrom and Rose 2004). Females in Virginia may achieve maximum pregnancy rates during their shortened breeding season to make up for the time that they are reproductively inactive. In order for adult females and autumn-born rats to survive to breed in spring, they apparently must stop breeding in the late autumn (Bergstrom and Rose 2004). In addition, Bergstrom and Rose (2004) also speculate that those females that reproduce throughout the summer and fall do not survive the winter in Virginia. It seems that the energies and resources of these females are drained and cannot be recovered before the onset of winter. Therefore, mortality may be closely related to the timing of reproduction, at least for autumn-breeding females. These speculations hopefully can be confirmed or at least tested in my field study.

By conducting a demographic study of *S. hispidus* at their northernmost distribution on the east coast of the United States, several aspects of population dynamics, such as monthly rates of growth and survival can be observed and compared to other northern populations of cotton rats. It is important to explore potential differences in the seasonal growth rates of Virginia populations to see if they contribute to both seasonal and overall survivorship. To reconstruct growth trajectories, data from monthly capture, tagging, weighing and release of these animals were used. The monthly progression of growth in tagged individuals was used to determine whether animals continue to have positive growth throughout the winter. By comparing growth rates within each season in Virginia populations, patterns should emerge that may explain higher and lower rates of survival during different times of the year.

Examinations of winter growth rates are important to our understanding of cotton rat population dynamics because at some other locations, such as in eastern Kansas, populations sometimes go extinct during the winter. Therefore, advantages may be associated with higher or lower growth rates during the winter months that can affect winter survivorship. By assessing the data exclusively from the winter months, trends may potentially surface identifying certain patterns of continued growth, nil growth or negative growth over the winter, which have the ability to positively or negatively affect winter survivorship. Nil or negative growth over the winter may either demonstrate some underlying benefits of small body size that outweigh the costs of growth or some benefits to being larger in body size.

An ultimate goal of this research is to compare growth rates in Virginia cotton rat populations to those of other populations. This will help us better understand the relationship between seasonal rates of growth, population density and survival. For instance, any differences in annual growth rates between Virginia and other subspecies may contribute to the continued persistence of the species in Virginia as it continues to move northward. Once we have a better understanding of growth rates and survivorship in this Virginia population, we may better understand growth rates and survivorship of other populations of hispid cotton rats and perhaps of small mammals in general.

The objectives of this study were to: (1) observe growth rates of male and female *S. h. virginianus* in order to understand the potential adaptive benefits of variation between and within seasons in relation to overall survivorship, (2) examine winter growth rates to determine if these rates may contribute localized extinctions of cotton rat populations observed during the winter months at other locations in the United States, and (3) compare growth rates in the Virginia population of cotton rats to those of other geographic populations, in an attempt to better understand the relationship between seasonal rates of body growth and survival, as well as the patterns of population density.

METHODS

Description of Study Area

The study site, located near Benefit Road in southern Chesapeake, Virginia, was an old field on property owned by The Nature Conservancy and is part of the watershed of the North Landing River. The entire field was 11.5-ha, but for the purpose of the study only a small portion of the field was used. The field is bordered along its north, west and east sides by forest and by a freshwater marsh on the south. The study grid was bisected by a ditch that filled with water most often in the winter, and depending on the amounts of recent rainfall, at different times of the year. In addition to the ditch, the grid encompassed a room-sized pool (4-m across) that was also subject to filling after heavy rainfall and during the winter months, when the water table rose above ground level on several low points on the grid (Figure 1).

Despite its overall uniform age, the field consisted of several different habitats. When the Nature Conservancy acquired the land, their intention was to convert it back into Dismal Swamp forest. Their efforts to achieve this goal included planting a variety of trees, including swamp chestnut oak (*Quercus michauxii*), bald cypress (*Taxodium distichum*) and sycamore (*Platanus occidentalis*). At the end of the year 2000 growing season, the land was withdrawn from agriculture and throughout the course of my study, changes to the plant community were observed. Loblolly pines (*Pinus taeda*), sweet gum (*Liquidambar styraciflua*) and red maples (*Acer rubrum*), all volunteers, have come to dominate the old field at a rapid pace. This was most apparent in the western section of the study grid where seeds scattered by the prevailing westerly winds have promoted the domination of fast-growing loblolly pines. At the time the grid was established in

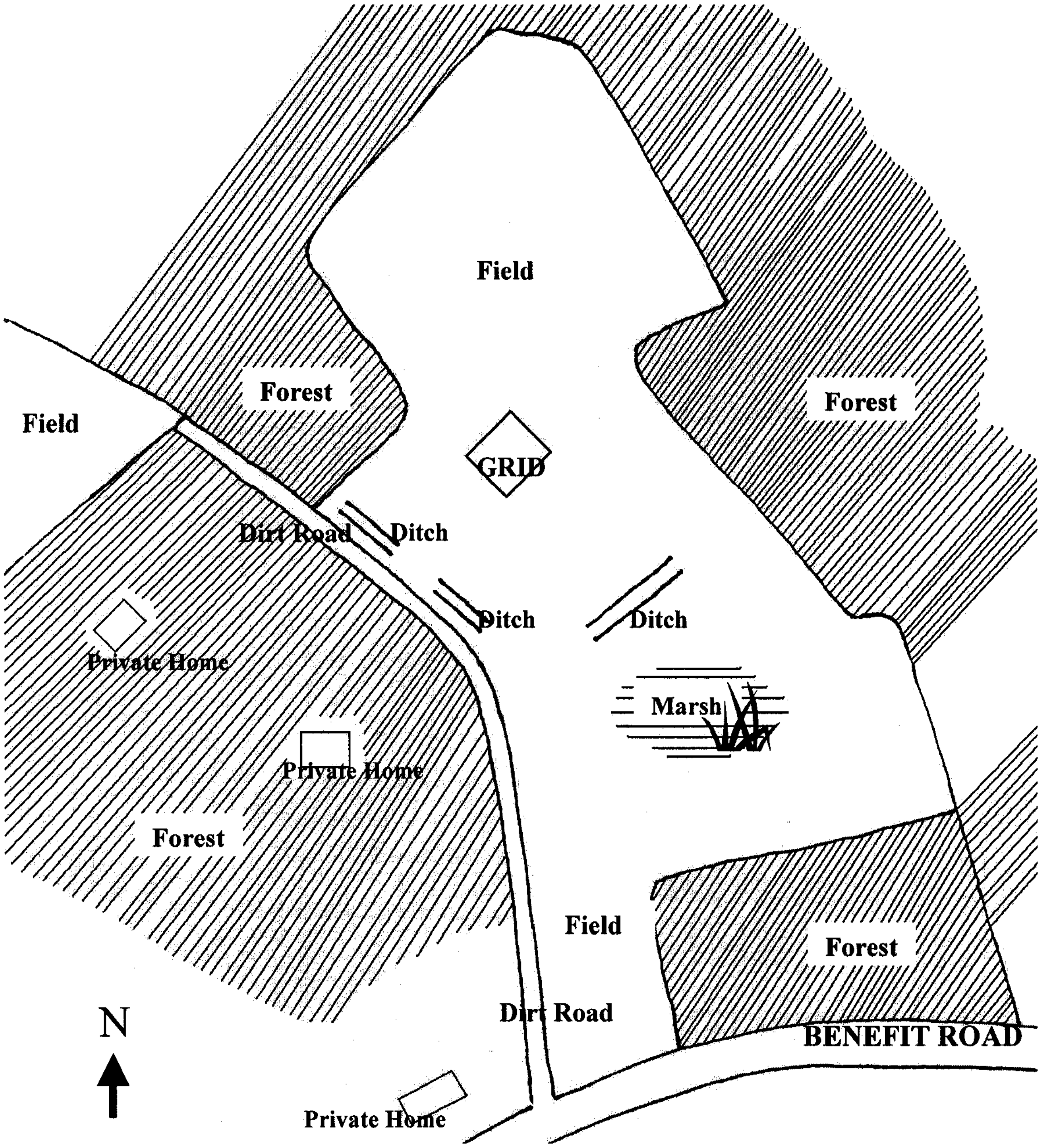

Fig. 1.—The study site was located off Benefit Road in Chesapeake, Virginia on land owned by the Nature Conservancy. The entire field measured 11.5 ha, but only a small portion of the site was used. The field is bordered to the north, east and west by forest. A small marshy area was south of the grid. Three private homes were situated west of the grid in the forested area.

December 2002, these pines were small, standing waist high, but over the past three growing seasons some have grown to be 4-m tall. In the few places on the grid where the pine saplings are dense, the forbs and grasses are slowly being excluded. As a result, the herbaceous habitat necessary to sustain *Sigmodon hispidus* is also being lost. Old-field succession to loblolly pines results in low densities of *S. hispidus* (Langley and Shure 1980). Other small saplings, such as red maple, swamp chestnut oak and elms (*Ulmus* spp.), are scattered across the grid.

Variation in vegetation was also observed between the growing and non-growing seasons. In late autumn of 2002, the majority of the grid was dominated by goldenrods (*Solidago* spp.), asters (*Aster* spp.), annual ragweed (*Ambrosia artemisiifolia*) and little bluestem (*Schizachyrium scoparium*), a 1-m tall grass. During the winter months, the vegetation was beaten down by heavy winds and rainfall. However, substantial ground cover and standing green vegetation still remained, provided by softrushes (*Juncus effuses* and *J. tenuis*), rosettes of forb species (*Eupatorium* spp.), as well as some other grasses (*Pancium* spp.). Softrushes are especially common in the northeast corner and in one other section near the center of the grid (both frequently inundated areas), while the forbs and grasses are widespread. Throughout the late spring and early summer the field was again covered with goldenrods, asters and ragweed. However, in the late summer other important forbs, such as dog fennel (*Eupatorium capillifollium*) and wild tomato (*Solanum carolinensis*), were observed. Over the subsequent growing and non-growing seasons, with the exception of the western portion of the grid where dense pines prevailed, the flora remained relatively static.

Monthly temperature and precipitation patterns based on 50-year monthly means were obtained using climate data from the Southeast Regional Climate Center from a collection site at Lake Kilby in Suffolk, Virginia. This site is located approximately 50 km west of the study grid. For this region, the summers are typically hot and winters are relatively mild. The highest monthly temperatures occurred in July (average 25.79 °C), while the coldest temperatures were seen in January (average 4.21 °C) (Figure 2). Monthly mean temperature patterns for northeastern Kansas, with which comparisons will be made, were similar from April to October, but were colder in winter than in Virginia. Kansas climate data were obtained from the High Plains Regional Climate Center for Lawrence, Kansas.

Monthly precipitation totals ranged from 80 mm in April and November to more than 140 mm in July and August; there being no identifiable dry season (Figure 3). In contrast, Kansas winters were dry and summers were wet. Based on 50-year monthly means, the wettest times of the year are in July, August and September for Virginia, while spring and early summer months were wetter in Kansas.

Precipitation and snowfall patterns were also obtained for the duration of my study (2002-2005). The spring of 2003 was wetter and the summer drier than normal, whereas rainfall amounts were well below normal for the first five months of 2004. However, winter was as wet as the spring and summer months (Figure 4). Overall, the driest time of the year was in both autumns with the exception of September 2003, which experienced increased rainfall due to the impact of Hurricane Isabelle. Snowfall was observed in January 2003, and the winter months of 2004 and 2005, but seemingly did not affect populations or my trapping efforts (Figure 5).

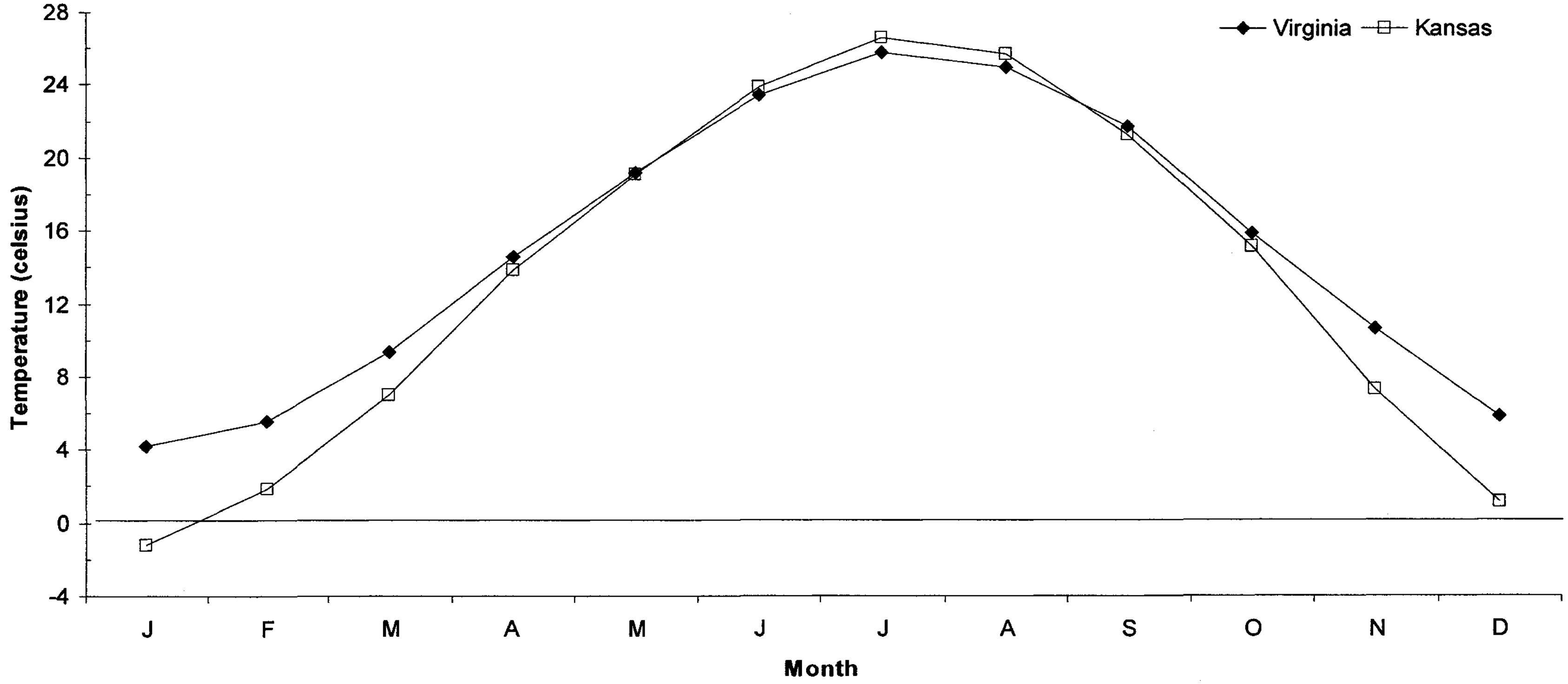

FIG. 2.—Monthly average temperatures (°C) based on 50-year mean from Lake Kilby in Suffolk, Virginia and Lawrence, Kansas. Both locations are at 37° N. Winters in Kansas were colder than in Virginia, but similar temperature patterns were observed over the summer months.

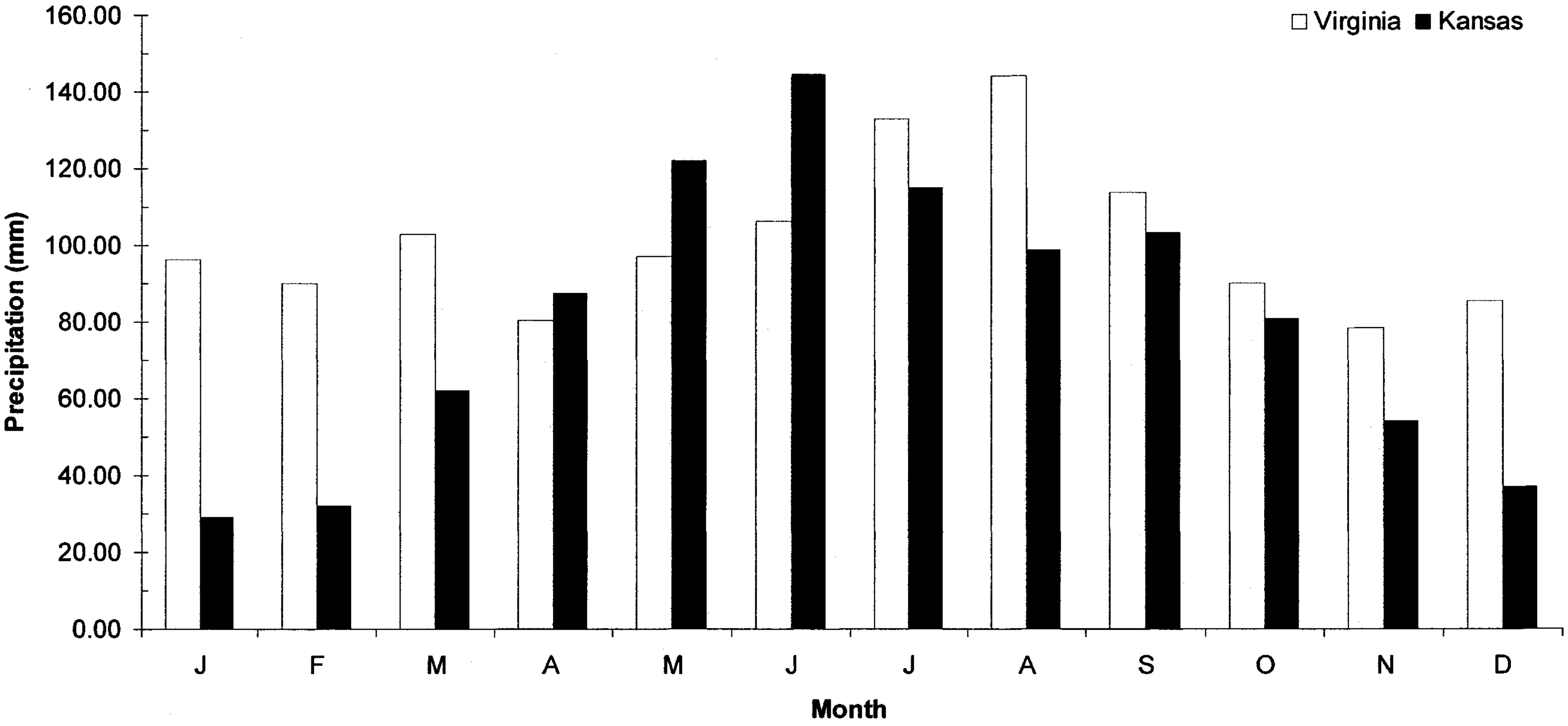

FIG. 3.—Monthly average precipitation totals (mm) based on 50-year mean from Lake Kilby in Suffolk, Virginia and Lawrence, Kansas. Monthly precipitation totals were more uniform throughout the year in Virginia, whereas Kansas summers were relatively wet and winter months were much drier.

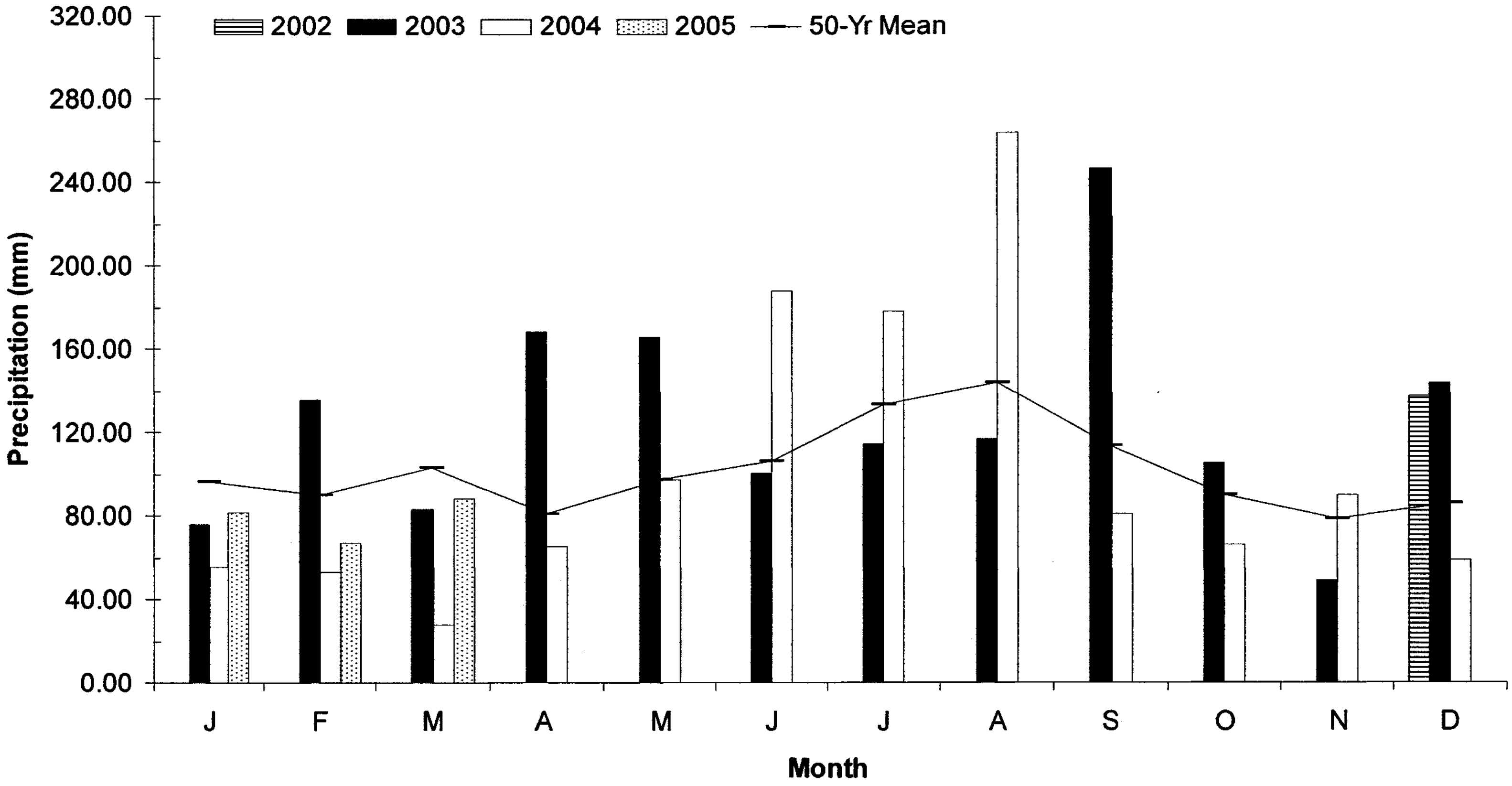

FIG. 4.—Precipitation totals (mm) during the study period, December 2002 to March 2005. In 2003, spring months were the wettest months, while summer months were drier than normal (50-year mean). Rainfall amounts were below normal for the first five months of 2004. Winter months were just as wet as spring and summer months.

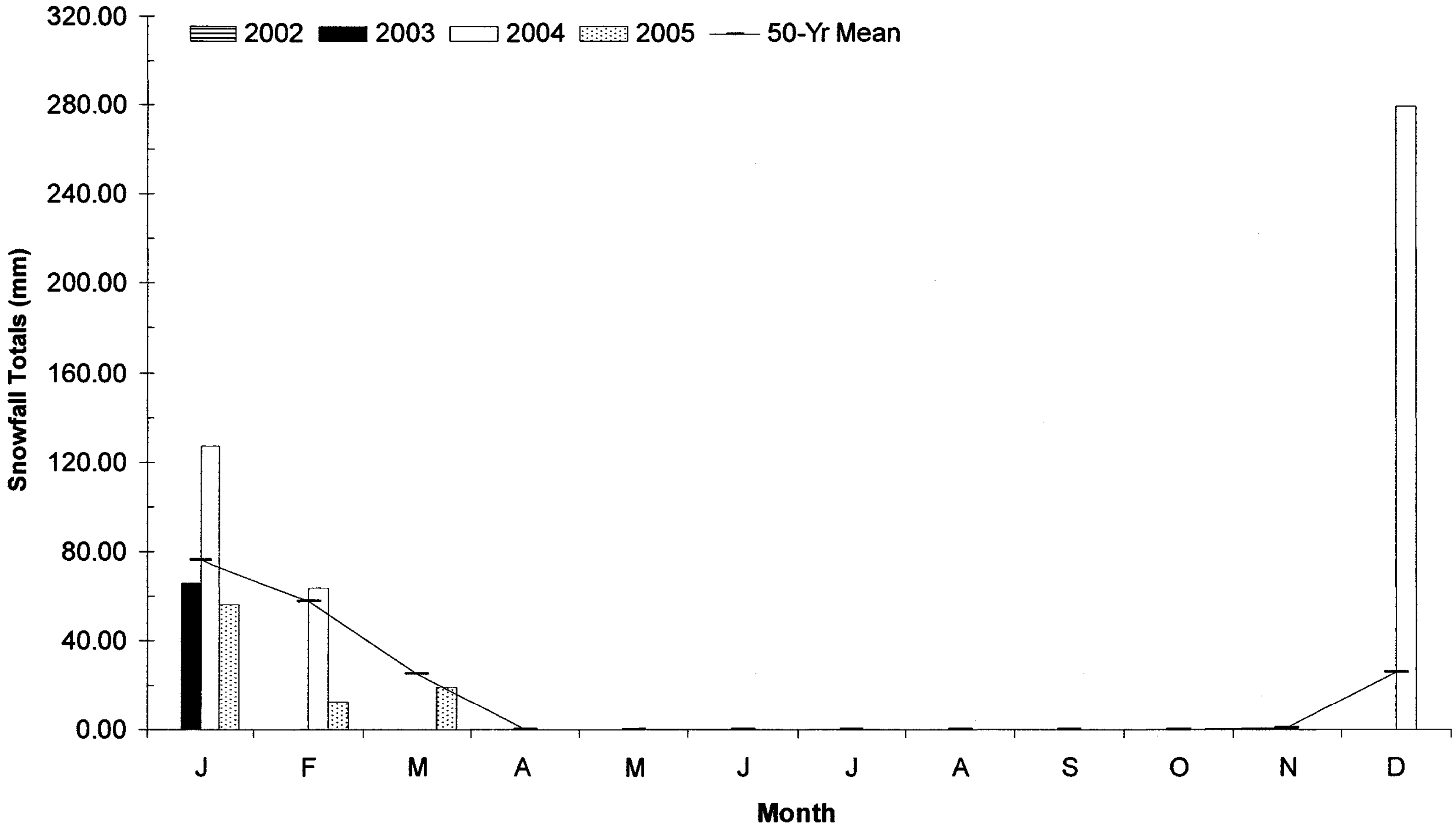

Fig. 5.—Snowfall totals (mm) observed throughout the study, December 2002 to March 2005. Snowfall was observed during the winter months with the exception of snowfall in March 2005 and was generally below normal (50-yr mean). Trapping efforts were not affected by snowfall, as trapping was never conducted with snow on the ground.

Some portions of the study site were subject to temporary flooding due to occasional heavy rain and the high water tables experienced during winter months. One of these areas included sections adjacent to the ditch that bisects the grid that often filled with water. Another reason the study site is susceptible to flooding is a result of its substrate. The clayey loams easily retain moisture and do not drain readily during periods of heavy rainfall. The northeast corner and the center of the grid near the small pond were often flooded to ankle- and calf-deep levels and usually remained that way for the duration of the winter. These saturated conditions are not suitable to support pines, but are ideal conditions for softrushes, sedges (*Carex* spp.), and other obligate wetland plants.

Detailed information about the structure of plant communities is important when conducting population studies, particularly in the case of *S. hispidus*. *S. hispidus* is herbivorous and occupies areas where covering herbaceous vegetation is abundant. Not only does the vegetation act as a primary food resource for *S. hispidus*, but dense cover probably also serves to reduce losses to overhead predation from birds, such as hawks and owls. Habitat with sparse vegetative cover is neither suitable to satisfy their nutritional needs nor to provide adequate protection. When we first investigated the study site in December 2002, the dominance of little bluestem grass promised to provide an ideal cotton rat habitat and preliminary trapping revealed substantial numbers of *S. hispidus* to be present.

The trapping grid was established inside an 11.5-ha portion of the field (Figure 6). The study grid measured 100-m x 100-m (1-ha) and comprised of 64 trap stations set at 12.5-m intervals. The grid is about 75-m from a small residential driveway that runs

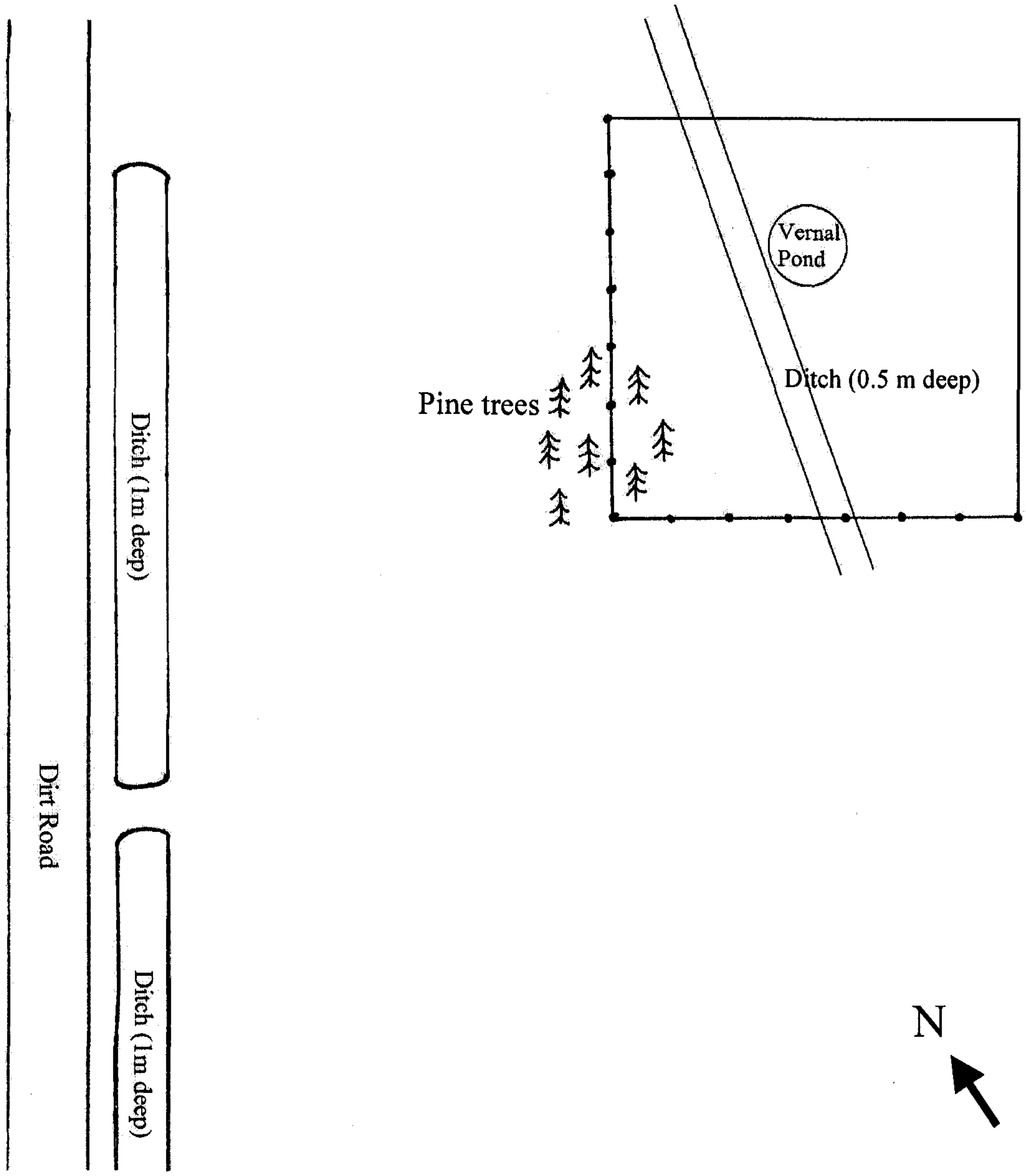

Fig. 6.—The trapping grid was established in the 11.5-ha field. The study grid measured 100 m x 100 m (1-ha) and consisted of 64 trap stations spaced at 12.5-m intervals. Pine trees first became dominant in the lower left quadrant of the grid and they continue to spread over the grid. The grid was bisected by a 0.5-m deep ditch and a small vernal pond was located in the center of the grid. The grid was ca. 75 m from a small dirt driveway which was bordered by forest to the east and two 1-m deep ditches to the west.

parallel to the study site. The forest of the northern and eastern boundaries is about 250 and 100-m, respectively, from the grid. Cotton rats are known to have larger home ranges than microtine rodents; therefore, the 12.5-m interval between trap stations seemed advisable (McNab 1963; Swihart et al. 1988).

Trapping Procedures

My study was conducted from December 2002 through July 2004; however, the collection of data from this site is ongoing and additional data through March 2005 have been incorporated into my results, enabling me to evaluate patterns of growth and survival for three winters. Data were collected each month for three consecutive days. We tried to consistently maintain the duration of time between trapping sessions; however, there were often times when extra time between these sessions elapsed. In order to prevent trapping during periods of the full moon, an extra week between trapping sessions sometimes was necessary. Small mammals are known to restrict movements to avoid nocturnal predators during the full moon (Daly et al. 1991). However, with the exception of winter, the dense vegetative cover found on the majority of the grid may have reduced exposure to predators (Stokes et al. 2001). Trapping sessions also were postponed due to inclement weather to reduce trap-induced mortality, particularly when growth and survival of marked individuals are being evaluated (Sauer 1985).

In May of 2003, we began to see widespread disturbance of traps across the grid. We deemed it to be a predator problem and trapping was suspended for the month of June in 2003. When trapping was resumed in July of 2003, it appeared that the problem had been rectified and the predator had moved on. In January of 2004, it became clear that disturbance problems due predation had resurfaced and it became necessary to attempt to remove the predator threat. In March 2004, we were successful in capturing and permanently removing a raccoon (*Procyon lotor*) from the study grid. However, throughout the following months, the disturbance problems did not subside. During April 2004, we captured and removed both a gray fox (*Urocyon cinereoargenteus*) and another raccoon from the study grid. Disturbance was not observed again until November 2004, when another gray fox was successfully captured and permanently removed. Since that time there have been no signs of disturbance on the grid. These predators were released at a location approximately 40 km from the study area.

During each trapping session, traps were baited and set during the day and checked every morning of the trapping period. *S. hispidus* is known to demonstrate crepuscular activity and hence traps must be open overnight (Eifler and Slade 1998). Air temperature, wind speed and overall weather conditions were estimated at the start of each day of trapping. At the end of the trapping session, the traps were locked open until the next period of active trapping. During the warmer months, it was necessary to lock the traps open in the mornings and reopen them in the afternoons to prevent heat-induced mortality of animals that otherwise would have been caught during the day.

At each station, two different types of live traps were used. One was a typical Fitch trap (Rose 1994) made with a 355-ml drink can attached to a mesh trap 23 cm long and with a 6.5 X 6.5 cm opening. The other trap was a modified Fitch trap in which the drink can is replaced with a #10 tin can (Rose 1973). The larger trap allowed us to place a substantial amount of hay to reduce winter mortality to nearly zero (Rose et al. 1977). The hay was only used during the winter months acting as both an additional food source and as insulation. Traps were baited with a combination of wild bird seed and sunflower seeds.

Each animal was given a numbered ear tag at the time of initial capture. Newly tagged individuals were identified by species, and tag number, station of capture, body mass and reproductive information were recorded. Although the main focus of the study was to capture and follow the progress of *S. hispidus*, we regularly captured and monitored several other small mammal species that were present in the study area. These species included meadow vole (*Microtus pennsylvanicus*), house mouse (*Mus musculus*), eastern harvest mouse (*Reithrodontomys humulis*), rice rat (*Oryzomys palustris*), pine vole (*Microtus pinetorum*) and two species of shrews (*Blarina* spp. and *Cryptotis parva*).

Body weight was obtained by using 100-g and 300-g Pesola ™ scales. Reproductive condition was determined for both males and females. Males were noted as having either descended (reproductive) or abdominal (non-reproductive) testes (McCravy and Rose 1992). For females, reproductive condition was based on three characteristics, including perforate or non-perforate vaginal opening, size of nipples (small, medium and large), and closed, slightly open or open pubic symphyses. Pregnancy was also recorded when apparent.

The same information was collected for recaptured animals. However, those animals that were recaptured within the same trapping session were counted solely as an additional capture and only tag number and station of capture were recorded. In some cases, recaptured animals might have lost an ear tag. These animals were retagged and later synonymized with the previously tagged individual it was most likely to be. Each animal was released at the station of capture.

Statistical Analysis

Standard programs, such as SPSS version 12.0 and JOLLY, were used to determine aspects of population dynamics such as density, rates of body and population growth, survival rates per month and season, and to evaluate patterns of reproduction. Mean masses for males and females were calculated for each month, season, mass class, and age class. Winter was defined as December, January, February; spring as March, April, May; summer as June, July August; and autumn as September, October, November. Animals were placed into one of seven mass classes based on mass at time of capture, using the criteria similar to other mean mass and growth rate studies on cotton rats (Cameron and Spencer 1983; Slade et al., 1984; Campbell and Slade 1993). Mass classes were broken down by increments of 20 grams, with the exception of mass class 1, which accounted for individuals weighing < 50 grams. Mean growth rates of individuals were also categorized in grams per week at the monthly, seasonal and mass class level. As a result of small sample sizes, mean mass and mean growth rates could not be calculated for some months, seasons, and mass classes.

Sex ratios were evaluated using Chi-square analysis to determine if there were significant differences between the numbers of males and females for entire duration of the study, as well as for the years 2003 and 2004 (SPSS 2003). Chi-square analysis was also conducted on age distributions to examine potential significant differences between the numbers of adult and juvenile males and females in the population. Residency patterns were also analyzed using Chi-square analysis to test for significant differences among three different residency classes of the population. Transients were defined as individuals observed in only one month, visitors as those caught during two consecutive months, and residents as individuals known to have lived at least three months on the study grid.

Survival rates and density were determined using the software package JOLLY (Hines 1996), an executable software program downloaded from the USGS website, which uses the Jolly-Seber Model. Density values were also calculated by hand using minimum number known alive (MNA) for a given month. The density of a population, as estimated by MNA, is calculated by adding the number of individuals captured during month *t* to those tagged animals not captured in month *t* but known to have survived into a following month. Such animals can only be counted for month *t* if they were caught in month $t + 1$ or beyond. Correlation analysis was performed on density values produced by JOLLY to evaluate a possible correlation between the first and second year of the study. Correlation analysis was also conducted on density estimates produced by JOLLY and MNA to determine if a significant correlation was present between the two methods of density estimation. In addition, Chi-square statistics were produced by JOLLY to assess estimates of density and survival as a suitable model for my data.

I also investigated potential differences between my study based on mark-recapture methods and previously reported necropsy data of Virginia cotton rat populations (Rose and Mitchell 1990; Bergstrom and Rose 2004). Correlation analysis was used to examine similarities in reproductive patterns for males and females (SPSS 2003). Correlation analysis evaluated reproductive patterns for males based on external reproductive features from the current study and testes weights from the necropsy study (Bergstrom and Rose 2004). Correlation analysis also examined female reproductive trends and pregnancy rate values obtained from necropsy data from the Bergstrom and Rose study (2004).

For analysis of mean mass, Student's t-tests (two-sample) were used to determine potential significant differences in overall mean masses between males and females (SPSS 2003). Two-sample t-tests were also performed on males compared to females in the years 2003 and 2004. Same-sex comparisons using two-sample t-tests were also conducted for both sexes between the years 2003 and 2004. Additional two-sample t-tests were performed on mean mass for male and female transients and residents between 2003 and 2004. Mean mass was also analyzed using model-I two-factor analysis of variance (ANOVA) to observe any potential significant differences between the sexes and months. A model-I two-factor ANOVA was also used to determine if there were significant differences between the sexes and among seasons. In order to observe any significant difference between the sexes and among seasons and mass classes for mean mass, a model-I three-factor ANOVA was used. Ryan-Einot-Gabriel-Welsch Multiple Range (REGWF) tests were performed for each ANOVA where factors proved to be significant (SPSS 2003).

Daily growth rates were determined by calculating changes in body mass of an individual from its first capture in one trapping period to its first capture in the next trapping period and dividing these values by the number of intervening days. Obviously pregnant females were excluded from these analyses because of the large weight gains associated with pregnancy. Juvenile growth was also excluded from growth rate analysis because of their exceptionally large gains in weight in the early stages of their life. To compare calculated growth rates with previously published growth rates (Cameron and

Spencer 1983; Slade et al. 1984; Eifler and Slade 1999), daily growth rates (grams per day) were converted to weekly growth rates (grams per week) by multiplying individual growth rates by seven. Individual growth rates were averaged by sex, month, season, and mass class. Student's t-tests (two-sample) were used to determine any significant difference between overall male and female growth rates for the entire study. Two-sample t-tests were also conducted between male and female growth rates for 2003 and 2004, as well as same-sex comparisons between the two years. Monthly and seasonal growth curves were constructed using mean growth rates of individuals. Growth rates were also analyzed using a model-I two-factor ANOVA to observe significant differences between sexes and seasons. In addition, a model-I three-factor ANOVA was used to determine if there were significant differences in growth rates between sex, season and mass class (SPSS 2003). When the factors of ANOVAs demonstrated significance, REGWF tests were performed to determine the exact interactions that were significant. In addition, individual growth trajectories for animals with long capture histories were plotted to reveal patterns of growth.

Additional comparisons were made between my study and previously reported necropsy data of Virginia cotton rat populations (Rose and Mitchell 1990; Bergstrom and Rose 2004). A one-sample, 1-tailed t-test was used to observe any potential significant difference between overall mean masses for males and females (SPSS 2003). To rule out differences based on the influence of temperature and precipitation, Chi-square analysis was conducted on mean yearly weather values from each Virginia population to the 50-year mean, as well as against each other.

In order to better understand the effect of survival on the population, statistical analysis was performed on survival rates produced by JOLLY (Jolly-Seber model). Daily survival rates were converted to monthly survival rates by multiplying the daily rate by 30. Survival rates were calculated with and without juveniles. Two-sample t-tests on monthly mean survival rates revealed no significant differences between the groups (SPSS 2003). Therefore, monthly survival rates with juveniles were used for all of the statistical analyses on survival. Two-sample t-tests were also conducted on monthly mean survival rates for males and females for the entire study to determine if significant differences were present. Monthly mean survival rates between males and females in 2003 and 2004 were also tested for significance using two-sample t-tests. In addition, monthly mean survival rates for same sex comparison across 2003 and 2004 were conducted using two-sample t-tests (SPSS 2003).

Factors that have the potential to influence survival are growth and the proportion of transient animals in the population. In order to explore these relationships within my population, the survival and growth rates, as well as survival and percentages of transients, were compared using correlation analysis (SPSS 2003). For survival and growth analysis, monthly growth rates were calculated by multiplying daily growth rates by 30. Correlation analysis was conducted monthly and seasonally for both males and females to determine if significant correlations were present. These analyses were also performed at the monthly and seasonal levels for monthly mean growth rates and subsequent survival (e.g., survival in March compared to February growth). For comparison of survival and the proportion of transients, correlation analysis was conducted using seasonal proportions of transients and seasonal survival rates. Seasonal proportions of transients were also compared with seasonal growth rates using correlation analysis (SPSS 2003).

Because winter survivorship was an important aspect of the study, the impact of survival throughout this season was examined without the use of JOLLY survival estimates. Winter patterns of survival based on individuals of each mass class were observed into successive seasons. Over the winter months, individuals from cohorts were noted as either present or not present in successive seasons and these patterns are presented graphically. Increases and decreases in mean mass into different mass classes were not taken into account; only the initial mass class at the start of the season was used for each individual. These observations were made for males and females in the winter of 2002-2003, and both autumn of 2003 and 2004.

RESULTS

During the 28-month study period, 864 animals of eight different species were tagged in 9,088 trap nights. Of these, *Sigmodon hispidus* accounted for 513 (59.42%) of the total number of individuals tagged and constituted the highest number of captures on the grid (Table 1). *Microtus pennsylvanicus* and *Reithrodontomys humulis* were the second and third most common with 135 (15.61%) and 129 (14.91%) tagged individuals, respectively. During the first months of trapping, 45 *Mus musculus* (5.20%) were tagged on the grid, but none were caught after May of 2003. *Oryzomys palustris, Blarina* spp., *Microtus pinetorum* and *Cryptotis parva* were captured much less frequently and together accounted for < 5% of tagged animals. Ten *O. palustris* tagged during January and February of 2003 were recaptured through April of 2003, but none was seen on the grid again until November and December of 2003. Thereafter, rice rats were not observed until 1-3 were caught intermittently from September 2004 to February 2005. *Blarina* spp. and *Cryptotis parva* were also captured sporadically throughout the study; many were dead in the trap. *Microtus pinetorum* was the rarest species on the grid. Two of these four individuals were captured in November and December 2003, and the other individuals were captured six months later in February and March 2004. In the last few months of the study, *S. hispidus* presence began to dwindle on the study grid and *M. pennsylvanicus* and *R. humulis* were the more common species.

The dynamics of the community are integral to our understanding of populations of small mammals; however, the following results will focus solely on the species of interest, *S. hispidus*. These results are based on data collected in December 2002 to February 2005, which includes three winter seasons. Except where specifically

TABLE 1.—Number of tagged males and females captured from December 2002 to February 2005. *Sigmodon hispidus* was the species with the most tagged individuals and *Microtus pinetorum* was the species with the fewest. The sexes of *Cryptotis sp.* and *Blarina sp.* cannot be determined externally.

Species	Males	Females	Unknown	Total
Sigmodon hispidus	248	265	0	513
Microtus pennsylvanicus	70	64	1	135
Reithrodontomys humulis	67	62	0	129
Mus musculus	31	13	1	45
Oryzomys palustris	11	9	1	21
Cryptotis parva	—	—	11	11
Blarina sp.	—	—	6	6
Microtus pinetorum	1	3	0	4
Total			23	864

mentioned, data from March of 2005 were only used to calculate density and growth and survival rates.

General Population Trends

For all tagged cotton rats, the sex ratio (265:248; females:males) was not significantly different from 1:1 ($X^2 = 0.56$, d.f. = 1, $p > 0.50$; Figure 7; Table 1). However, for the total number of animals captured and accounted for once per month, more females were captured than males (652:538; Table 2). These include only individuals that were physically captured and not those known to be alive. This sex ratio was significantly female-biased ($X^2 = 10.92$, d.f. = 1, $p < 0.001$) for the entire study (Figure 7).

When each year of study was examined separately based on total individuals captured (n = 1190), only the year 2003 (315:254) demonstrated a significantly female-biased sex ratio ($X^2 = 6.54$, d.f. = 1, $p < 0.01$; Figure 7). The sex ratio in 2004 (244:208) was not significantly different from 1:1 ($X^2 = 2.87$, d.f. = 1, $p > 0.05$). In addition to female bias observed in the total number captures (652:538), female bias was also present at the seasonal level, with males only more dominant in the summer of 2003 and the spring of 2004 (Figure 8). Females were most dominant in the winters of 2003-2004 and 2004-2005.

During my study, the population was dominated by adults. Of the 538 males captured, 466 (87%) were adults, using the maturity criterion of 50 g body mass (Rose and Mitchell, 1990), and 72 were juveniles. Similarly, 566 of the 652 (87%) female individuals captured were adults and the remaining 86 were juveniles (Table 3). No juvenile males were recorded in the last winter (2004-2005) and less than 5% of cotton

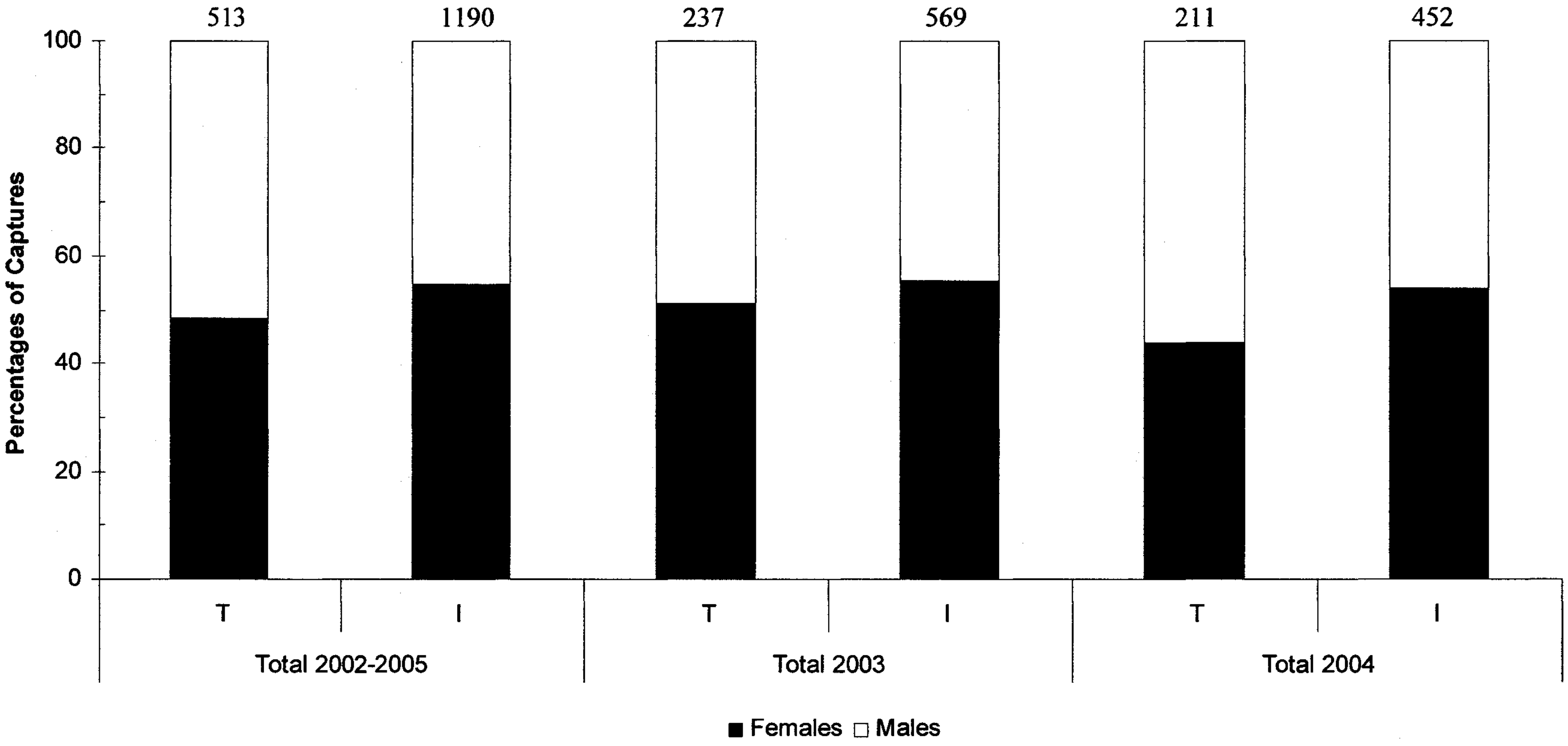

FIG. 7.—Percentages of males vs. females for tagged individuals (T) and individuals captured once per month (I), including juveniles, for the study period December 2002 to February 2005, and separately the years 2003 and 2004. No significant differences were present for the sex ratio of tagged individuals, but because of their longer residency on the grid, females captured once per month had significantly ($p < 0.001$) higher numbers than males for the entire study, and for the calendar years of 2003 and 2004.

TABLE 2.—Total number of animals captured and accounted for once per month of each species and the total number of animals captured of each sex of each species, December 2002 to February 2005. Numbers exclude those individuals known to be alive but not captured. Numbers in parentheses indicate the total number of multiple captures.

Species	Males	Females	Unknown	Total
Sigmodon hispidus	538 (694)	652 (874)	0	1190 (1568)
Microtus pennsylvanicus	141 (181)	124 (153)	1	266 (335)
Reithrodontomys humulis	96 (104)	90 (115)	0	186 (219)
Mus musculus	43 (44)	19 (19)	1	63 (64)
Oryzomys palustris	20 (25)	14 (14)	1	35 (40)
Cryptotis parva	—	—	11	11 (11)
Blarina sp.	—	—	6	6 (6)
Microtus pinetorum	1 (2)	3 (3)	0	4 (5)
Total	840 (1050)	902 (1178)	20	1762 (2248)

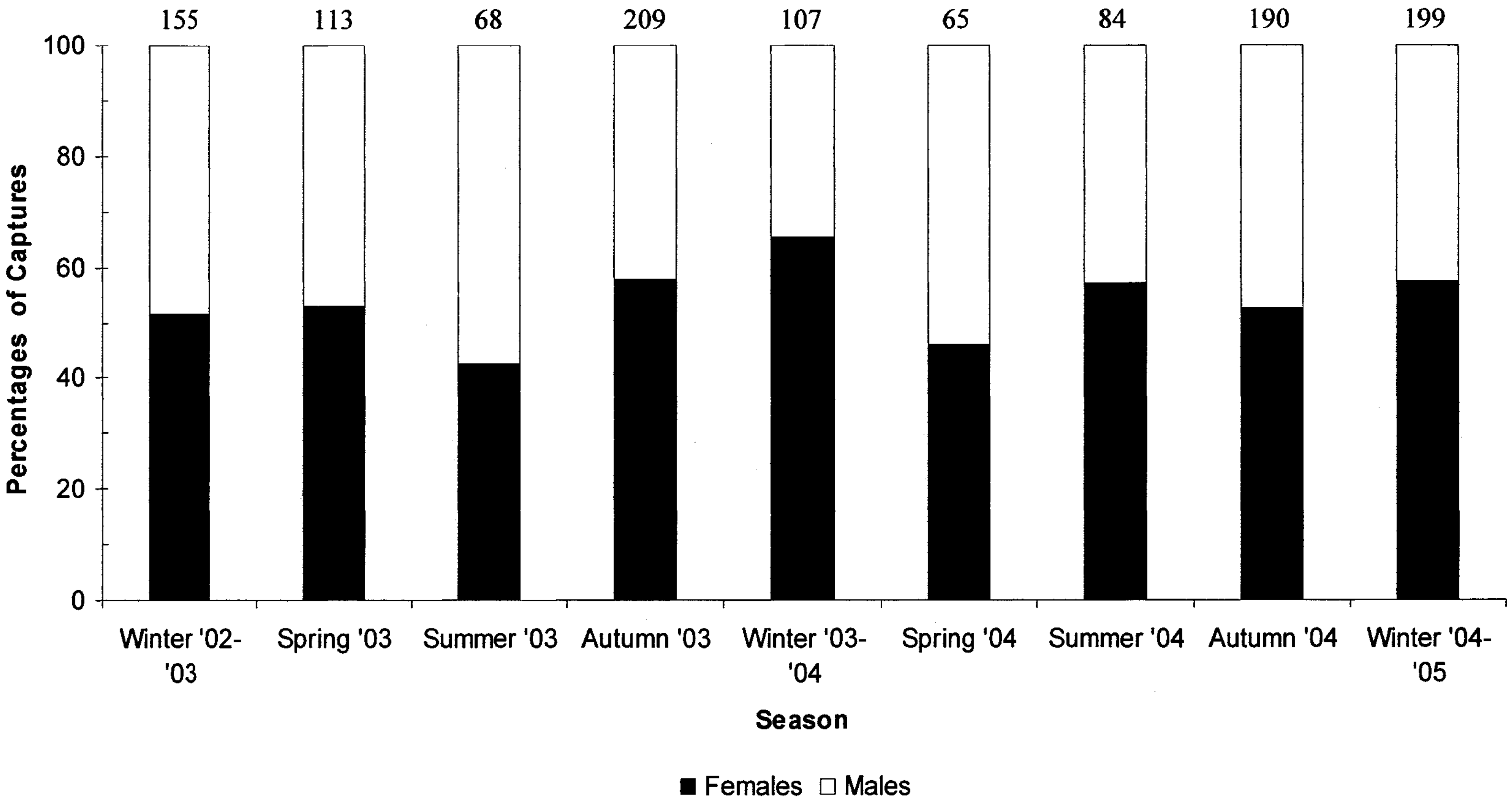

FIG. 8.—Seasonal percentages of males vs. females captured, including juveniles, from winter 2002-2003 to winter 2004-2005. Increases in the percentages of females were seen in the autumn of 2003, and winters of 2003-2004 and 2004-2005. Increases in males were seen in the summer of 2003 and spring of 2004. Winter consisted of months (Dec-Feb), spring (Mar-May), summer (Jun-Aug) and autumn (Sept-Nov). Sample sizes per season noted at top of each column.

TABLE 3.—Total numbers of male and female juvenile and adult *Sigmodon hispidus* captured during December 2002 to February 2005. Juveniles weighed < 50 g and adults weighed ≥ 50 g. Winter consisted of months (Dec-Feb), spring (Mar-May), summer (Jun-Aug) and autumn (Sept-Nov).

	Juveniles		Adults	
	Males	Females	Males	Females
Winter 2002-2003	1	5	74	75
Spring 2003	0	0	53	60
Summer 2003	12	4	27	25
Autumn 2003	14	33	74	88
Winter 2003-2004	1	7	36	63
Spring 2004	11	1	24	29
Summer 2004	16	11	20	37
Autumn 2004	17	25	73	75
Winter 2004-2005	0	0	85	114
Total	***72***	***86***	***466***	***566***
Grand Total	158		1032	

rats were judged to be juveniles in the first (2002-2003) and second winters (2003-2004) (Figure 9). Bursts of juveniles appeared in the spring of 2004 and in both summers and autumns. Juvenile females were not recorded in the first spring or the last winter (Figure 9). Approximately 10% of females in the first winter and less than 10% in the second winter and second spring were juveniles (Table 3). There was no significant difference between the total numbers of male and female juveniles captured ($X^2 = 1.24$, d.f. = 1, $p > 0.25$); however, significant differences existed between the total numbers of male and female adults captured ($X^2 = 9.69$, d.f. = 1, $p < 0.005$; Table 3).

Patterns of residency are important because population theory considers resident animals to be paramount in understanding the dynamics of populations. Animals that pass through populations may contribute little to such important parameters as reproduction and survival. Throughout the study, more cotton rats of both sexes were residents than transients or visitors. For each residency class, these numbers were based on individuals actually observed and accounted for once during a given month, plus those known to be alive but not necessarily observed that month. In some cases, animals disappeared for 2-3 months and then returned to the study grid (6.85% of tagged males (n = 17), 5.66% of tagged females (n = 15)).

Significantly more total female residents were caught than male residents (543:428) ($X^2 = 13.62$, d.f. = 1, $p < 0.001$; Table 4). By contrast, equal numbers of male and female visitors were observed ($X^2 = 0.00$, d.f. = 1, $p > 0.99$; Table 4) and significantly more male than female transients were observed ($X^2 = 6.95$, d.f. = 1, $p > 0.01$; Table 4). Monthly comparisons of male and female residents confirmed the overall pattern that residents outnumbered transients and visitors (Figure 10). These patterns

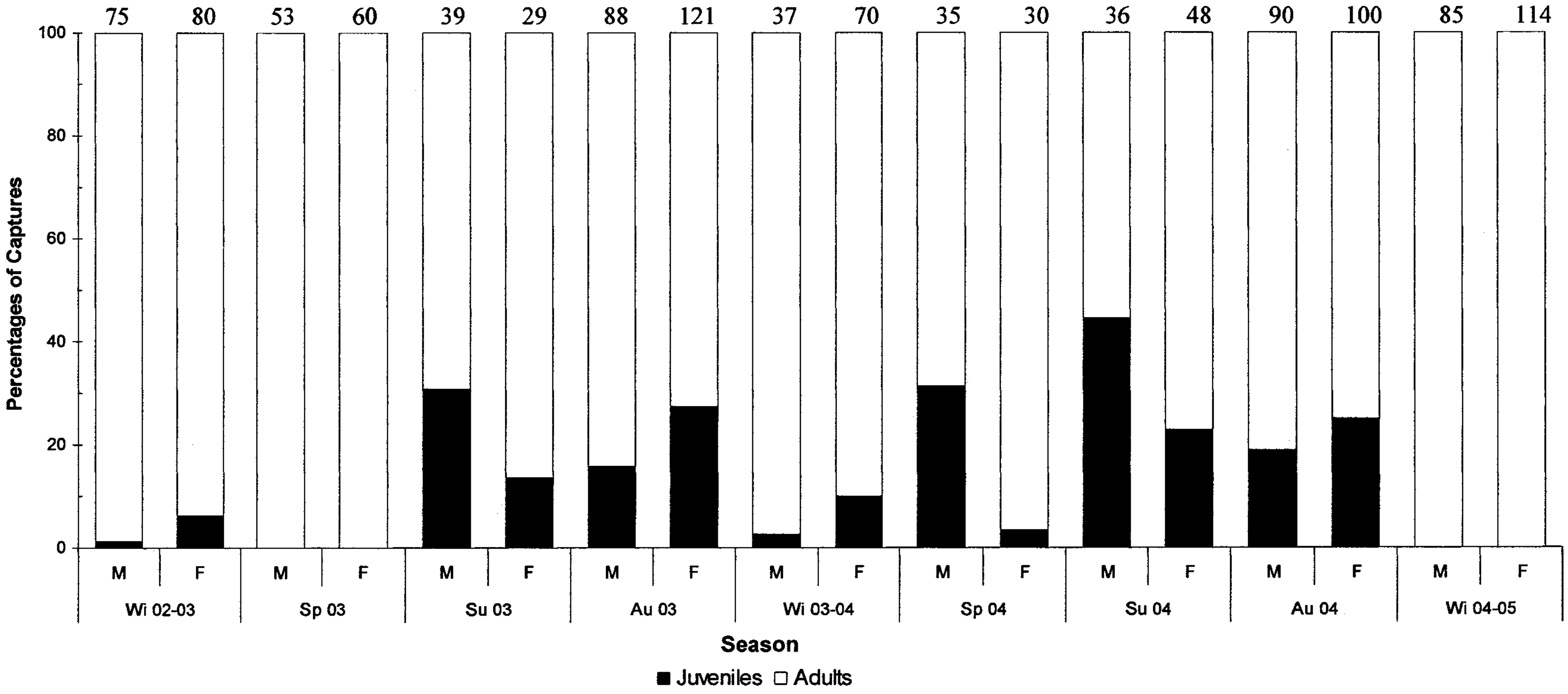

FIG. 9.—For each sex, seasonal pattern of juveniles (solid bars) vs. adults (open bars) captured from winter 2002-2003 to winter 2004-2005. Increases in percentages of juveniles were observed in the summer and autumn of 2003, and spring, summer and autumn of 2004. Less than 10% of juveniles were present in the winters of 2002-2003 and 2003-2004. No juveniles were seen in winter 2004-2005. Juveniles were animals weighing < 50 g and adults were animals weighing ≥ 50 g.

TABLE 4.—Total numbers of male and female transients, visitors and residents observed during December 2002 to February 2005. Transients were individuals observed in only one month, visitors during two consecutive months, and residents were individuals known to have lived at least three months on the study grid.

	Transients		Visitors		Residents	
	Males	Females	Males	Females	Males	Females
Winter 2002-2003	19	26	13	10	50	44
Spring 2003	9	9	5	4	47	45
Summer 2003	12	7	5	0	34	35
Autumn 2003	16	14	15	12	68	102
Winter 2003-2004	10	10	8	9	27	70
Spring 2004	20	3	3	1	18	34
Summer 2004	16	6	0	14	25	34
Autumn 2004	14	9	18	11	77	90
Winter 2004-2005	13	6	8	14	82	89
Total	***129***	***90***	***75***	***75***	***428***	***543***
Grand Total	219		150		971	

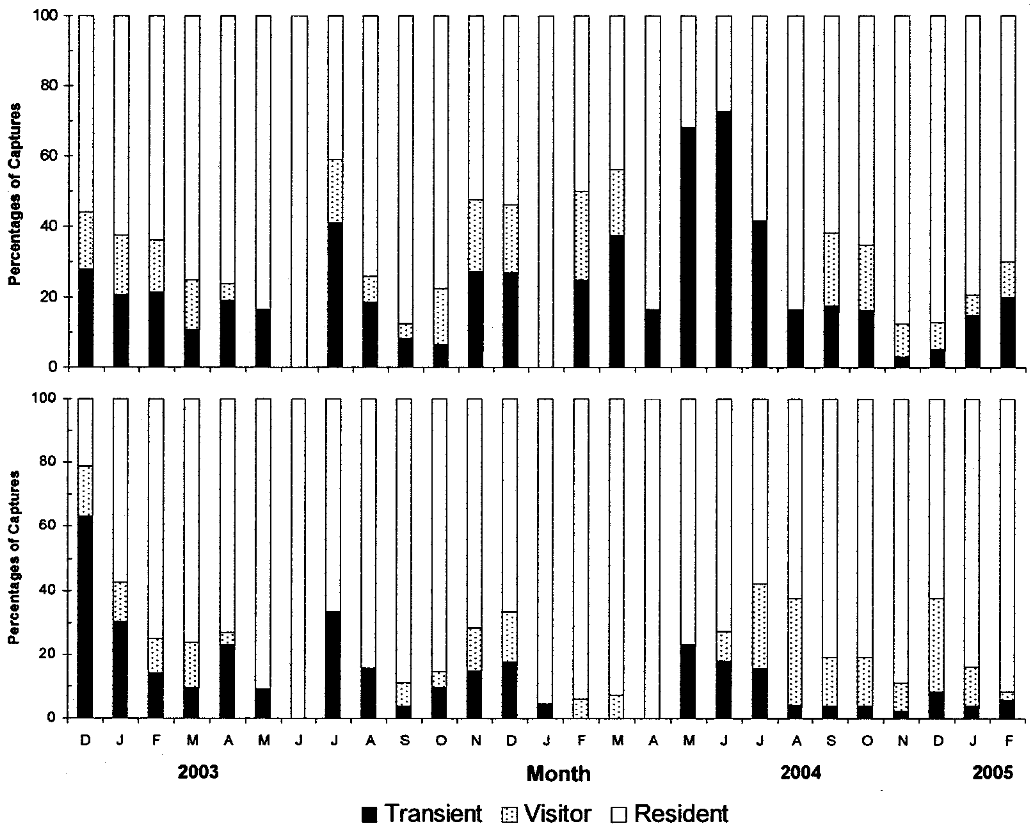

Fig. 10.—Monthly patterns of percentages of male (top) and female (bottom) transients, visitors, and residents captured during the study period. Definitions of transients, visitors, and residents are found in Table 4. Residents of both sexes were more numerically dominant than transients or visitors throughout the study, but male transients were more numerous than female transients. Minimum number of individuals in a given residency class were 0 and the maximum number of individuals was 102.

also clearly showed that transient males were more numerous than transient females, except in December 2003.

For seasonal distributions, the highest proportions of transient males were observed in the winter of 2002-2003, summer of 2003, spring of 2004 and the summer of 2004 (Figure 11). In the spring of 2004, male transients were slightly more numerous than resident males and no visitors were observed. The numbers of visitors noticeably increased in both autumns of the study (Table 4). A similar trend of large numbers of residents was observed in both autumns and the winter of 2004-2005. When total numbers of male transients, visitors and residents were compared, significant differences emerged: male transients were more numerous than visitors ($X^2 = 14.29$, d.f. = 1, $p < 0.001$; Table 4), male visitors were less numerous than residents ($X^2 = 160.50$, d.f. = 1, $p < 0.001$) and thus male residents were much more numerous than transients ($X^2 = 247.73$, d.f. = 1, $p < 0.001$). For females, more residents were seen than transients or visitors (Figure 11). Residents were more dominant in both autumns, as well the winters of 2003-2004 and 2004-2005. Significantly more resident females were observed than visitors ($X^2 = 354.41$, d.f. = 1, $p < 0.001$) and transients ($X^2 = 324.18$, d.f. = 1, $p < 0.001$). No significant difference was observed in the number of female transients versus visitors ($X^2 = 1.36$, d.f. = 1, $p > 0.1$; Table 4).

Despite differences in total numbers of male and female cotton rats captured, some general seasonal trends in transiency and residency were observed. Although female transients were fewer than males overall, relatively greater numbers of female transients were seen in the autumn of 2003 and the winter of 2003-2004 (Table 4). Similar increases in the numbers of male visitors were also present in both autumns of the

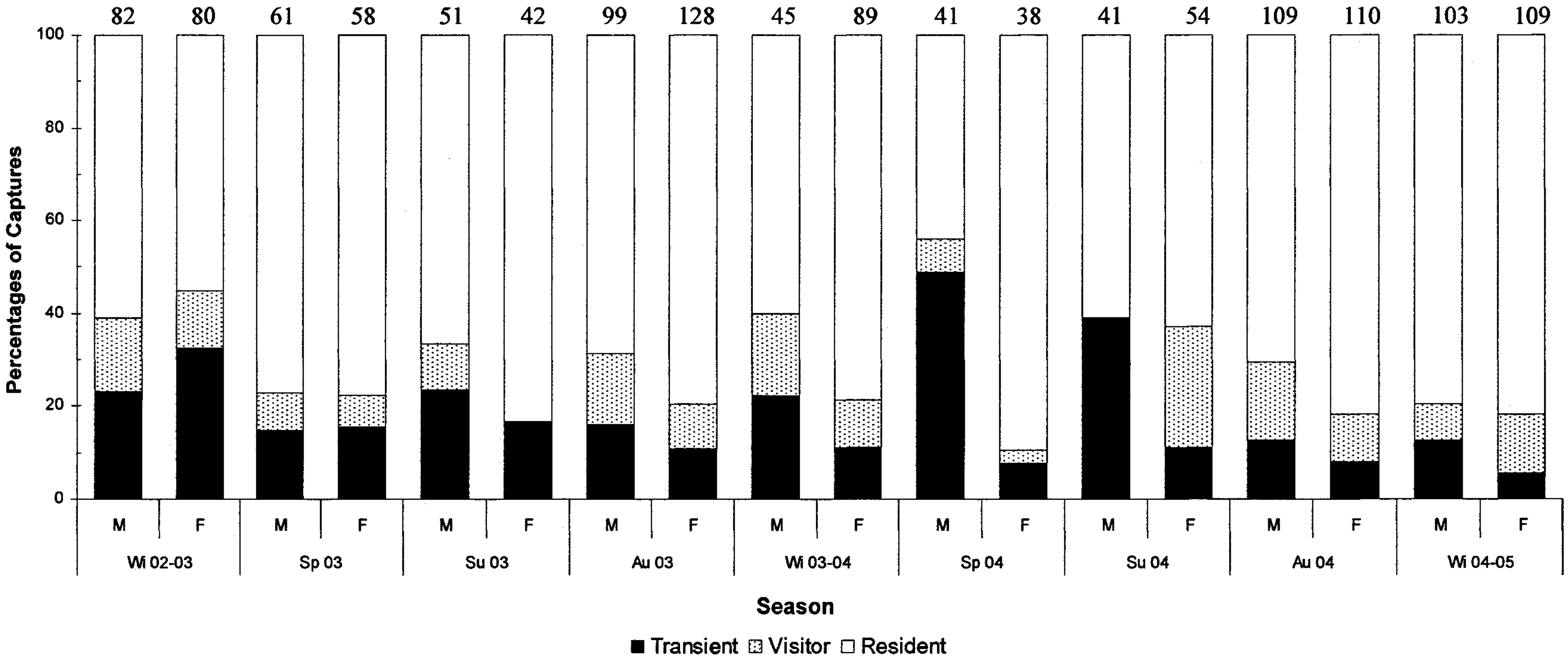

FIG. 11.—Seasonal patterns of percentages of male and female transients, visitors, and residents captured during the study period. Male residents dominated the population and large increases in the percentages of transient males were observed in the spring and summer of 2004. Female residents clearly dominated the population; percentages of female transients and visitors were low. No visitors were observed for females in the summer of 2003 and for males in the summer of 2004.

study. There were significantly more female than male visitors in the summer of 2004 ($X^2 = 14.00$, d.f. = 1, $p < 0.001$; Table 4). Significantly more female than male residents were observed in the autumn of 2003 ($X^2 = 6.8$, d.f. = 1, $p < 0.01$), winter of 2003-2004 ($X^2 = 19.06$, d.f. = 1, $p < 0.001$) and the spring of 2004 ($X^2 = 4.92$, d.f. = 1, $p < 0.05$; Table 4).

Population Density

Goodness-of-fit tests demonstrated that JOLLY model-B was the best model for my data ($X^2 = 46.29$, d.f. = 33, $p = 0.062$). Initial late winter estimates were about 60/ha, numbers that fell by half in May 2003 before a density of 60/ha was observed again in late summer (Figure 12). By the end of the autumn breeding season in October and November 2003 population density reached > 100/ha. Density declined to 30-40/ha during the second winter. The population recovered during 2004 and population density again reached 100/ha by September 2004 and increased to 101/ha in November and 124/ha in January as young were being recruited. The apparent decline into the last month of study is not accurate because population estimators rely on some animals being alive in the following months and the future captures and survival of these animals were not known. The significant correlation between the first and second years of the study ($r = 0.640$, $n = 11$, $p < 0.05$) indicated that density patterns did not differ between years.

In addition to density estimates produced by JOLLY, minimum number alive per month was also calculated by hand based on those individuals captured and those known to be alive (Figure 12). These values are commonly used to provide a more conservative estimate of population density. There was significant correlation between density values

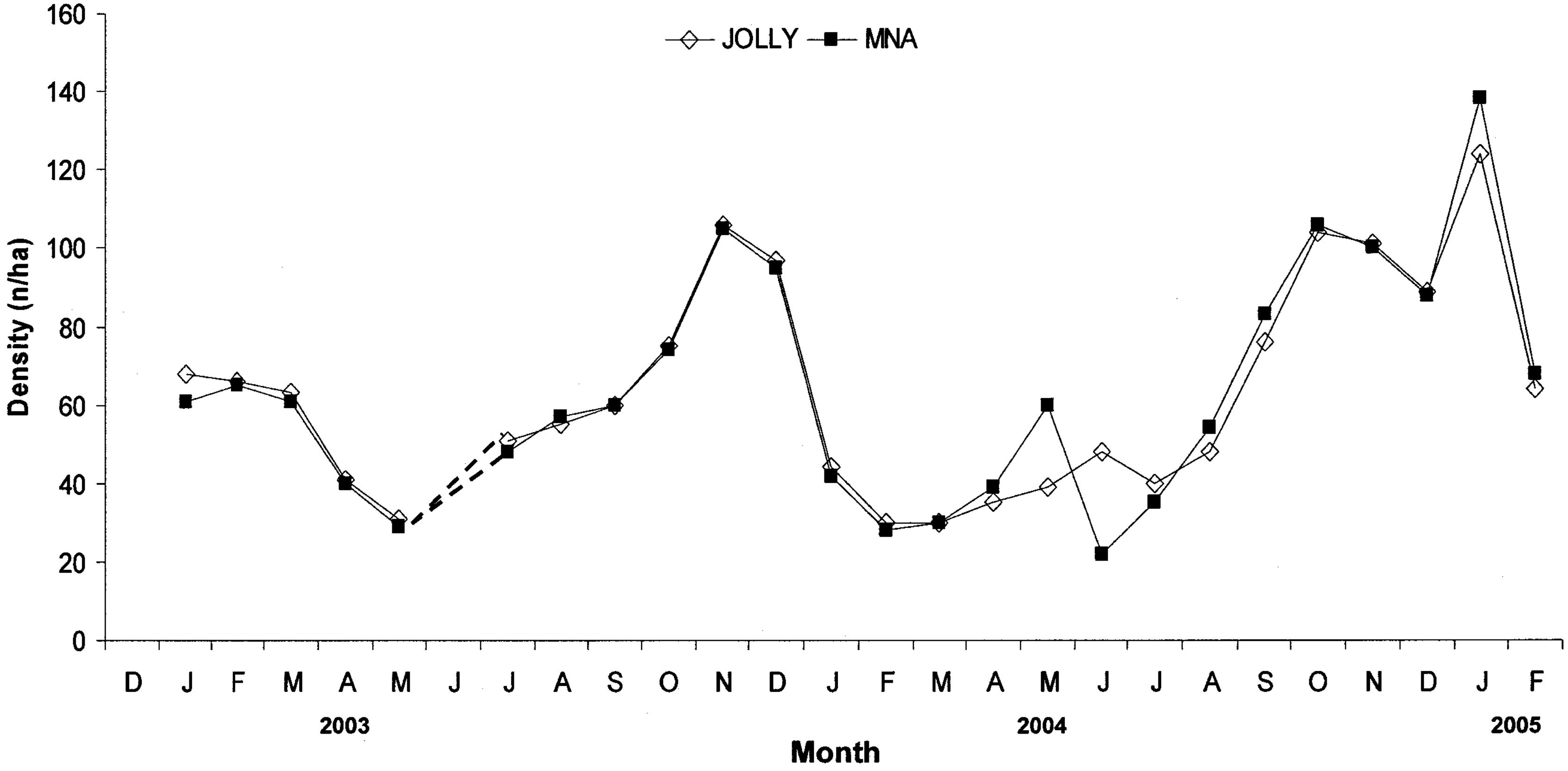

Fig. 12.—Monthly patterns of overall population density from December 2002 to February 2005. Density estimates (n/ha) were determined by software package JOLLY and through minimum numbers alive (MNA). Dashed lines represent the gap in data collection for June 2003. Increases in density were observed in both autumns and in the spring months of 2004. Decreases in density were seen in the late spring of 2003 and the winter of 2003-2004.

produced by JOLLY and those determined by minimum number alive methods ($r = 0.963$, $n = 25$, $p < 0.001$).

Patterns of Reproduction

Distinctive breeding and non-breeding seasons were evident based on external features for both sexes. In both 2003 and 2004, reproductive males of adult size were not observed until March (Figure 13). A small percentage of males were reproductive in January 2003 and January 2005. In 2003, males remained reproductively active into November, but no reproductive males were seen in November of 2004.

Male reproductive patterns observed in my study did not significantly deviate from trends previously observed with necropsy data based on percentage of convoluted epididymides (Bergstrom and Rose 2004; $r = 0.732$, $n = 27$, $p < 0.01$; Figure 14). Low percentages of convoluted epididymides were associated with periods of reproductive inactivity, while increased proportions of convoluted epididymides demonstrated periods when males are reproductively active. Males were reproductively active in both February 1988 and 1989 and no reproductive males were observed after both October 1988 and 1989. Despite the overall significance in male reproductive patterns, males in my study were reproductively active in October and into November 2003.

Almost all adult females were reproductively inactive over the winter months (Figure 15). Females were reproductively active in the spring, as well as in the late summer into early autumn, with the proportion of non-reproductive females gradually increasing from about August through the end of the year. In April of 2003, 70 percent of females were reproductively active and all females were reproductively active in May

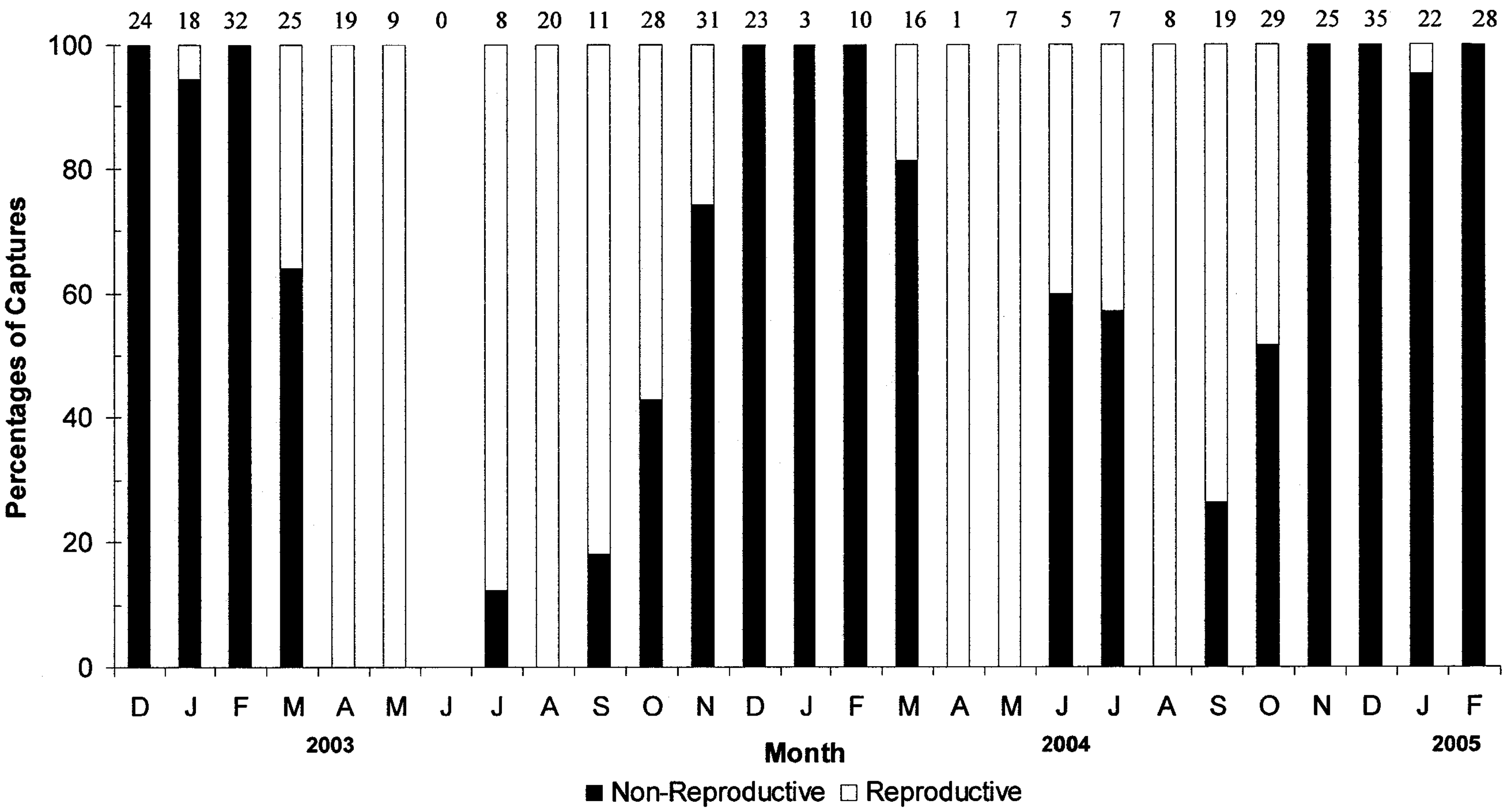

FIG. 13.—Monthly pattern of percentages of non-reproductive vs. reproductive adult males captured from December 2002 to February 2005. All males were observed to be reproductive in April, May and August of 2003 and 2004. Males were non-reproductive in the winter months (December-February) with the exception of small percentages in the Januarys 2003 and 2005. Non-reproductive males were also dominant in November 2004. No trapping was conducted in June 2003 due to predator disturbances.

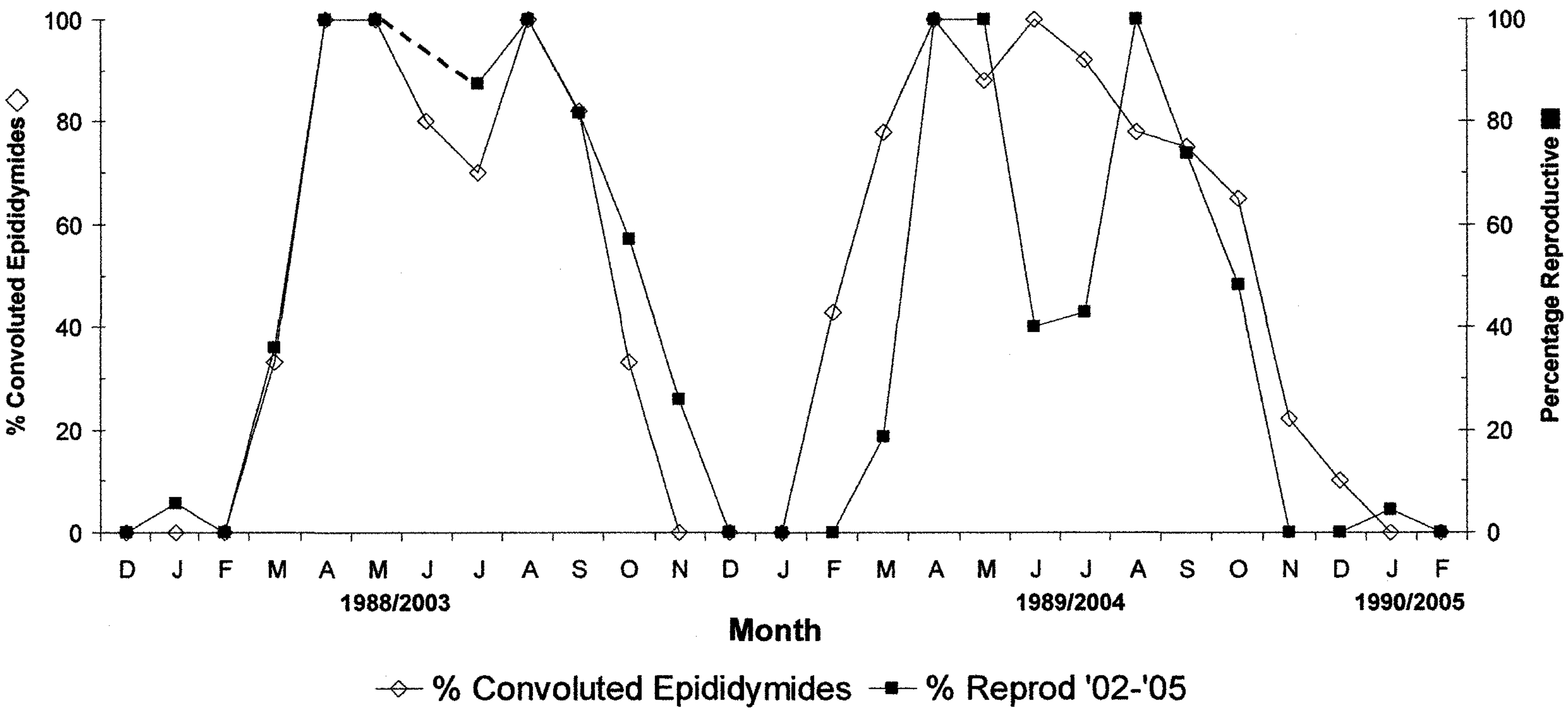

FIG. 14.—Patterns of male reproductive activity in the present study compared to male percent convoluted epididymides indicating reproductive competency using data from necropsied Virginia males from September 1987 to December 1989 (Bergstrom and Rose 2004). The dashed line indicates the gap in data collection for June 2003, when trapping was not conducted. Patterns of percentages of convoluted epididymides closely followed the percentages of reproduction for live-trapped males. Reproductively active males were observed over the winter months, but were associated with low proportions of convoluted epididymides. Increases in the proportion of convoluted epididymides were associated with months in which males were highly reproductive, as seen in the late spring to early autumn months.

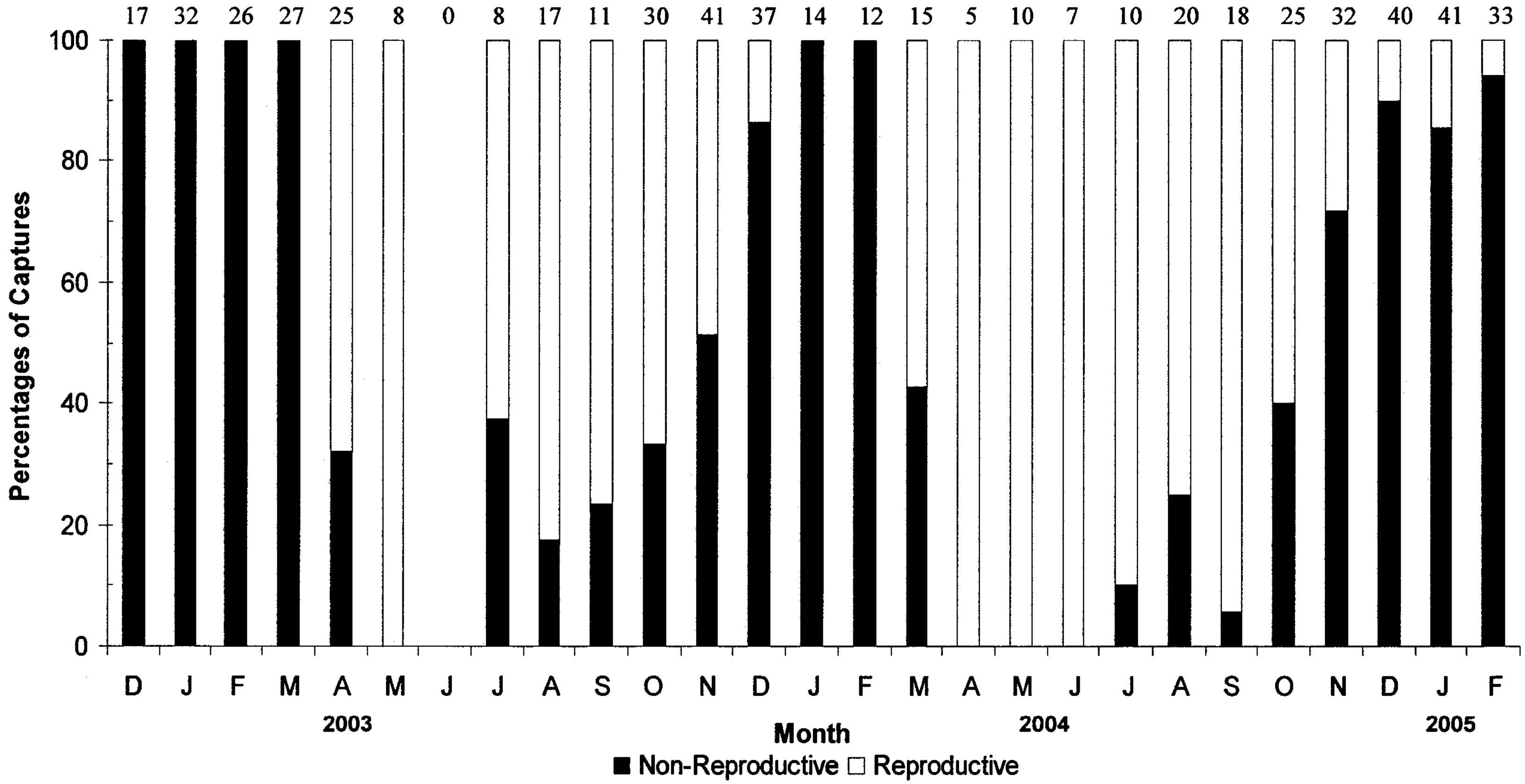

FIG. 15.—Monthly pattern of percentages of non-reproductive vs. reproductive adult females captured from December 2002 to February 2005. Higher percentages of non-reproductive females were observed over the late autumn and winter months. Females demonstrated the highest percentages of reproductive activity in the spring and summer months. All females were judged reproductive in May 2003 and April-June 2004. Reproductive females possessed slightly open to open pubic symphyses, medium-to-large nipples and perforate vaginal openings. No trapping was conducted in June 2003.

of 2003 and April, May and June of 2004. Females were reproductively competent through November in 2003 and 2004.

During the period when female cotton rats were reproductively active, 20.65% were recorded as being pregnant. Pregnant females, seen first in May of both years, were observed through November (Figure 16). Pregnant females were most numerous in the autumn months, with the most pregnant females recorded in August, September and October of 2004. Three females were recorded as being pregnant multiple times in their trapping history, but only one survived over the winter to be observed as pregnant in another breeding season.

Female reproductive patterns present in my study were not significantly different from previously reported necropsy data based on pregnancy rate values (Bergstrom and Rose 2004; $r = 0.782$, $n = 26$, $p < 0.01$; Figure 17). High proportions of reproductive females were seen in the spring and in late autumn with a cessation of breeding in the winter months of both studies. Despite the overall significantly similar reproductive patterns between the two studies, the onset of increased breeding activity in the spring was later in the 1987-1989 study than in my study. A high percentage of reproductive females was present in both April months of my study, which was similar to Virginia cotton rats in Bergstrom and Rose (2004). In both studies, 100 percent of females were reproductive by May. Virginia females from Bergstrom and Rose (2004) remained reproductively active through October in 1988 and through November in 1989, trends similar to the current study.

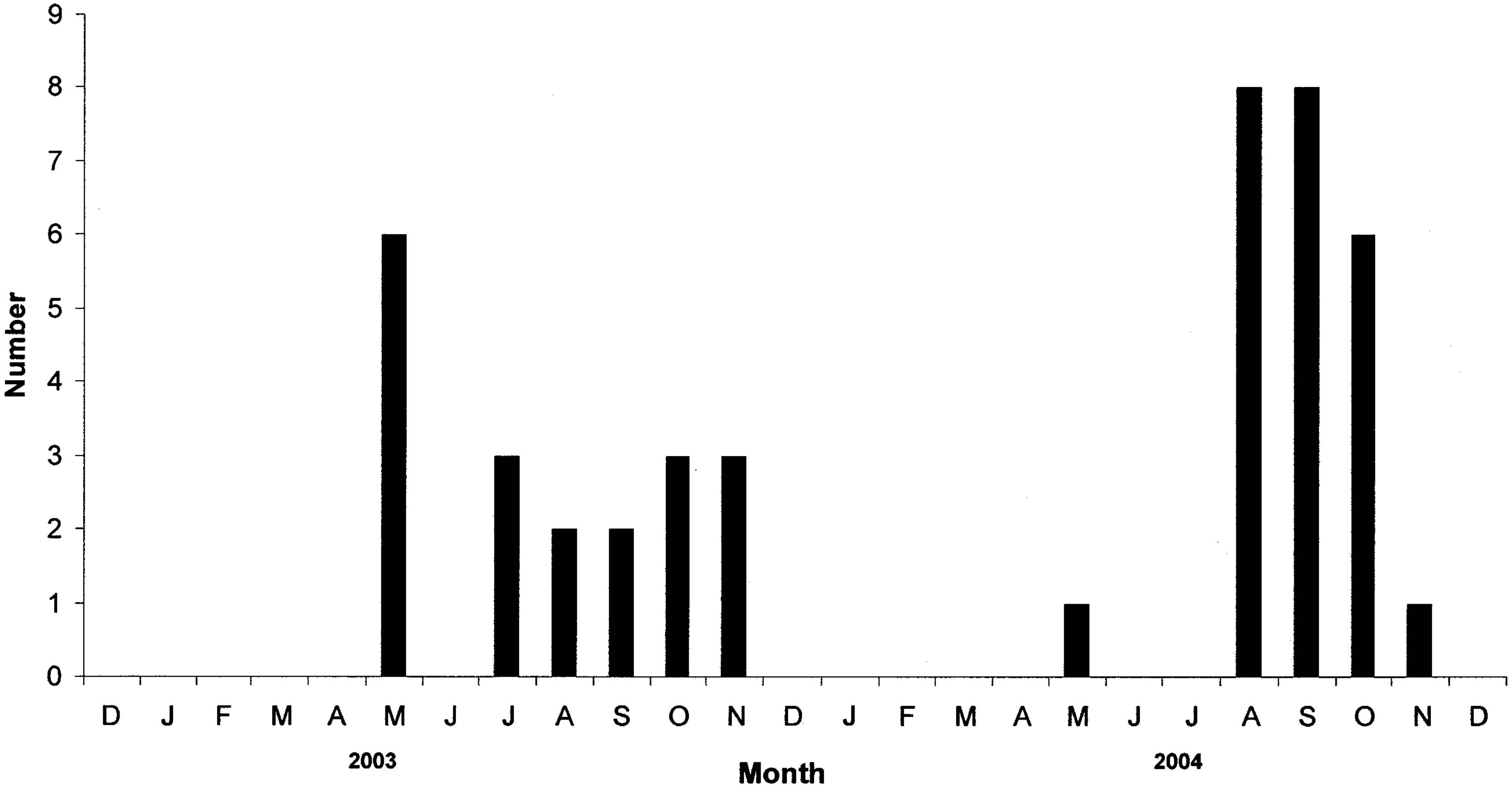

Fig. 16.—Numbers of pregnant females observed during the study period. Pregnant females were observed in March 2003 and 2004 and during the mid-summer through the late autumn months. No pregnant females were observed in any winter month. No trapping was conducted in June 2003.

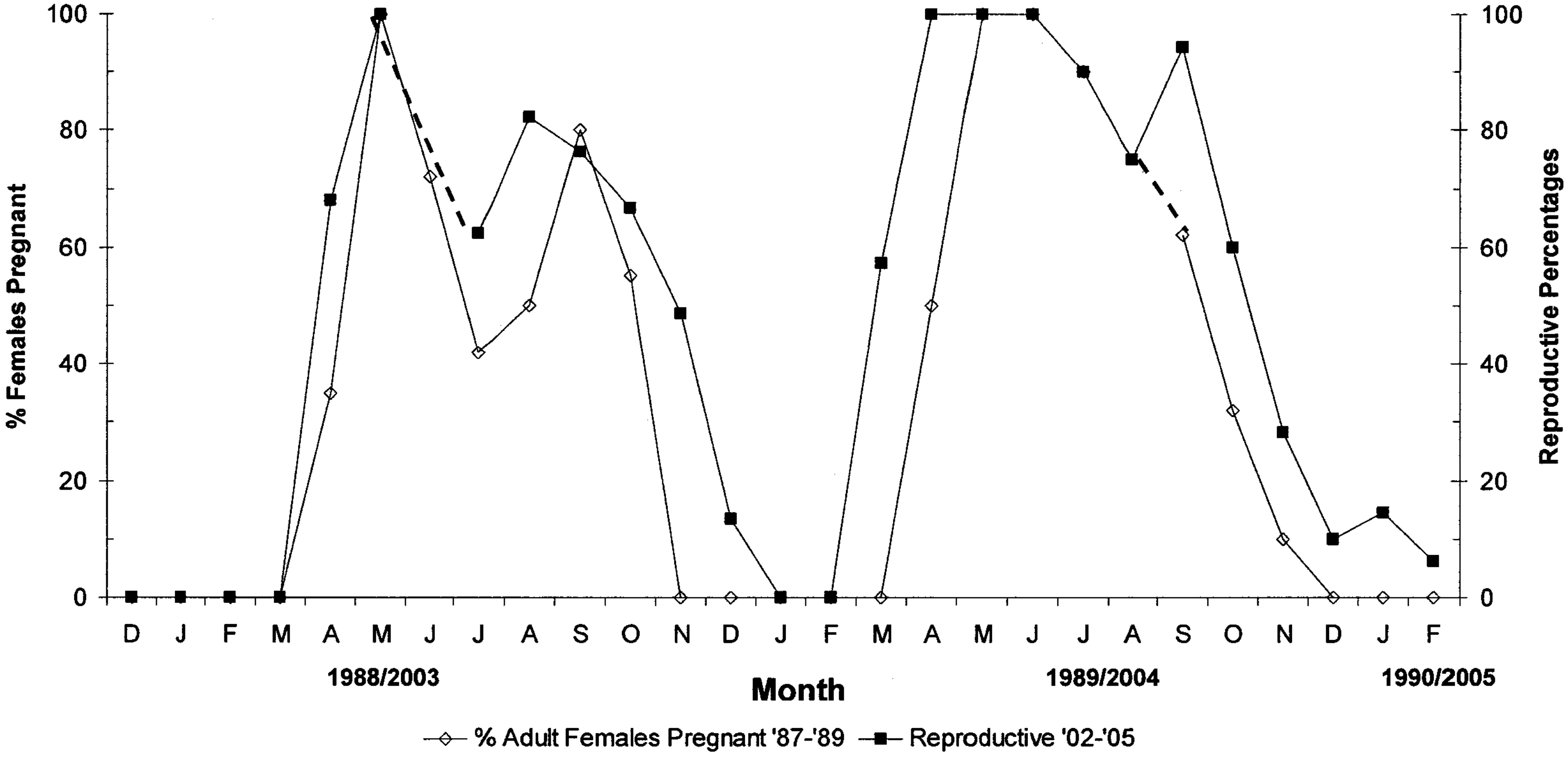

FIG. 17.—Patterns of female reproductive activity in present study compared to reproductive activity data obtained from necropsied Virginia females collected from September 1987 to December 1989 (Bergstrom and Rose, 2004). Dashed lines indicate gaps in the data collection for August 1989 and June 2003. Patterns of reproductive activity for both studies closely mimicked each other. Females had the lowest rates of reproductive activity over the winter months (December-February) with increased rates of activity in the late spring through mid-autumn months.

Body Mass

The overall mean body mass for adult males was 99.51 ± 1.327 g (n = 466) and for adult females, excluding pregnant females, mean mass was 92.23 ± 1.132 g (n = 522). Juvenile masses were also excluded from this analysis. These means were significantly different (t = 4.007, p = 0.001). These results were not significantly different from Virginia cotton rat body masses reported by Rose and Mitchell (1990), but were significantly greater than those reported by Bergstrom and Rose (2004). In the Rose and Mitchell study (1990), mean body mass was 101.48 ± 2.027 g for males (n = 152) and 94.26 ± 1.872 g for females (n = 148; Rose and Mitchell 1990). In comparison to my study, these means did not differ significantly for males (t = -1.481, p = 0.139) or females (t = -1.797, p = 0.073). However, significant differences were present for males (t = 5.341, p = 0.001) and females (t = 3.875, p = 0.001) when compared to Virginia populations reported by Bergstrom and Rose (2004). In the Bergstrom and Rose (2004) study, the mean mass for Virginia males was 92.40 ± 26.1 g (n = 234) and 87.80 ± 24.0 g for females (n = 239).

The mean masses for male and female cotton rats in the years 2003 (104.71 ± 2.002 g for males, 92.52 ± 1.490 g for females) and 2004 (97.92 ± 2.218 g for males, 92.49 ± 2.251 g for females) were significantly different in 2003 (t = 4.555, p = 0.001), but not in 2004 (t = 1.931, p = 0.054). Statistical significance was also tested for the same sex between years of the study. Males were significantly heavier in 2003 than in 2004 (t = 2.281, p = 0.024), but females were not (t = 0.714, p = 0.476).

In an attempt to better understand the observed mean mass differences for Virginia populations of cotton rats, mean mass of residency classes in this study were tested for statistical significance using two-sample t-tests. Both male transients and residents were significantly heavier in 2003 than 2004 ($t = 3.23$, $p = 0.002$; $t = 3.32$, $p = 0.001$, respectively; Table 5). In addition, male residents were significantly heavier than transients in both 2003 and 2004 ($t = -2.655$, $p = 0.01$; $t = -4.632$, $p = 0.001$). However, no significant differences in mean mass were found between females transients in 2003 and 2004 ($t = 0.329$, $p = 0.744$; Table 5) or between female residents in the two years ($t = -0.613$, $p = 0.540$). Female residents were not significantly heavier than transients in either 2003 or 2004 ($t = -1.705$, $p = 0.092$; $t = -1.50$, $p = 0.145$).

Statistical analysis was also performed on weather data for each individual Virginia study period to observe differences that have the potential to affect mean body mass. Temperature did not significantly deviate from the 50-year mean for this area (1983-1984: $X^2 = 0.0001$, d.f. = 1, $p > 0.05$; 1987-1989: $X^2 = 0.006$, d.f. = 1, $p > 0.05$; 2002-2005: $X^2 = 0.047$, d.f. = 1, $p > 0.05$; Table 6). The years 1983-1984 and 1987-1989 were study periods corresponding to earlier studies (Rose and Mitchell 1990; Bergstrom and Rose 2004, respectively). No significant differences were present when the 1983-1984 study period was compared to the 1987-1989 and 2002-2005 study periods ($X^2 = 0.004$, d.f. = 1, $p > 0.05$; $X^2 = 0.052$, d.f. = 1, $p > 0.05$). Also, no significant difference was also observed between the periods 1987-1989 and 2002-2005 ($X^2 = 0.088$, d.f. = 1, $p > 0.05$).

Precipitation also did not significantly deviate from the 50-year mean in this area. (1983-1984: $X^2 = 0.021$, d.f. = 1, $p > 0.05$; 1987-1989: $X^2 = 0.0305$, d.f. = 1, $p > 0.05$; 2002-2005: $X^2 = 0.107$, d.f. = 1, $p > 0.05$). Additionally, no significant differences were found between the 1983-1984 study period and the 1987-1989 and 2002-2005 study

TABLE 5.—Mean masses (g) of male and female transients and residents observed for the years 2003 and 2004. Numbers in parenthesis are the total numbers per year excluding juveniles and pregnant females.

	Transients		Residents	
Year	Males	Females	Males	Females
2003	89.16 (56)	81.66 (56)	104.91 (199)	90.49 (228)
2004	63.91 (55)	78.28 (25)	92.86 (164)	92.32 (266)

TABLE 6.—Mean temperatures (°C) and annual precipitation totals (mm) for the 50-year means, as well as for individual study periods obtained from the Southeast Regional Climate Center from a collection site at Lake Kilby in Suffolk, Virginia. Mean temperatures are reported in degrees Celsius and precipitation totals are in millimeters.

	Mean Temperatures	**Precipitation Totals**
50-year Means	1501.39	1220.47
1983-1984	1498.09	1257.05
1987-1989	1479.55	1362.20
2002-2005	1562.10	1303.53

TABLE 7.—Results for model-I 2-factor ANOVA on mean mass with sex and month as factors for data collected from December 2002 through February 2005.

Source	df	MS	F	P
Sex	1	0.099	7.451	0.006
Month	1	0.066	4.975	0.000
Sex * Month	25	0.027	2.046	0.003
Error	933	0.013		
Total	982			

periods ($X^2 = 0.165$, d.f. = 1, $p > 0.05$; $X^2 = 0.032$, d.f. = 1, $p > 0.05$, respectively). Nor were significant differences in precipitation totals found between the 1983-1984 and 2002-2005 study periods ($X^2 = 0.051$, d.f. = 1, $p > 0.05$).

A model-I two-factor ANOVA using sex and months as factors on log transformed data confirmed that there were significant mass differences between the sexes (F = 7.451, d.f. = 1,958, p = 0.006) and also significant differences among months (F = 4.975, d.f. = 25,958, p = 0.001; Table 7). The sex-month interaction term was also significant (F = 2.046, d.f. = 22,958, p = 0.003) as mean body mass for each sex was not significantly different in all months. It should be noted that due to small monthly sample sizes, some sex-month combinations were excluded from the analysis (males from January 2004 (n = 3) and April 2004 (n = 1) and females from May 2003 (n = 2)).

Ryan-Einot-Gabriel-Welsch Multiple Range (REGWF) F-tests were conducted on both the month and sex-month interaction terms to show which month and sex-month combinations were significantly different from one another. For the monthly factor, May of 2004 was significantly different from all other months, except for May 2003 (Appendix 1). In general, mean mass observed in the spring months was significantly higher than all other months. For the sex-month interaction factor, mean mass for males from December 2002 was significantly lower than mean mass for males in both May 2003 and 2004 (Appendix 2). In addition, male mean mass from May 2004 was significantly higher than mean mass for males from October 2003, March 2004, July 2004, November 2004 and the winter months of 2004 through February 2005. Female mean mass from May 2004 was significantly higher from all other sex-month combinations with the exceptions of females in April of 2003 and June and July of 2004.

Monthly mean mass of cotton rats for the study was plotted for both sexes (Figure 18). Mean masses increased steadily from January to May for males and less quickly for females. Mean mass of females changed little from October through March with the exception of a slight decrease in mean mass from January to February 2004. Additional increases in mean mass for both males and females were observed during June and July. Mean masses of both sexes were heaviest in May (142 g for males; 152 g for females) and lowest over the winter months (84 g for males; 74 g for females).

When monthly mean mass values were combined into seasons (Figure 19), the heaviest female cotton rats were found in spring and the lightest females in autumn of both years. Cotton rat males were heaviest in the spring of 2004 and next heaviest in the spring of 2003. Spring-to-summer decreases in mean mass were observed for both sexes, followed by steady increases for males but not females. The most pronounced decrease in mean mass was seen in males over the summer of 2004.

A model-I two-factor ANOVA, which used sex and season as factors, was performed on log transformed data. Data previously excluded from monthly ANOVA for mean mass due to small monthly sample size were incorporated into this analysis. Significant differences were present between sexes (F = 15.060, d.f. = 1,980, p = 0.001) and among the seasons (F = 6.089, d.f. = 7,980, p = 0.001; Table 8). The sex-season interaction term was also significant (F = 1.937, d.f. = 7,980, p = 0.05). REGWF tests, performed on the season factor, showed that mean masses for the springs of 2003 and 2004 were both significantly higher than masses from all three winters and the autumn of 2004 (Appendix 3). Both summers and the autumn of 2003 were not significantly different from other seasons.

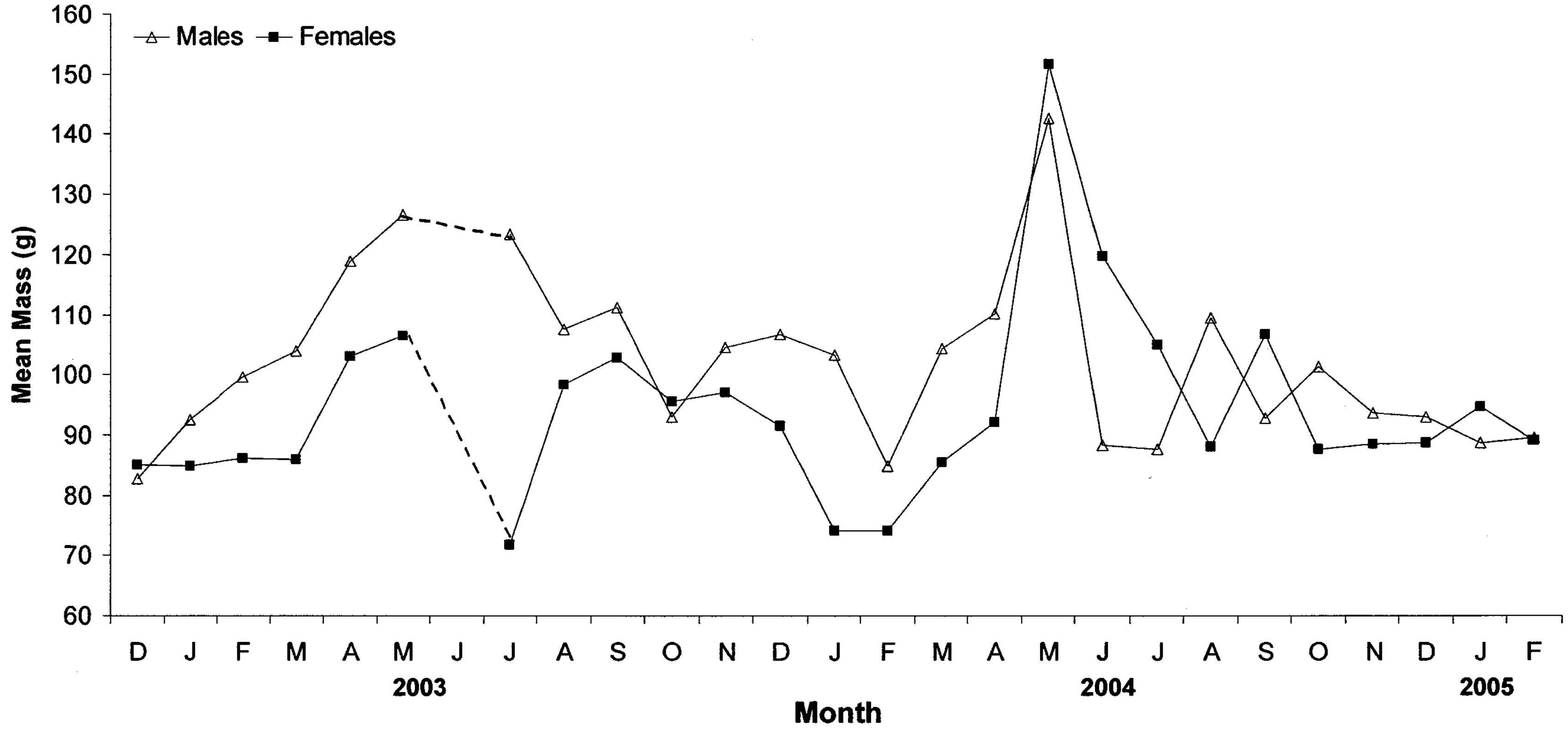

Fig. 18.—Monthly mean masses (g) for males and females over the time period December 2002 to February 2005. Dashed lines indicate no trapping was conducted in June 2003. Increases in mean mass were present in the spring months, while decreases and plateaus in mean mass were present in the winter months. Pregnant females were excluded from all mean mass estimates.

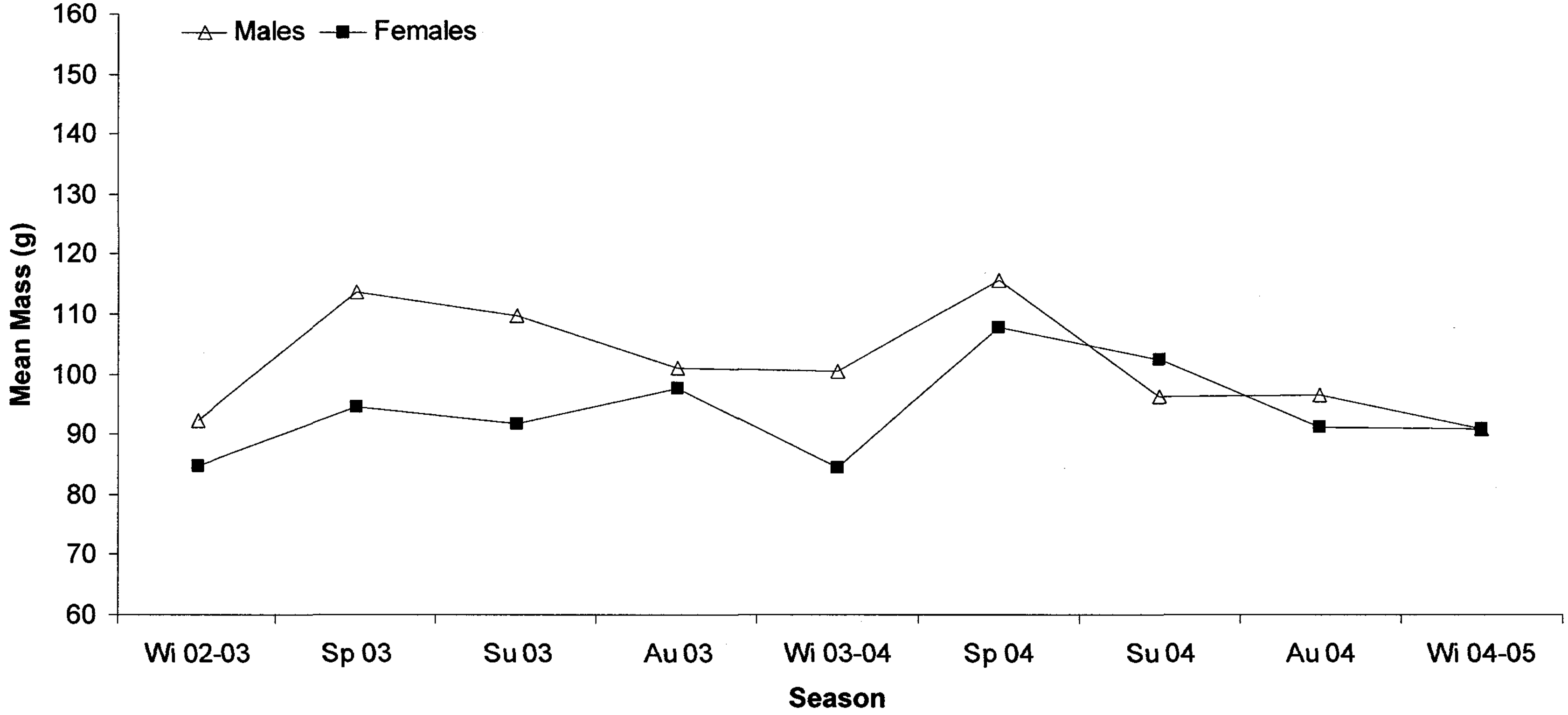

FIG. 19.—Seasonal mean mass (g) for males vs. females from winter 2002-2003 to winter 2004-2005. Increases mean mass for both males and females were observed in both spring followed by slight decline in mean mass into the summer and autumn. A slight decrease in mean mass for males compared to females was present in the winter of 2003-2004.

TABLE 8.—Results for model-I 2-factor ANOVA on mean mass with sex and season as factors for data collected from December 2002 through February 2005.

Source	df	MS	F	P
Sex	1	0.215	15.060	0.000
Season	8	0.087	6.089	0.000
Sex * Season	8	0.028	1.937	0.051
Error	970	0.014		
Total	988			

TABLE 9.—Results for model-I 3-factor ANOVA on mean mass with sex, season and mass class as factors for data collected from December 2002 through February 2005.

Source	df	MS	F	P
Sex	1	1.751	0.037	0.847
Season	3	22.495	0.477	0.699
Mass Class	6	126260.785	2674.729	0.000
Sex * Season * Mass Class	13	91.239	1.933	0.024
Error	928	47.205		
Total	974			

The REGWF test for the sex-season interaction term showed that male mean mass for the spring seasons was significantly higher than male mean mass in the winters of 2002-2003 and 2004-2005 and male mean mass in the autumn of 2004 (Appendix 4). Mean masses for females in the spring of 2003 and 2004 were significantly higher than female mean mass in the winter of 2003-2004. Sex-season interactions that were not different from any other sex-season combinations were females in both springs, males in both summers, males and females in autumn of 2003 and males in the winter of 2003-2004. Male mean mass was not significantly different between summer and autumn seasons, nor was female mean mass significantly different between summer and autumn seasons.

After cotton rats were divided into seven mass classes, mean masses for both sexes were determined at both the monthly and seasonal levels. Since no significant difference was previously established among the same months across the study from the REGWF test results, mean masses were combined for monthly and seasonal comparisons among the mass classes. However, statistical analysis was performed only on the seasonal values due to small sample sizes. A model-I three-factor ANOVA with sex, season and mass class as factors on untransformed data determined that significant differences were present between the mass class factor (F = 2674.729, d.f. = 6,967, p = 0.001) and the interaction factor (F = 1.933, d.f. = 12,971, p = 0.024; Table 9). All other factors tested demonstrated no significant difference. The only significant difference within a sex was female mean mass in mass class 7 from the spring, which was significantly higher than the mean mass from females in the autumn. Otherwise, when all mass classes with small sample sizes were excluded from the statistical analysis, the distribution of mass classes was similar among seasons (Appendix 5).

In the monthly breakdown of mean mass class, cotton rat males in mass class 1 appeared in May and were seen through December (Table 10). Female cotton rats had similar patterns; mass class 1 was not observed until May, with the exception of the month of January (Table 10). Males in mass class 7 were present year-round (except February); however, their numbers were small in comparison to other mass classes. For example, in January, March, April, June and December, only one male was observed in this mass class. The heaviest mass classes for both sexes were most prevalent in May through November. There was a trend for the majority of animals to be found in the intermediate mass classes, especially during the winter months, but more were seen in the smaller mass classes in the late summer and autumn months. Seasonal mass classes for both males and females further demonstrated that lightest and heaviest mass classes were underrepresented during the winter months (Figures 20 and 21; Table 11).

Despite no significant differences in mean mass for winter months, as demonstrated by the REGWF tests from the model-I two-factor ANOVA on the monthly data, slight variations in winter mean mass were observed in all three winters (Figure 18; Appendix 1). Males gained mass in the first winter, but declined in mass over the second winter, and then during the last winter, mass remained relatively unchanged. Females did not increase in mean mass over the winter months, but mass remained stable except in the second winter (2003-2004), when mean mass decreased slightly.

TABLE 10.—Mean mass per mass class per month in mass classes 1-7 during the study period. Mean masses from entire study were condensed into a single set of monthly data after no significant differences across months were found. Numbers in parentheses were individuals captured once per month. Each mass class column holds both male and female values (M = Males, F = Females). Totals were calculated per sex in each mass class per six months. Totals per sex and grand totals of individuals for the entire study found in continuation of table 5. Mass Classes 1 = 0-49g, 2 = 50-69g, 3 = 70-89g, 4 = 90-109g, 5 = 110-129g, 6 = 130-149g, 7 = 150+g, similar to classes as defined by Cameron and Spencer, 1983; Slade et al., 1984; Campbell and Slade, 1993. Pregnant females were excluded from these mean mass calculations.

Month	Mass Class 1		Mass Class 2		Mass Class 3		Mass Class 4		Mass Class 5		Mass Class 6		Mass Class 7	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
January	(0)	43.33 (3)	59.17 (6)	60.67 (15)	80.58 (19)	79.82 (39)	98.44 (9)	97.05 (21)	118.40 (6)	118.00 (6)	134.00 (2)	132.60 (5)	167.00 (1)	158.00 (1)
February	(0)	(0)	64.67 (6)	62.62 (13)	80.38 (24)	79.00 (33)	98.04 (25)	96.59 (17)	117.86 (14)	117.80 (5)	130.00 (1)	138.67 (3)	(0)	(0)
March	(0)	(0)	60.00 (1)	63.83 (6)	81.50 (6)	81.72 (22)	98.62 (21)	98.91 (11)	119.56 (9)	122.00 (2)	133.33 (3)	(0)	170.00 (1)	(0)
April	(0)	(0)	(0)	(0)	(0)	82.00 (5)	102.80 (5)	98.59 (18)	116.80 (10)	117.20 (5)	134.50 (4)	131.00 (2)	150.00 (1)	(0)
May	23.55 (11)	22.00 (1)	(0)	(0)	(0)	(0)	104.00 (1)	106.50 (2)	119.67 (6)	117.00 (2)	138.50 (4)	146.00 (2)	157.80 (5)	167.60 (5)
June	26.20 (5)	39.33 (3)	51.33 (3)	60.00 (2)	(0)	(0)	(0)	(0)	(0)	122.00 (1)	132.00 (1)	141.33 (3)	152.00 (1)	172.00 (1)

TABLE 10.—(Continued).

Month	Mass Class 1		Mass Class 2		Mass Class 3		Mass Class 4		Mass Class 5		Mass Class 6		Mass Class 7	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
July	27.18 (11)	31.75 (8)	60.83 (6)	55.25 (4)	78.00 (1)	76.00 (2)	102.00 (2)	98.00 (4)	(0)	114.00 (2)	(0)	132.00 (2)	164.80 (5)	152.00 (1)
August	30.16 (12)	29.75 (4)	60.75 (4)	61.00 (9)	81.63 (8)	80.50 (4)	102.80 (5)	96.00 (4)	119.40 (5)	119.00 (4)	134.00 (2)	137.33 (3)	174.25 (4)	155.00 (2)
September	34.00 (13)	31.71 (14)	58.57 (7)	59.33 (3)	74.43 (7)	82.20 (5)	100.00 (5)	101.86 (8)	116.25 (4)	119.40 (5)	133.00 (2)	148.00 (1)	164.80 (5)	150.67 (3)
October	28.50 (8)	33.05 (20)	60.30 (10)	58.18 (17)	77.67 (18)	84.17 (6)	96.10 (9)	98.71 (7)	120.64 (11)	118.22 (9)	134.50 (4)	142.43 (7)	162.40 (5)	(0)
November	32.70 (10)	36.67 (24)	56.29 (7)	60.67 (15)	78.36 (14)	79.38 (24)	100.56 (18)	95.14 (7)	118.00 (12)	118.67 (15)	136.57 (7)	134.50 (4)	161.00 (2)	157.50 (4)
December	37.50 (2)	43.43 (9)	59.06 (16)	63.59 (15)	79.50 (24)	78.50 (40)	101.35 (20)	96.96 (24)	118.38 (13)	117.09 (8)	139.50 (8)	136.33 (7)	160.00 (1)	(0)
Total per sex (n)	**72**	**86**	**66**	**99**	**121**	**180**	**120**	**123**	**90**	**64**	**38**	**39**	**31**	**17**
Grand Total (n)	158		165		301		243		154		77		48	

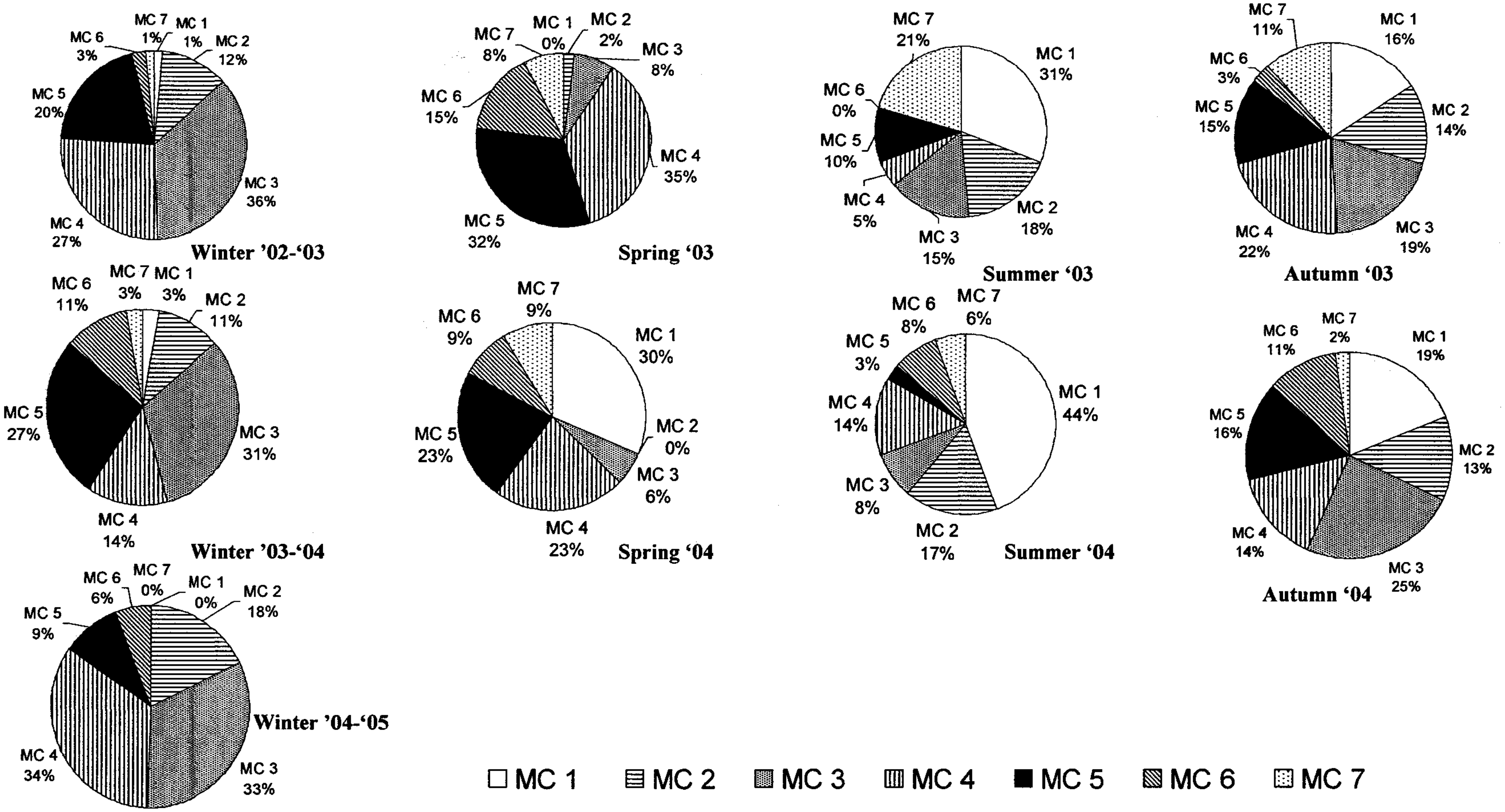

FIG. 20.—Seasonal percentages in the number of individual males per mass class for the study period. Definitions of mass classes can be found in the legend of Table 7. Mass class 1 was most numerous in the spring, summer and autumn, while intermediate mass classes (3 and 4) were most prevalent overall.

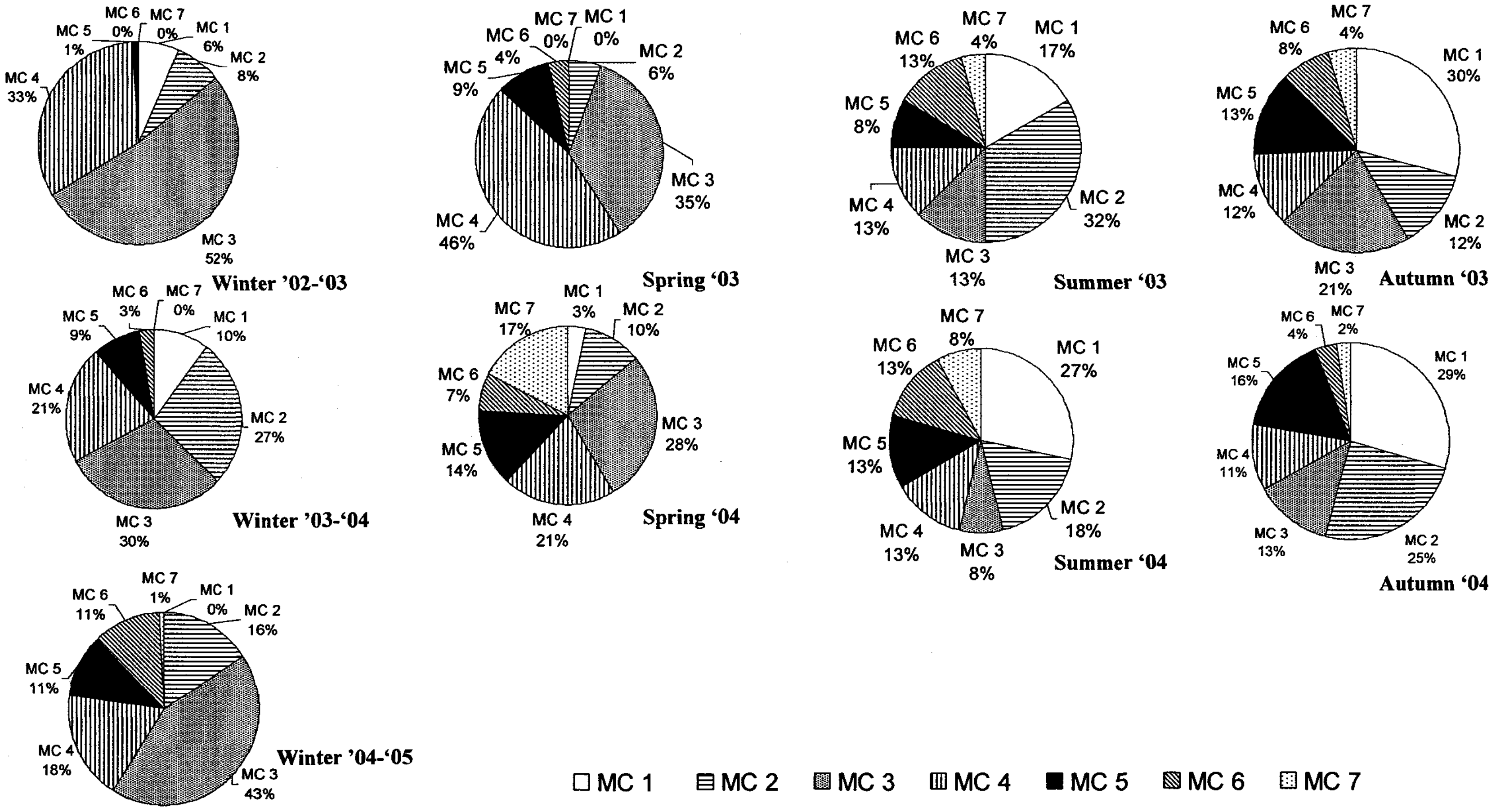

FIG. 21.—Seasonal percentages in the number of individual females per mass class for the study period. Definitions of mass classes can be found in the legend of Table 7. Trends are similar to those seen for males in that mass class 1 was most numerous in the warmer seasons, while intermediate mass classes (3 and 4) were overall the most numerous mass classes.

Table 11.—Mean mass (g) per mass class per season in mass classes 1-7 during the study period. Numbers in parentheses were individuals captured once per month. Each mass class column holds both male and female values (M = Males, F = Females). Mass class criteria are defined in the legend of Table 5.

Season	Mass Class 1		Mass Class 2		Mass Class 3		Mass Class 4		Mass Class 5		Mass Class 6		Mass Class 7	
	M	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
Winter '02-'03	47.00 (1)	44.00 (5)	54.89 (9)	57.67 (6)	80.78 (27)	78.83 (42)	98.05 (20)	99.12 (26)	118.13 (15)	116.00 (1)	132.50 (2)	(0)	167.00 (1)	(0)
Spring '03	(0)	(0)	60.00 (1)	64.00 (3)	82.75 (4)	82.00 (19)	100.26 (19)	100.36 (25)	118.47 (17)	117.20 (5)	135.00 (8)	131.00 (2)	158.25 (4)	(0)
Summer '03	22.67 (12)	29.50 (4)	63.14 (7)	59.63 (8)	79.83 (6)	82.00 (3)	104.00 (2)	98.67 (3)	117.25 (4)	127.00 (2)	(0)	137.33 (3)	170.13 (8)	150.00 (1)
Autumn '03	33.07 (14)	34.24 (33)	58.17 (12)	59.14 (14)	77.24 (17)	80.56 (24)	98.89 (19)	96.62 (13)	119.62 (13)	118.40 (15)	137.00 (3)	140.33 (9)	162.60 (10)	152.80 (5)
Winter '03-'04	28.00 (1)	43.43 (7)	63.75 (4)	63.53 (19)	77.33 (12)	79.38 (21)	103.60 (5)	98.13 (15)	118.60 (10)	113.67 (6)	141.25 (4)	142.00 (2)	160.00 (1)	(0)
Spring '04	23.55 (11)	22.00 (1)	(0)	63.67 (3)	79.00 (2)	81.25 (8)	98.00 (8)	95.33 (6)	118.50 (8)	119.50 (4)	137.33 (3)	146.00 (2)	158.67 (3)	167.60 (5)
Summer '04	32.50 (16)	33.91 (11)	53.33 (6)	59.00 (7)	84.00 (3)	76.00 (3)	102.00 (5)	96.00 (5)	128.00 (1)	114.40 (5)	133.33 (3)	137.60 (5)	156.00 (2)	161.33 (3)
Autumn '04	31.41 (17)	34.20 (25)	59.08 (12)	59.48 (21)	77.41 (22)	81.91 (11)	99.69 (13)	101.78 (9)	118.07 (14)	118.93 (14)	134.90 (10)	140.00 (3)	166.00 (2)	159.00 (2)
Winter '04-'05	(0)	(0)	63.21 (15)	63.33 (18)	80.68 (28)	78.12 (49)	99.25 (29)	94.50 (21)	118.88 (8)	119.67 (12)	136.60 (5)	135.20 (13)	(0)	158.00 (1)
Total	***72***	***86***	***66***	***99***	***121***	***180***	***120***	***123***	***90***	***64***	***38***	***39***	***31***	***17***
Grand Total	158		165		301		243		154		77		48	

Growth Rates

Growth rates were calculated for all adult cotton rats caught two times or more for the entire study (335 males, 396 females; Figure 22). The overall mean growth rate per week for males was 3.22 ± 0.262 g/week and for females, excluding pregnant females, was 2.12 ± 0.207 g/week. These means were significantly different ($t = 3.307$, $p = 0.001$). Mean growth rates for the years 2003 (3.37 ± 0.268 g/week for males, 3.21 ± 0.403 g/week for females) and 2004 (3.17 ± 0.348 g/week for males and 1.72 ± 0.242 g/week for females) showed no significant differences between the sexes for 2003 ($t = 0.232$, $p = 0.747$), but were different for 2004 ($t = 3.425$, $p = 0.001$). No significant differences were detected for males between 2003 and 2004 ($t = 0.457$, $p = 0.648$), but female growth was significantly faster in 2003 than 2004 ($t = 3.179$, $p = 0.002$).

Growth rate varied over the course of the year (Figure 22). Positive growth rates for females, more pronounced than for males, occurred in the early to late spring and again in the late summer to early autumn. Females also exhibited a large peak in growth rate during August in 2003; in contrast, negative growth for females was seen in September 2004. Although males generally had positive growth, negative growth was observed in the second winter (2003-2004) and nil growth in the third winter (2004-2005). For females, near negative or nil growth was observed in the first two winters and negative growth was seen in the last winter (2004-2005).

As a result of small sample size in at least five months of the study, monthly growth rates were combined into seasons for statistical analysis. Seasonal growth curves exhibited trends of positive growth during the spring and autumn seasons and decreases in growth rates before the onset of winter. Overall, males had slightly higher rates of

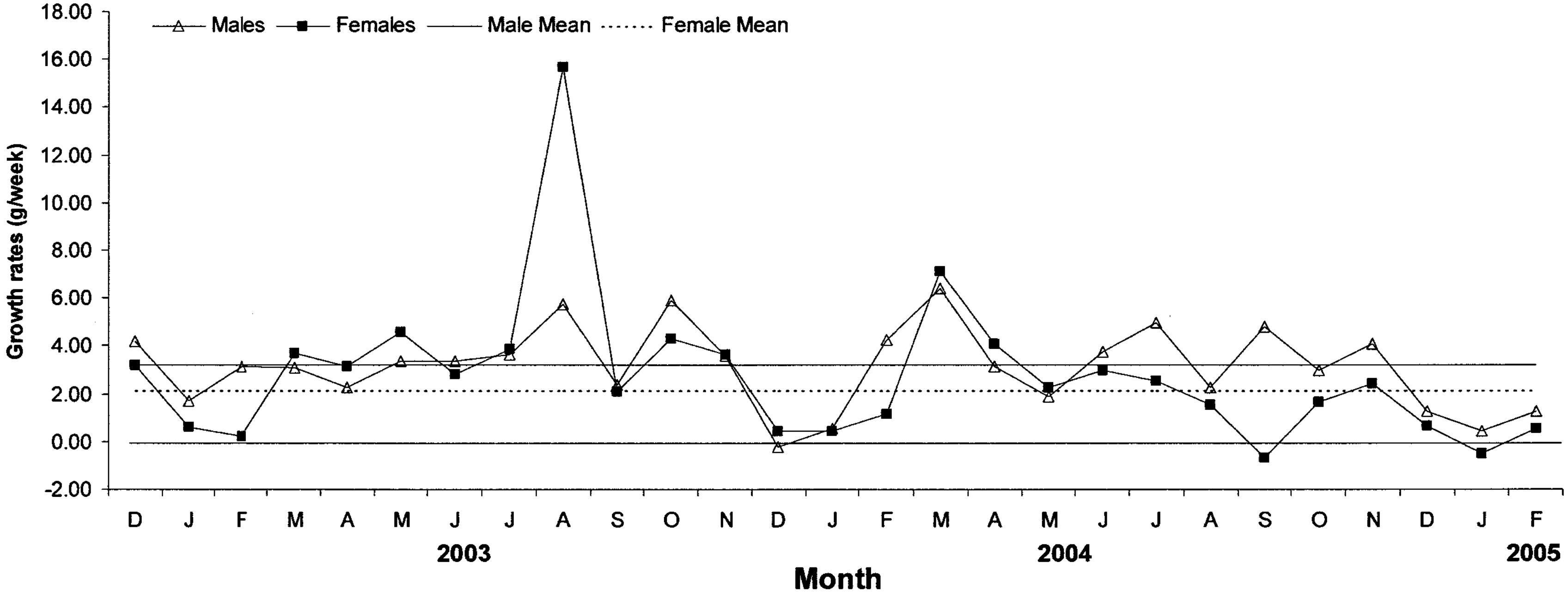

FIG. 22.—Pattern of monthly mean growth rates (g/week) for males and females for the study period. Increases in mean growth rates were observed in early spring, early summer and late autumn months. Decreases in mean growth rates were observed over the early autumn and winter months. A spike in female mean growth rates was observed in August 2003. Juveniles and obviously pregnant females were excluded from the growth rate analysis. Solid line indicates mean growth rate for males and dashed line indicates mean growth rate for females. An additional solid line at 0.00 on the y-axis represents zero growth rate.

seasonal growth (Figure 23), but no significant differences were found between the sexes (F = 0.072, d.f. = 1,729, p = 0.789) using a model-I two-factor ANOVA with sex and season as factors on the untransformed data (Table 12). However, significant differences were observed among seasons (F = 14.315, d.f. = 7,723, p = 0.001) and for the sex-season interaction (F = 5.800, d.f. = 7,723, p = 0.001) because not all growth rates for each sex were significantly different in all seasons.

REWGF tests on the season factor showed generally that cotton rat growth rates in all three winter seasons (2.15 ± 0.328 g/week for winter 2002-2003, 0.98 ± 0.247 g/week for winter 2003-2004, 0.84 ± 0.420 g/week for winter 2004-2005) were not significantly different from each other (Appendix 6). However, growth rates in all three winter seasons were significantly lower than growth rates in the summer of 2003 (6.99 ± 1.186 g/week) and spring of 2004 (4.90 ± 0.636 g/week). In addition, growth rates in winters of 2003-2004 and 2004-2005 were significantly lower than growth rates in spring 2003 (3.31 ± 0.243 g/week) and both autumn seasons (3.77 ± 0.337 g/week for autumn 2003, 2.93 ± 0.377 g/week for autumn 2004). Spring growth rates did not differ, but those of summer 2003 were significant higher than rates in the summer of 2004 (2.50 ± 0.614 g/week). No differences were seen in the two autumns.

REWGF tests performed on the sex-season interaction showed that growth rates of cotton rat males were not significantly different from one another in the three winters (3.17 ± 0.409 g/week for winter 2002-2003, 1.69 ± 0.531 g/week for winter 2003-2004 and 1.77 ±1.026 g/week for winter 2004-2005; Appendix 7). Male growth rates in both autumns (4.07 ± 0.477 g/week and 4.08 ± 0.584 g/week, respectively) were not significantly different, but they were significantly higher than those of both winters 2003-

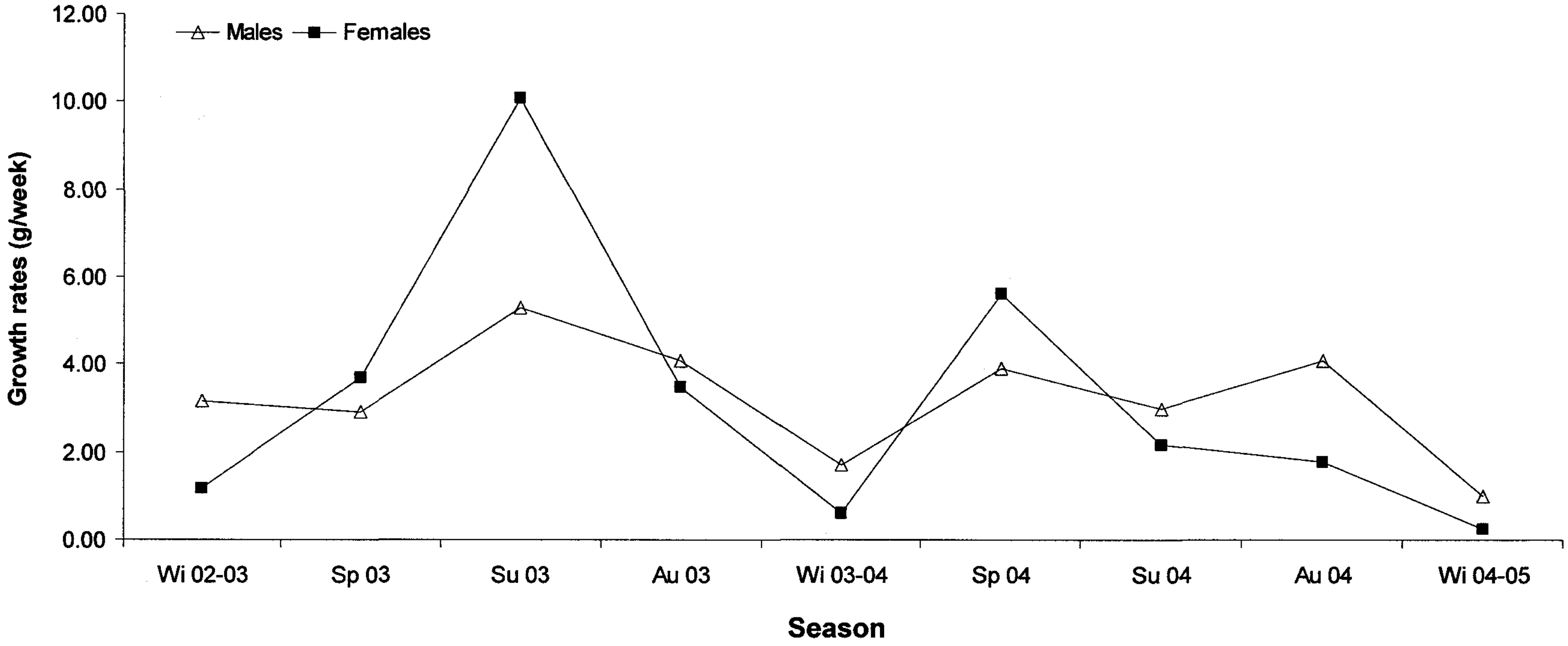

FIG. 23.—Seasonal patterns of mean growth rates (g/week) for males and females for the study period. Steady and increased in mean growth rates were observed in the spring, summer and autumn seasons, accompanied by decreases in mean growth rates in the winter seasons.

Table 12.—Results for model-I 2-factor ANOVA on growth rates with sex and season as factors for data collected from December 2002 through March 2005.

Source	df	MS	F	P
Sex	1	1.193	0.072	0.789
Season	8	238.259	14.315	0.000
Sex * Season	8	96.535	5.800	0.000
Error	713	16.644		
Total	731			

Table 13.—Results for model-I 3-factor ANOVA on growth rates with sex, season and mass class as factors for data collected from December 2002 through March 2005.

Source	df	MS	F	P
Sex	1	49.198	5.046	0.025
Season	3	171.693	17.611	0.000
Mass Class	6	186.447	19.124	0.000
Sex * Season * Mass Class	7	23.697	2.431	0.018
Error	625	9.749		
Total	665			

2004 and 2004-2005. In addition, male growth rates were not significantly different between spring seasons (2.92 ± 0.279 g/week for 2003, 3.89 ± 1.037 g/week for 2004) or between summer seasons (4.44 ± 1.008 g/week for 2003, 3.17 ± 0.719 g/week for 2004).

Growth rates for cotton rat females in all three winters (1.17 ± 0.477 g/week for winter 2002-2003, 0.62 ± 0.246 g/week for winter 2003-2004 and 0.25 ± 0.218 g/week for winter 2004-2005) were not significantly different from each other. Female growth rates in all three winters were also not significantly different from those of summer 2004 (2.15 ± 0.918 g/week) or autumn 2004 (1.79 ± 0.441 g/week). Female growth rates in the spring of 2003 (3.73 ± 0.397 g/week) did not differ from those of spring 2004 (5.62 ± 0.781 g/week). However, female growth rates in the spring 2004 were significantly higher than those of all three winters, as well as for summer 2004 (2.15 ± 0.918 g/week). Female growth rates in the summer of 2003 (11.12 ± 2.346 g/week) were significantly greater from every other growth rate for sex or season. In comparison to growth between spring seasons, autumn growth rates did not significantly differ between 2003 (3.47 ± g/week) and 2004 (1.79 ± 0.441 g/week).

A model-I three-factor ANOVA with sex, season and mass class was also performed on the untransformed growth rate data (Table 13). Due to inadequate sample sizes within certain mass class groups, fewer growth rates were incorporated in this three-factor ANOVA and do not reflect the entire scope of growth rate study (281 for males and 384 for females). The only factors of interest examined in depth were mass class and the sex, season and mass class interaction factor.

Significant differences were observed for both the mass class factor (F = 19.12, d.f. = 6,658, p = 0.001) and the interaction factor between sex, season and mass class factors (F = 2.43, d.f. = 7,657, p = 0.018). When REGWF tests were performed on the mass class factor, mass class 1 (6.14 ± 0.335 g/week) and mass class 2 (4.63 ± 0.449 g/week) had significantly different growth rates from each other and both mass classes had significantly higher growth rates than all other mass classes (3-7; Appendix 8). Growth rates in mass classes 3 (2.34 ± 0.222 g/week), 4 (2.58 ± 0.329) and 5 (1.66 ± 0.327 g/week) were not significantly different from each other, but the growth rates in these mass classes were significantly higher than mass classes 6 (0.04 ± 0.796 g/week) and 7 (-0.41 ± 0689 g/week). In addition, mass classes 6 and 7 were not significantly different from each other.

REGWF tests were also used to examine sex-season-mass class interactions (Table 14; Appendix 9). For male cotton rats, autumn growth rates in mass class 1 (2.36 ± 0.639 g/week) were significantly lower than summer growth rates (8.49 ± 0.662 g/week). Because of small and nil sample sizes no male growth rates in mass class 1 could be calculated for the spring or winter. Male growth rates in autumn for mass class 2 (7.40 ± 0.494 g/week) were significantly higher than for males from mass class 2 in summer (1.95 ± 0.692 g/week) and winter (2.77 ± 0.561 g/week). Male growth rates for mass class 2 were not observed in the spring. Growth rates for mass class 3 were not significantly different among winter (2.17 ± 0.351 g/week), summer (1.43 ± 0.804 g/week) and autumn (4.85 ± 0.686 g/week). Small spring samples prevented male growth rates for mass class 3 to be calculated. For mass class 4, male growth rates in winter (1.95 ± 0.679 g/week) and summer (0.36 ± 0.132 g/week) were significantly lower than spring (3.86 ± 0.570 g/week) and autumn (4.17 ± 0.549 g/week), but no significant differences were detected between winter and summer, and spring and autumn, growth

TABLE 14.—Growth rates (g/week) from results from Model-I 3-Factor ANOVA conducted in SPSS in g/week ± standard error. All growth rate data were lumped into seasons from all years of the analysis Numbers of males and females per season in mass classes 1-7 are in parentheses. Male and female values indicated as M = Males, F = Females. Entries with no growth rates are the result of small sample size and were not calculated. Mass classes defined in the legend to Table 5. Negative growth rates are emphasized in bold type.

	Winter		Spring		Summer		Autumn	
Mass Class	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
1	— (1)	3.30 ± 1.195 (5)	— (0)	— (1)	2.36 ± 0.351 (15)	6.63 ± 1.170 (9)	8.49 ± 0.662 (17)	6.67 ± 0.364 (50)
2	2.77 ± 0.561 (15)	1.16 ± 0.392 (24)	— (0)	— (3)	1.95 ± 0.692 (6)	14.05 ± 0.258 (8)	7.40 ± 0.494 (16)	4.89 ± 0.397 (30)
3	2.17 ± 0.351 (43)	0.95 ± 0.267 (80)	— (2)	4.16 ± 0.583 (17)	1.43 ± 0.804 (4)	— (3)	4.85 ± 0.686 (27)	3.14 ± 0.743 (30)
4	1.95 ± 0.679 (30)	0.70 ± 0.638 (38)	3.86 ± 0.570 (10)	5.82 ± 1.038 (17)	0.36 ± 0.132 (6)	5.07 ± 2.028 (6)	4.17 ± 0.549 (19)	1.96 ± 0.885 (15)
5	1.57 ± 0.763 (15)	**-2.03 ± 2.242** (4)	2.73 ± 0.373 (15)	4.19 ± 0.922 (5)	0.18 ± 0.057 (7)	— (2)	2.33 ± 1.013 (10)	1.23 ± 0.647 (21)
6	— (2)	**-1.02 ± 0.574** (10)	3.39 ± 0.620 (14)	— (1)	0.03 ± 0.020 (4)	3.12 ± 4.005 (7)	**-0.17 ± 1.046** (9)	**-2.77 ± 1.451** (8)
7	— (0)	— (0)	— (1)	— (0)	0.06 ± 0.033 (4)	— (2)	**-0.79 ± 1.276** (5)	— (1)

rates. No significant differences were present among seasonal growth rates for mass class 5; however, higher rates of growth were seen in spring (2.73 ± 0.373 g/week) and autumn (2.33 ± 1.013 g/week) than in other seasons. Despite the fact that males in mass class 6 did not exhibit significant differences in growth rates among seasons, higher rates of growth were present in the spring (3.39 ± 0.620 g/week) and almost zero and negative growth rates were observed in the summer (0.03 ± 0.020 g/week) and autumn (-0.17 ± 1.046 g/week. These trends were similar to those present in mass class 5. Only one male growth rate was recorded in the winter for mass class 6 and was not included in the analysis. For mass class 7, male growth rates of almost zero or negative growth were observed in the summer (0.06 ± 0.033 g/week) and autumn (-0.79 ± 1.276 g/week). Sample sizes for winter and spring for mass class 7 were too small to be included in the ANOVA analysis.

For females (Table 14), REGWF tests showed that winter growth rates in mass class 1 (3.30 ± 1.195 g/week) were significantly lower than growth rates in the summer (6.63 ± 1.170 g/week) and the autumn (6.67 ± 0.364 g/week; Appendix 8). Summer and autumn growth rates for mass class 1 were not significantly different from one another. Only one female growth rate for mass class 1 was observed for the spring and this rate was excluded from the analysis. For mass class 2, female growth rates in summer (14.05 ± 2.580 g/week) were significantly higher than any other mass class growth rate observed for either sex. Winter growth rates in mass class 2 (1.16 ± 0.392 g/week) were significantly lower than autumn growth rates (4.89 ± 0.397 g/week). Not enough female growth rates for the spring season were observed for mass class 2 to include in the analysis. For mass class 3, spring and autumn growth rates were not significantly different from each other (4.16 ± 0.583 g/week for spring, 3.14 ± 0.743 g/week for autumn), but these growth rates were significantly higher than winter growth rates (0.95 ± 0.267 g/week). Not enough females in mass class 3 were observed for summer growth rates to be calculated. Female growth rates for mass class 4 were not significantly different between winter (0.70 ± 0.638 g/week) and autumn (1.96 ± 0.885 g/week), but these seasonal growth rates were significantly lower than spring and summer growth rates (5.82 ± 1.038 for spring and summer, 5.07 ± 2.028 g/week). In addition, spring and summer growth rates for mass class 4 were not significantly different. For mass class 5, growth rates in the autumn (1.23 ± 0.647 g/week) and winter (-2.03 ± 2.242 g/week) were not significantly different from each other, but both were significantly lower than spring growth rates (4.19 ± 0.922 g/week). Too few female growth rates were observed for mass class 5 in summer. Autumn and winter growth rates for mass class 6 were not significantly different from each other (-2.77 ± 1.451 g/week for autumn, -1.02 ± 0.574 g/week for winter), but both were significantly lower than summer growth rates for this mass class (3.12 ± 4.005 g/week). Not enough growth rates for mass class 6 for the spring were recorded to include in the analysis. For mass class 7, no females were observed in mass class 7 for the winter and spring and fewer than three growth rates were recorded for the autumn and summer, too few to use the analysis; therefore, these rates were excluded from the analysis.

Seasonal growth rates for each mass class were plotted using all the available growth rate data for cotton rats; previously excluded data were used here (Figure 24). Among seasons, the highest growth rates for both sexes were observed in summer. During spring, autumn and winter seasons, growth rates did not go above 10 g/week and

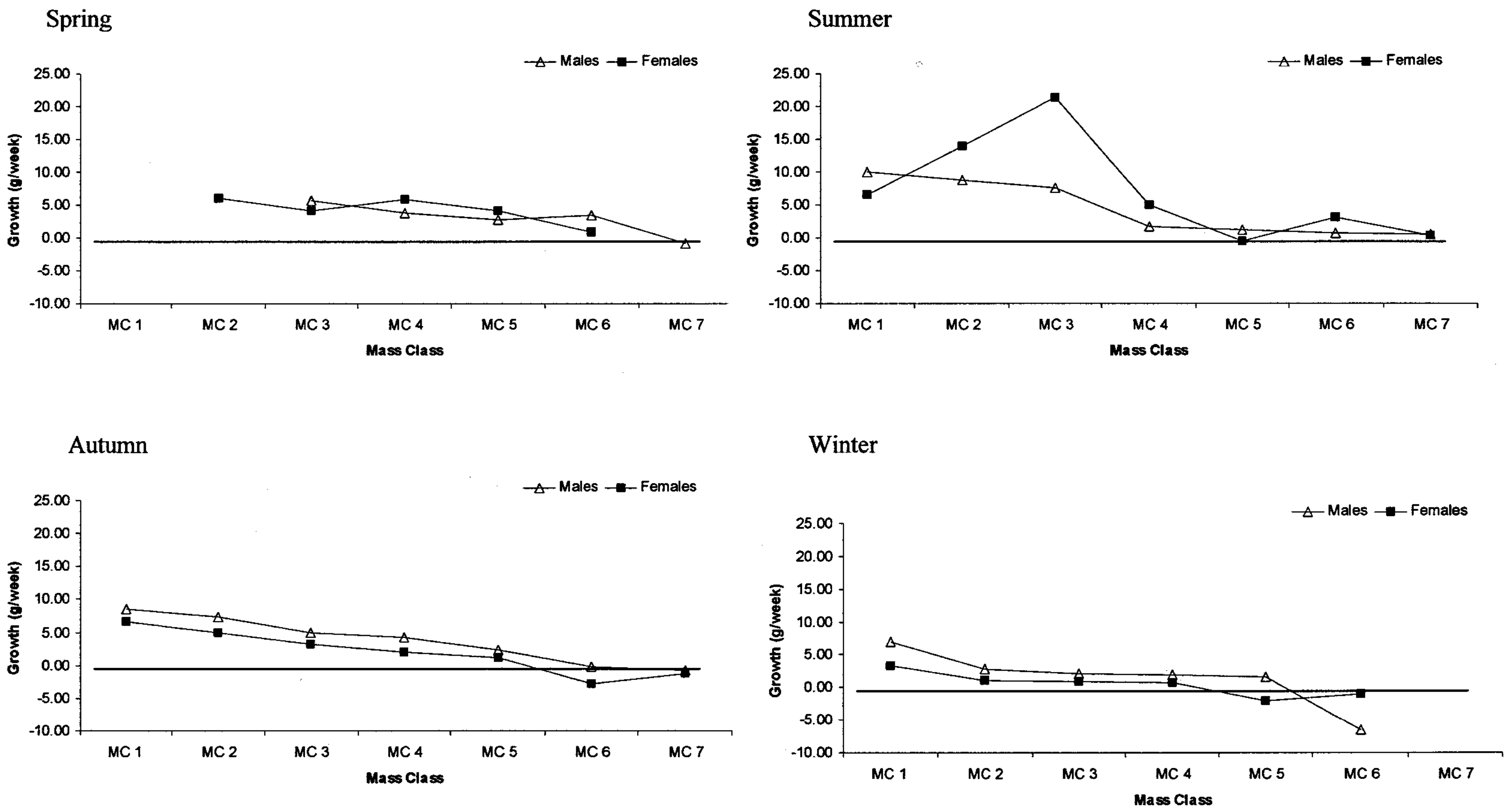

FIG. 24.—Overall mean growth rates (g/week) for all seasons observed for males and females per mass class (MC). Except for summer, mean growth rates per mass class were similar for both sexes in each season. An increase in summer mean growth rates with females for mass class 3 was clearly present.

negative growth was observed during these seasons in the heaviest mass classes. Males demonstrated higher rates of growth than females in the autumn and winter among most mass classes, but females more often than not had higher growth rates than males in the spring and summer.

In spring, male growth rates remained stable for intermediate mass classes (mass classes 3 and 4) and for mass classes 5 and 6. Females also demonstrated stability in growth rate for the intermediate mass classes, but growth rates decreased in mass classes 5 and 6, a pattern also seen in males (Figure 24). No males or females were observed in mass class 1 in the spring.

Positive growth for all mass classes was seen in the summer season (Figure 24). Males and females of mass classes 1 and 2 showed higher rates of growth than the other mass classes, while slightly lower rates of growth were seen in the intermediate mass classes (3 and 4). Near nil growth was observed in the heaviest three mass classes for both sexes. In summer, females of the lightest four mass classes had extreme positive growth trends.

As in the summer season, almost all masses classes in autumn had positive growth rates (Figure 24). However, only one autumn growth rate was calculated for females in mass class 7. Males and females exhibited a slight decrease in growth rate across the mass classes throughout this season, the lightest mass classes had the highest growth rates and the heaviest mass classes had lower rates of growth. Negative growth was observed for both sexes in mass classes 6 and 7.

Winter growth rates had a more stable pattern of growth (Figure 24). For both sexes, mass class 1 demonstrated the highest growth rates and the heavy mass classes (5 and 6) exhibited negative growth. Growth rates for the intermediate mass classes (3 and 4) remained stable throughout the winter. No growth rates were observed in mass class 7.

Growth rates were also determined for individual cotton rats with long capture histories. Growth trajectories were based on changes mass from successive months of capture. For months with gaps in the trapping record, mean mass was determined by interpolation. Male growth trajectories confirmed winter growth rate trends in that males showed positive growth during the winters of 2002-2003 and 2004-2005, while nil and negative growth was seen in the winter of 2003-2004 (Figure 25). For females, growth trajectories were consistent with the trend that no growth and negative growth was observed during the winter months (Figure 26). Young born in the summer months had lower positive growth than autumn-born individuals (Figure 27). Autumn-born young had better over-winter growth compared to summer-born animals.

Survival

Monthly survival rates of cotton rats were calculated for the total population and then separately for males and females. Goodness-of-fit tests demonstrated that JOLLY results was a good model for males (X^2 = 24.10, d.f. = 14, p = 0.055) and females (X^2 = 19.61, d.f. = 16, p = 0.238). Survival rates were calculated with and without juveniles, but two-sample t-tests revealed no significant differences among these mean monthly survival rates for males (0.624 ± 0.054 for males with juveniles, 0.508 ± 0.064 for males without juveniles) or females (0.693 ± 0.044 for females with juveniles, 0.673 ± 0.040 for females without juveniles; t = -0.323, p = 0.749 for males, t = 0.310, p = 0.758 for females; Figure 28). Therefore, survival rates with juveniles were used in my study. In

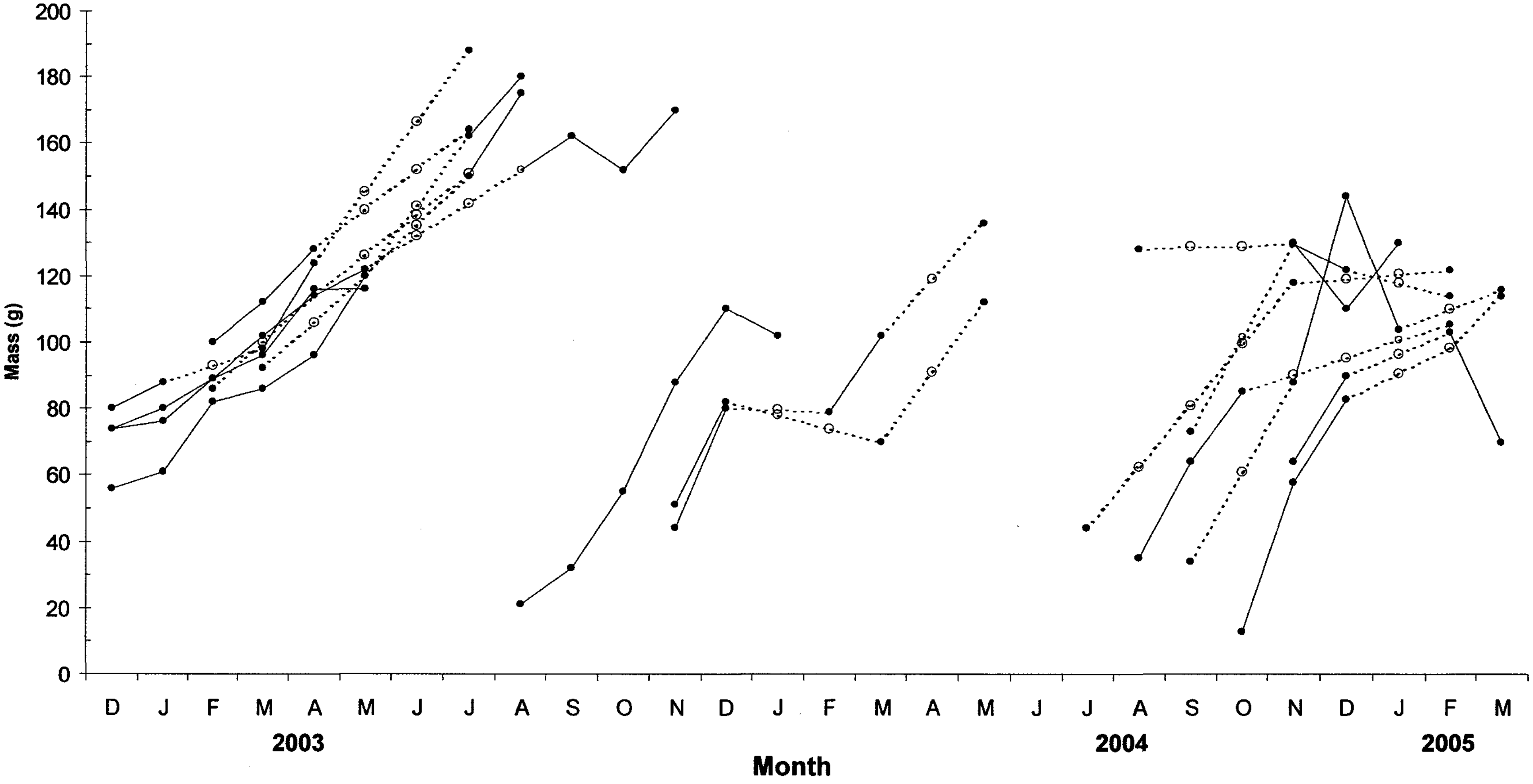

FIG. 25.—Growth trajectories based on change in mass (g) per month for males with long capture histories. Closed circles represent actual mass values and open circles and dashed lines represent interpolated mass values. Males showed positive growth over the winter of 2002-2003 and 2004-2005, but nil and negative growth in the winter of 2003-2004.

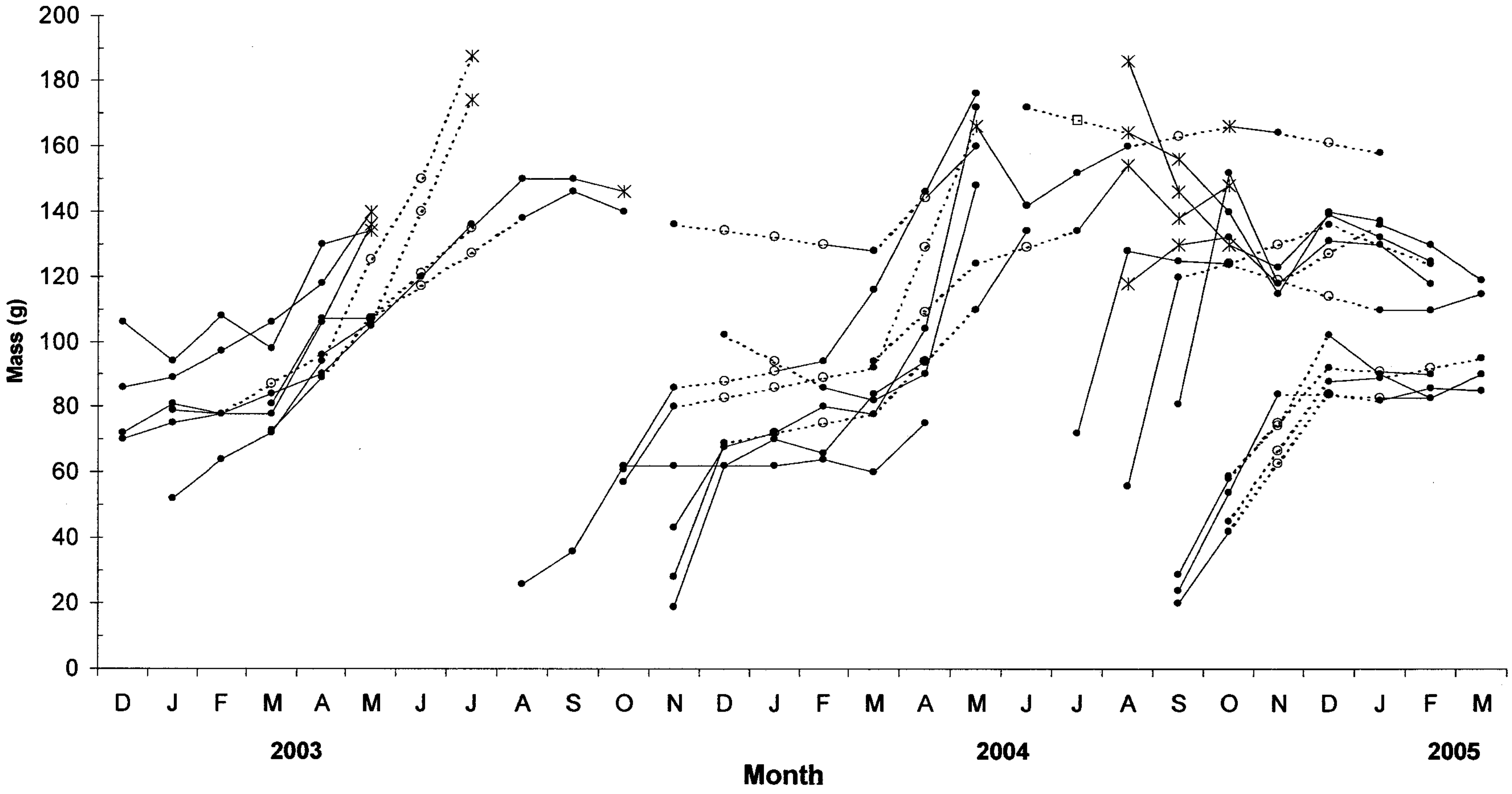

Fig. 26.—Growth trajectories based on change in mass (g) per month for females with long capture histories. Closed circles represent actual mass values and open circles and dashed lines represent interpolated mass values. Xs represent months when females were considered pregnant. Females demonstrated nil and negative growth throughout the winter months.

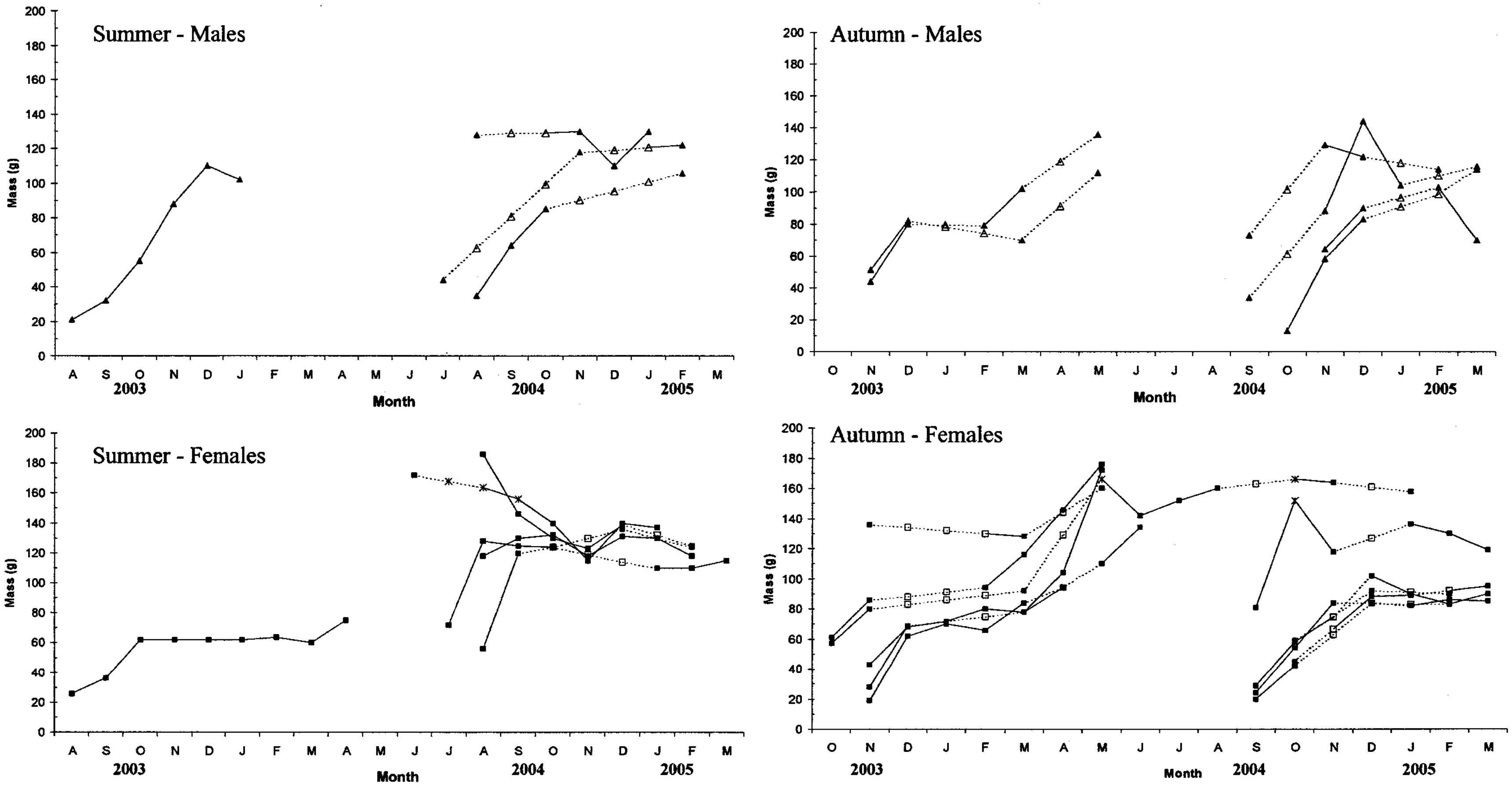

FIG. 27.—Growth trajectories of males (top) and females (bottom) using mass (g) per month of animals born or first tagged in summer and autumn. Closed shapes represent points of actual mass values and open shapes and dashed lines represent interpolated values. Xs represent pregnant females. Autumn-born animals showed more positive winter growth than summer-born animals.

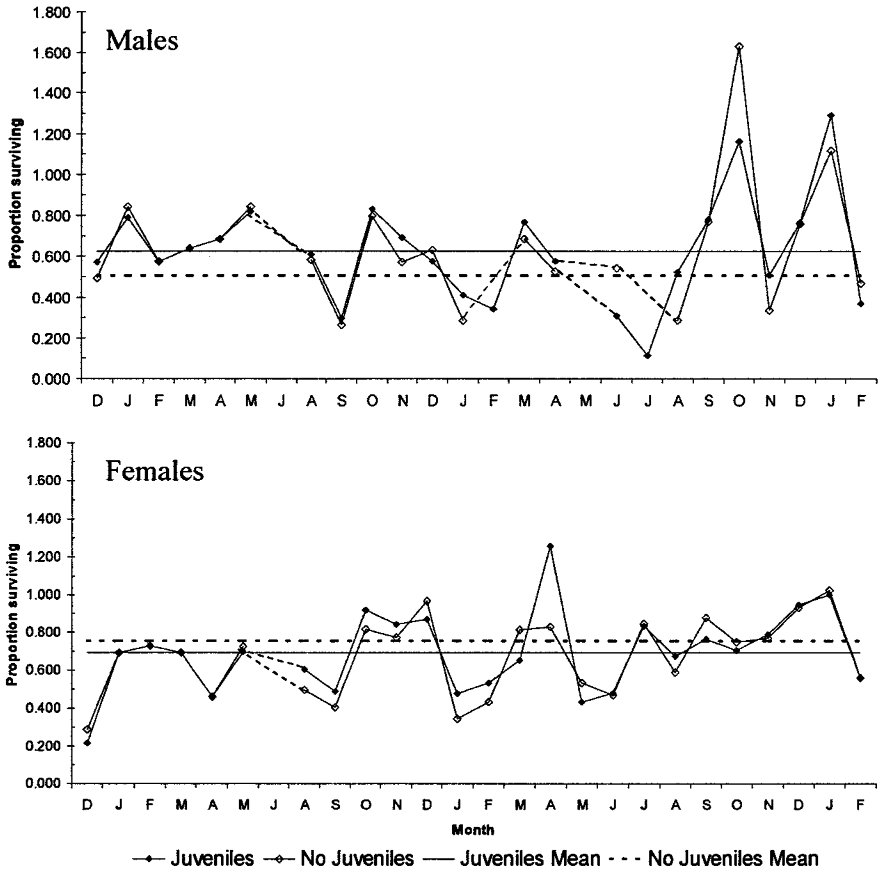

FIG. 28.—Comparison of monthly survival rates with and without juveniles for males (top) and females (bottom). Dashed lines represent breaks in the survival data for both sexes in June 2003, when no data were collected, and for males in April of 2004. Similar patterns of monthly survival were observed with both the presence and absence of juveniles. Solid line indicates mean survival rates for juveniles and dashed line indicates mean survival rate without juveniles.

addition, because JOLLY the estimates probabilities for both death or disappearance and persistence on the grid but does not evaluate failure to capture animals, transients were also incorporated into these survival analyses. The exclusion of transients from JOLLY analysis did not produce any meaningful results.

Overall, cotton rat females had slightly higher mean rates of survival per month than males, 0.693 ± 0.044 and 0.624 ± 0.054, respectively. Two-sample t-tests on these survival rates revealed no significant differences between these mean survival rates ($t = -1.133$, $p = 0.263$). Mean survival rates for 2003 (0.655 ± 0.045 for males, 0.678 ± 0.053 for females) and 2004 (0.638 ± 0.098 for males, 0.777 ± 0.070 for females) did not differ significantly between the sexes for 2003 ($t = -0.321$, $p = 0.752$) or 2004 ($t = -1.323$, $p = 0.200$). In addition, no significant differences were detected between males in 2003 and 2004 ($t = 0.469$, $p = 0.644$) or females in 2003 and 2004 ($t = -0.769$, $p = 0.450$).

Monthly survival rates fluctuated during the year, but males and females displayed similar patterns (Figure 29). Decreases in survival rates were observed for both sexes towards the end of all three winters, and decreased survival was also seen in the late summer of 2003. Unlike females, males in July 2004 experienced a sharp drop in survival, followed by a steady increase in survival through October 2004. Increases in survival rates for both sexes occurred in the spring months and again in autumn months for both years. These increases in survival rates were generally followed by decreased survival rates that continued into the winter months. Females in March 2004 showed one of the largest increases in survival rates across the entire study.

Patterns of seasonal survival rate for both sexes confirmed the trends seen in the monthly patterns of survival (Figure 30). Seasonal survival rates for females

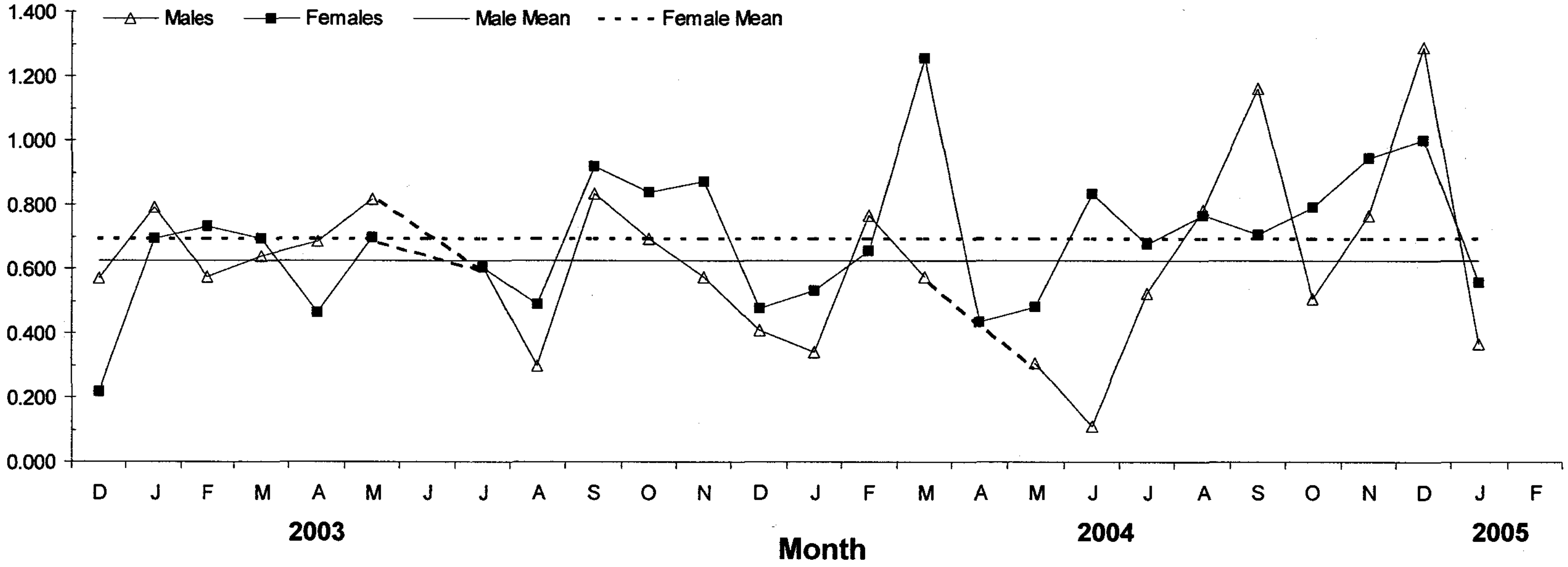

FIG. 29.—Comparison of monthly survival rates for males and females for the study period. Dashed lines represent breaks in the survival data for both sexes in June 2003, when no data were collected, and for males in April of 2004. Increases in survival were seen in the spring and autumn months, while decreases in survival were observed in the late summer and winter months. Rates of survival greater than 1 are not an accurate representation of survival for either sex, representing smaller sample sizes of females in March 2004. While survival estimates will tend to be less accurate toward the end of the study because future capture histories and potential survival of these animals are not known, as seen for males in September 2004 and December 2004. Solid line indicates mean survival rates for males and dashed line indicates mean survival rate for females.

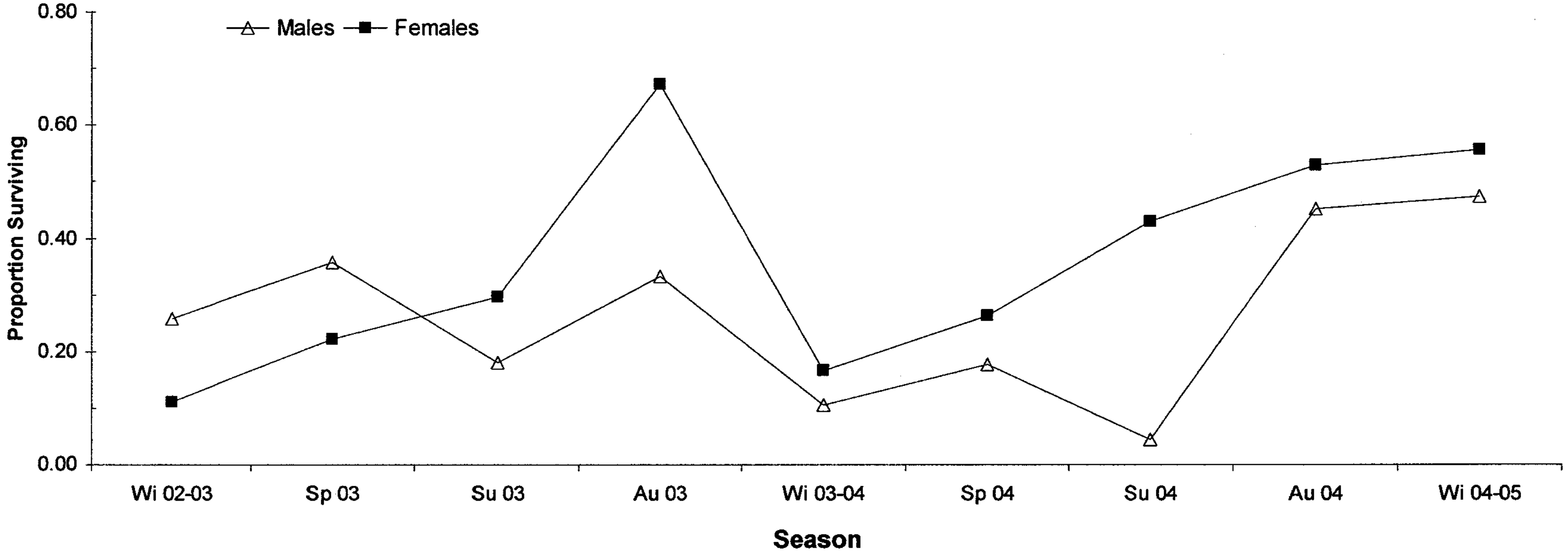

Fig. 30.—Comparisons of seasonal survival rates for males and females during the study period. Increases in survival were observed in the autumn, while decreases were seen over the winter '03-'04 and summer '04 for males.

were relatively stable with occasional increases in survival throughout the study, except for a decrease in survival in winter 2003-2004. Increases in survival rates were observed in both autumns for both sexes. Males demonstrated lower rates of survival than females in both summers and, unlike females, decreased survival was observed.

Since previous cotton rat studies had suggested that effects of weather and mean mass adversely affect survival rates (Sauer 1985; Campbell and Slade 1993; Eifler and Slade 1998), other factors, such as growth rate and proportions of transients in the population, were tested against survival rates in this study. Correlation analysis was conducted to determine if significant relationships were present between rates of survival and mean growth per month. Previously calculated growth rates per day were converted into monthly values. This analysis was performed for both sexes, using both monthly and seasonal growth and survival rates, as well as monthly and seasonal growth and subsequent survival, e.g., survival in March compared to February growth. There was no significant relationship between mean monthly growth rates and survival rates for males ($r = -0.080$, $n = 47$, $p > 0.05$) or for females ($r = 0.072$, $n = 47$, $p > 0.05$). Nor were significant relationships seen for seasonal growth and survival rates for either males ($r = -0.244$, $n = 7$, $p > 0.05$) or females ($r = 0.025$, $n = 7$, $p > 0.05$). No significant relationship was observed between monthly growth and subsequent monthly survival for either males ($r = 0.295$, $n = 45$, $p > 0.05$) or females ($r = -0.019$, $n = 46$, $p > 0.05$), nor were there significant relationships for seasonal growth and subsequent seasonal survival for males ($r = 0.222$, $n = 6$, $p > 0.05$) or females ($r = 0.494$, $n = 6$, $p > 0.05$).

Despite the fact that significant relationships were not demonstrated using correlation analysis, at certain points in the study growth might have influenced survival.

For cotton rat males, decreases in mean growth rates in January 2003 were associated with an increase in survival rate for January 2003 (Figure 31). Similar trends were also observed in September 2003. During periods of stable growth, survival rates either were stable or increased, as seen in mid-spring through early-summer of 2003 and in mid-summer to late-autumn of 2004. In some instances, the opposite trend was observed, such as in both August 2003 and June 2004 when increases in mean growth rates were associated with sharp decreases in survival. In the late autumn of 2003 through mid-spring of 2004, patterns of growth and survival appeared to closely follow each other, which suggests that something other than growth influenced survival during this period.

Similar patterns of mean growth rates and survival were observed for female cotton rats (Figure 32). Overall, periods of stable or decreased growth were associated with stable and increased survival rates. Stable periods of growth and survival rates were observed in mid-spring through mid-summer of 2003, autumn of 2003 and mid-summer through mid-autumn of 2004. In the winter months of 2002-2003, decreased growth coincided with an increase in winter survival. The opposite trend was observed in August 2003, when a sharp increase in mean growth rate was associated with a slight decrease in survival. As seen with males, patterns of growth and survival appeared to closely follow one another during the winter months of 2003-2004 through the mid-summer 2004, being slightly greater in females than males.

Seasonal patterns of rates of growth and survival for cotton rats confirmed those seen in monthly comparisons. For males, decreases in rates of growth were associated with increases in survival, observed in the spring of 2003 (Figure 33). Increases in growth rates were associated with decreased survival rates, seen in both summers.

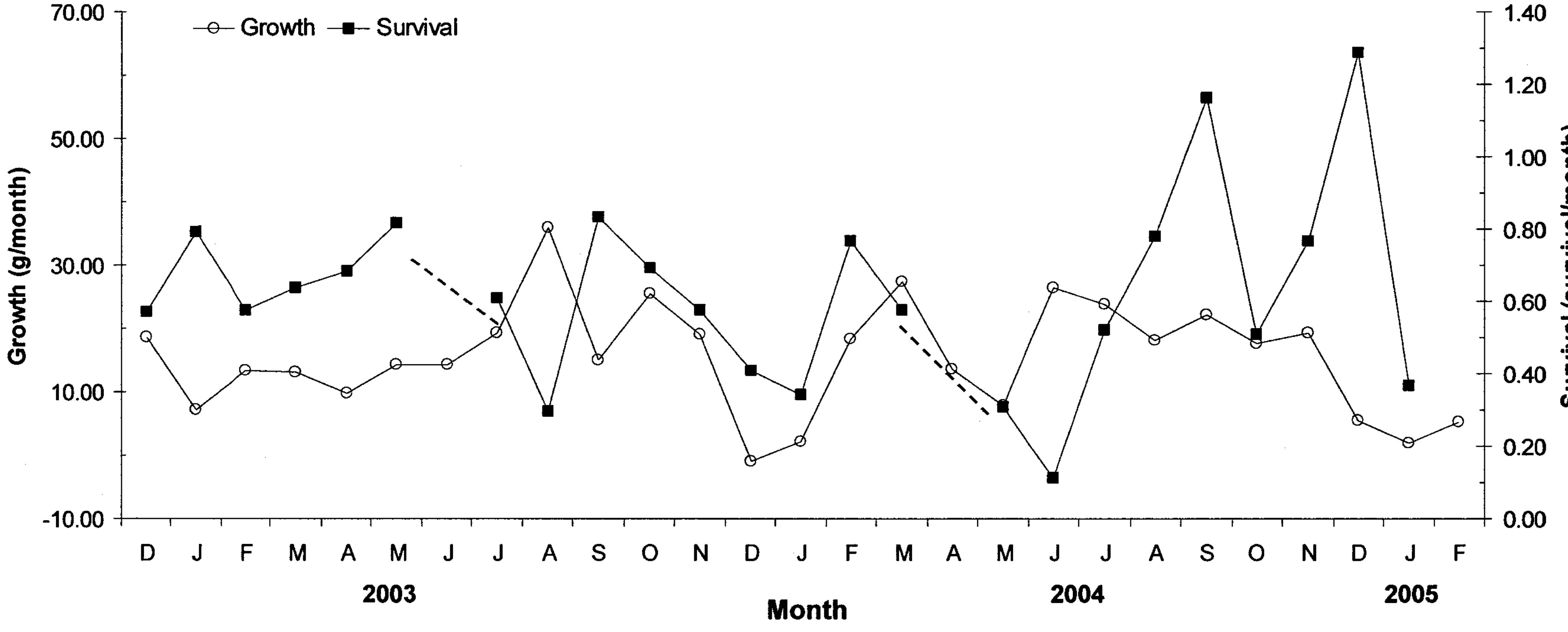

Fig. 31.—Male growth per month (g/month) versus male survival per month during the study period. Dashed lines represent breaks in the survival data for June 2003 and April 2004. First survival data point is for December 2002. Periods of stable growth were associated with increases in the rates of survival, while increases in mean growth rates were associated with decreases in survival. Decreases in mean growth rates, particularly over the winter months, were associated with decreases in survival rates, seen especially in the winter of 2003-2004. Explanations of rates of survival greater than 1 can be found in the legend of Figure 28.

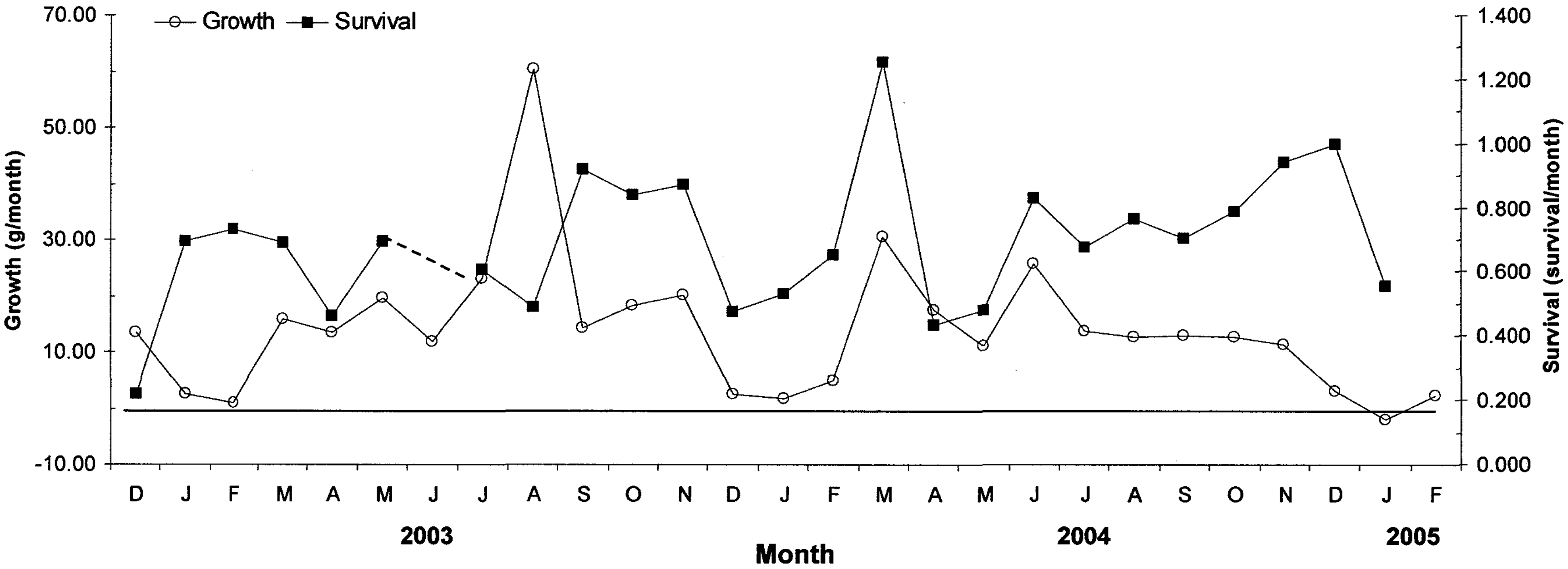

FIG. 32.—Female growth per month (g/month) versus female survival per month for the study period. First survival data point is for December 2002. Overall, periods of stable mean growth rates coincided with increased survival, while increases in mean growth rates were associated with decreased survival. Decreases in mean growth rates over the winter months were associated with lower rates of survival, but only slightly lower than average female survival. Explanations of rates of survival greater than 1 can be found in the legend of Figure 28.

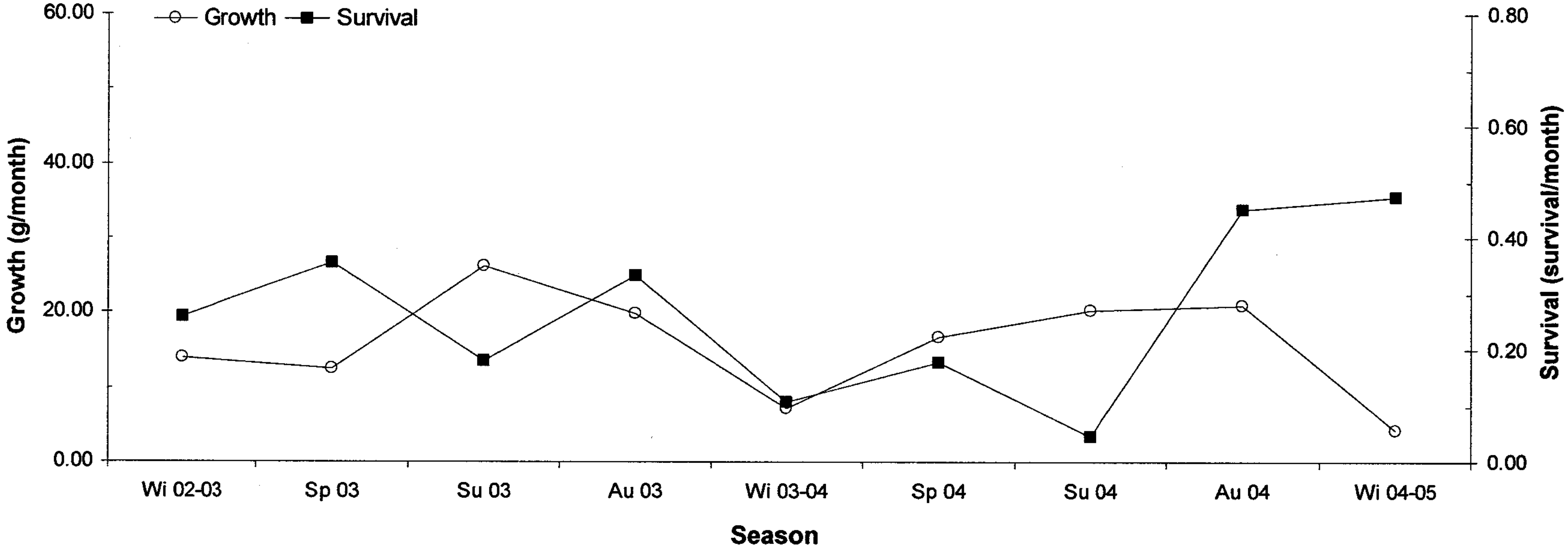

FIG. 33.—Male seasonal growth (g/month) versus male seasonal survival during the study period. Overall, decreases in seasonal growth were associated with increased survival, as observed in the spring of 2003. Increased growth associated with decreases survival was seen from spring to summer of both years.

Patterns of growth and survival rates during the winter of 2003-2004 and spring of 2004 closely followed one another. For females, stable rates of both growth and survival were observed during the winter of 2002-2003 and spring 2003 (Figure 34). Despite the large increase in growth in summer of 2003, survival in that summer remained relatively stable then. Decreases in growth rates had positive effects on survival, seen in the autumn of 2003 and all the seasons from summer 2004 through the end of the study. As with males, female seasonal growth and survival rates for the winter of 2003-2004 and spring of 2004 followed the same patterns.

For mean monthly growth rates and subsequent survival, males exhibited positive subsequent survival at times of stable and decreased growth, as seen in February through May of 2003 and August through December of 2004 (Figure 35). Slight increases in growth rates in June and July of 2003 seemed to have a negative effect on survival in both July and August 2003. Patterns of monthly growth and subsequent survival followed one another from September 2003 to July 2004. However, decreased growth in December 2003 and January 2004 coincided with positive survival in January and February 2004.

Concordant patterns of monthly growth and subsequent survival in cotton rats were more pronounced in females than in males (Figure 36). The stable and decreased growth rates observed in winter months of 2002-2003, mid-spring of 2003 and mid-summer of 2004 were associated with stable and increased subsequent survival. Increases in growth for March 2003, March 2004 and June 2004 were associated with negative survival the following months. Increased subsequent survival in mid-autumn of 2003 through the spring of 2004 was related to decreased growth rates in these seasons.

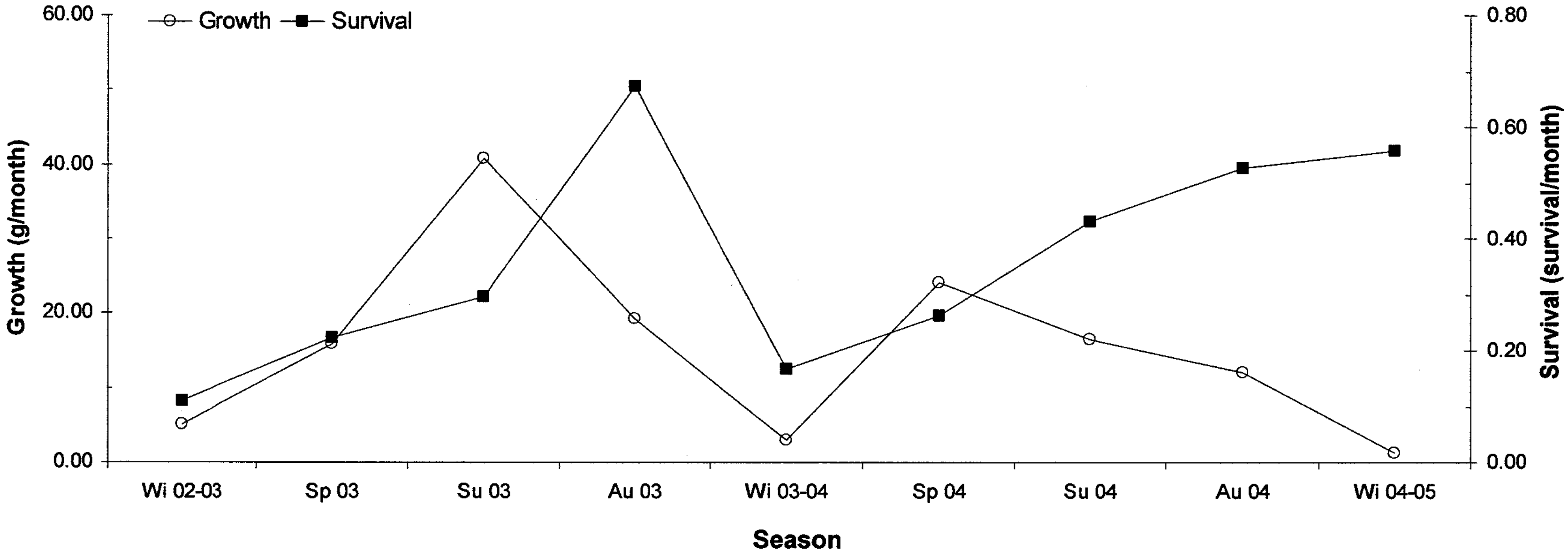

FIG. 34.—Female seasonal growth (g/month) versus female seasonal survival per month for the study period. Overall, periods of increased seasonal growth were associated with lower rates of survival (summer 2003 and spring 2004), while decreases in seasonal growth were associated with increased and higher survival (autumn 2003 and 2004, and summer 2004).

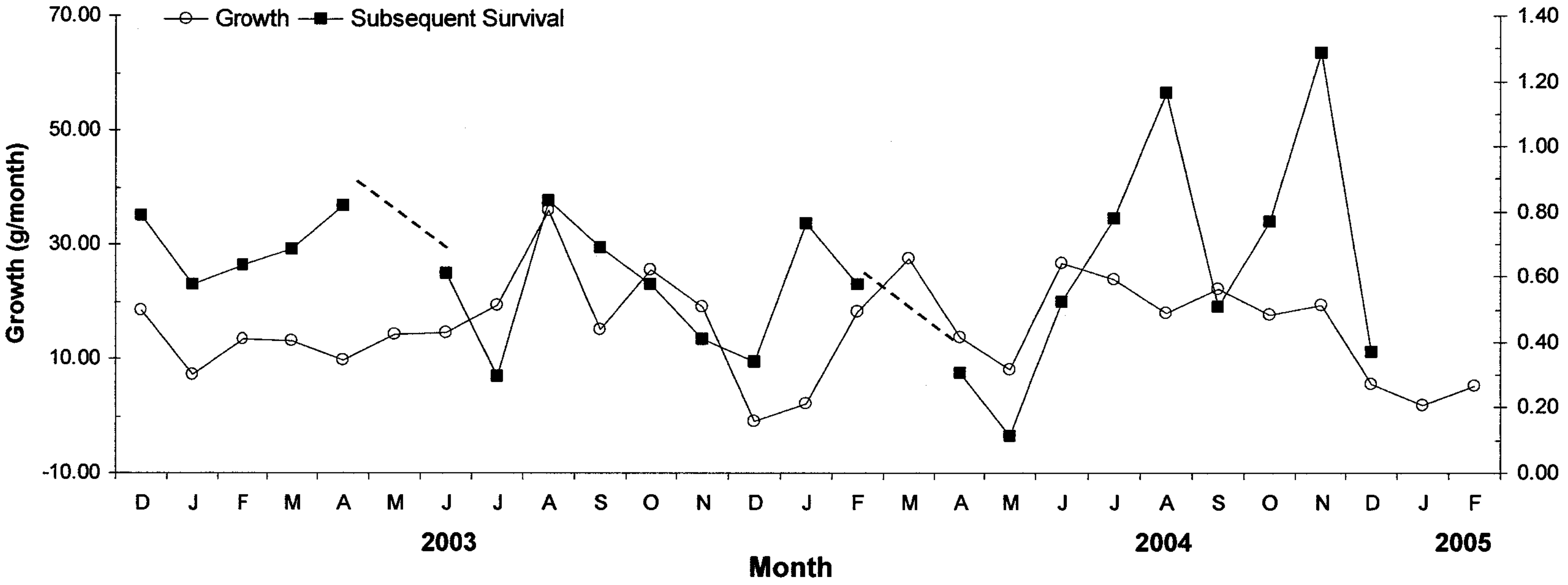

FIG. 35.—Mean male growth rates (g/month) versus subsequent survival per month during the study period, e.g., effect of December growth on January survival. The first survival data point is for January survival and the trend line is shifted to the left to better illustrate the effect of growth on subsequent survival. Periods of stable growth were associated with stable and increased rates of subsequent survival. Increases in growth negative effects on subsequent survival. Decreases in growth rate in the winter months appeared to have positive effects on subsequent survival. Explanations of rates of survival greater than 1 can be found in the legend of Figure 28.

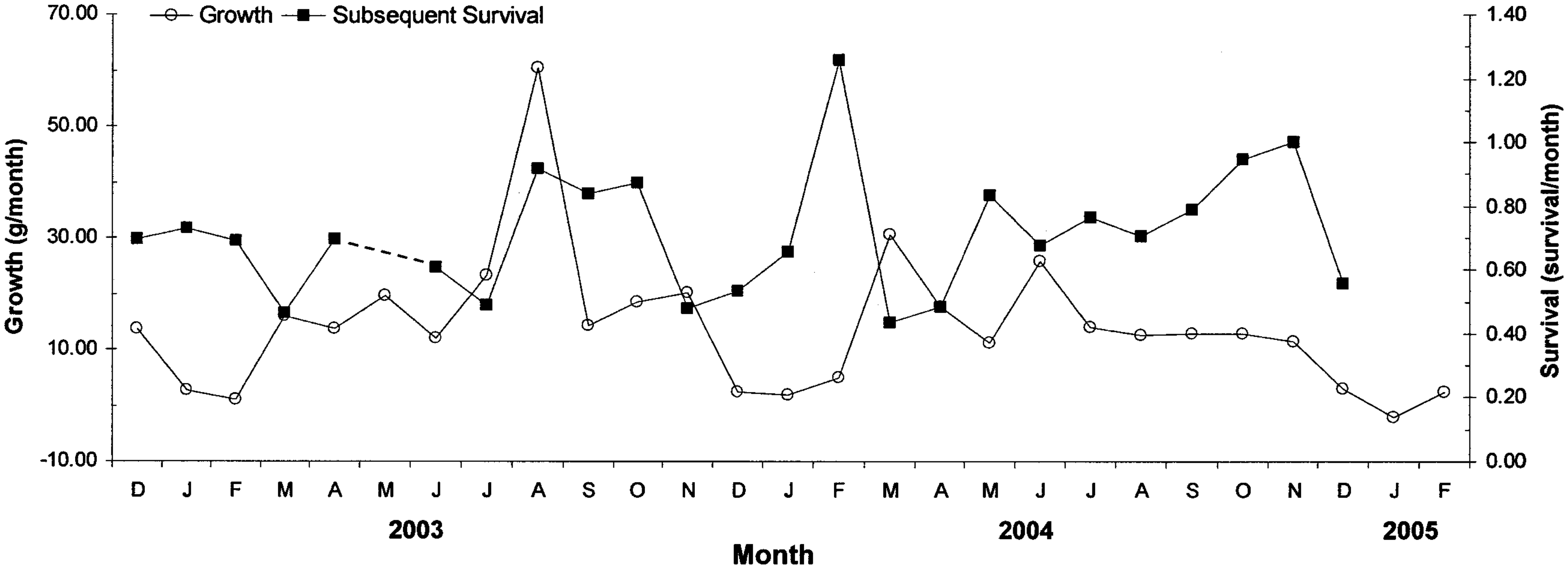

FIG. 36.—Mean female growth rates (g/month) versus subsequent survival per month for the study period. The first survival data point is for January survival and the trend line is shifted to the left to better illustrate the effect of growth on subsequent survival. Periods of stable or decreased mean growth were associated with periods of stable and increased monthly subsequent survival. Increases in mean growth were associated with decreased subsequent survival. Explanations of rates of survival greater than 1 can be found in the legend of Figure 28.

In particular, decreases in growth from November 2003 to February 2004 reflected stable and increased subsequent survival in winter of 2003-2004.

Patterns of seasonal growth and subsequent seasonal survival supported those patterns previously demonstrated for monthly growth and subsequent survival. These seasonal patterns better illustrated the potential for longer lasting effects of growth on survival. For males, with one exception, subsequent survival patterns closely followed patterns of growth (Figure 37). The exception was in spring 2004, when an increase in growth rate was negatively associated with summer 2004 survival and was followed by an increase in survival, similar to the summer and autumn 2004 pattern. For females, seasonal growth for the first half of the study mimicked subsequent survival patterns. Despite fluctuations in seasonal growth rates for the latter half of the study, subsequent survival rates continued to increase (Figure 38).

Proportions of transient cotton rats were also compared against both seasonal survival and growth rates within the population. Correlation analysis was conducted between seasonal survival rates and seasonal proportions of transients for sexes. There proved to be significant negative correlations for males ($r = -0.768$, $p < 0.05$) and females ($r = -0.715$, $p < 0.05$) using log-transformed seasonal growth, survival and proportion of transient data. For males, increased proportions of transients were associated with a decrease in seasonal survival (Figure 39). The highest percentages of transients were seen in spring and summer of 2004, which corresponded with the lowest seasonal survival rates. Stable and lower proportions of female transients were associated with stable and increased seasonal survival rates (Figure 39). Consistent increases in seasonal

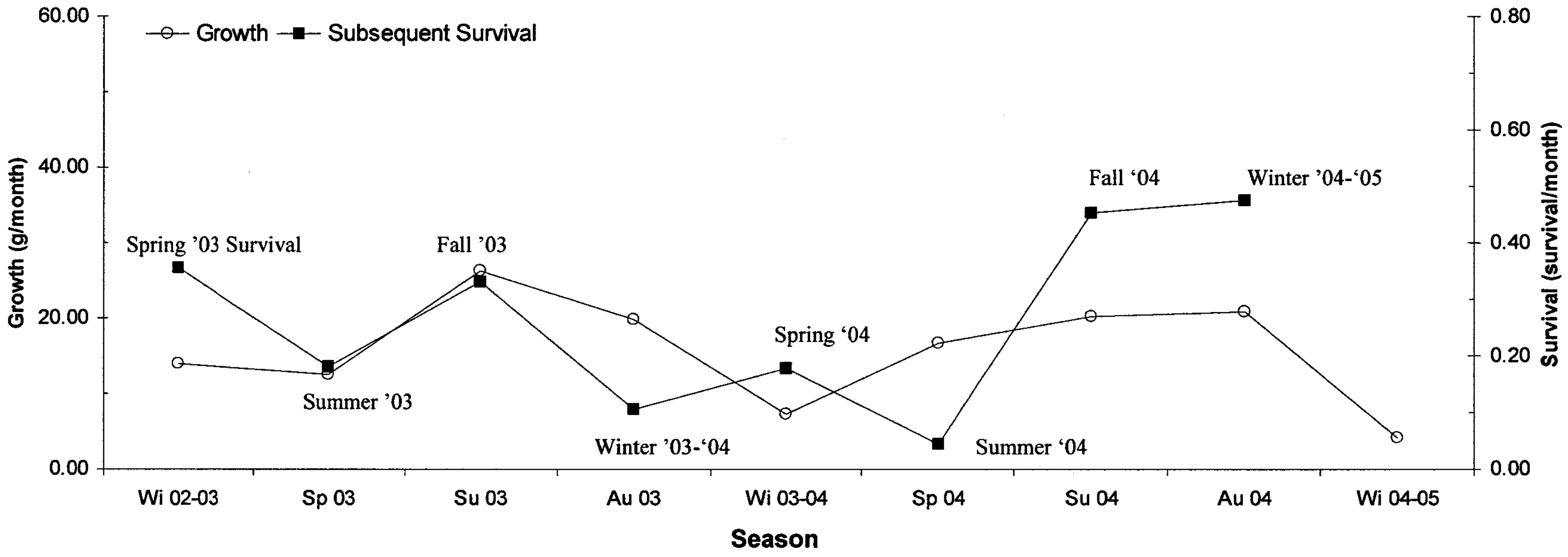

FIG. 37.—Male seasonal growth (g/month) versus subsequent survival during the study period. The first survival data point is for spring 2003 survival. Patterns of seasonal growth and subsequent seasonal survival closely mimicked one another. Increased growth in spring 2004 was associated with decreased subsequent survival in summer 2004. Periods of stable and decreased seasonal growth in summer and fall of 2004 were associated with increased and stable subsequent survival in the spring of 2004, autumn of 2004 and winter 2004-2005.

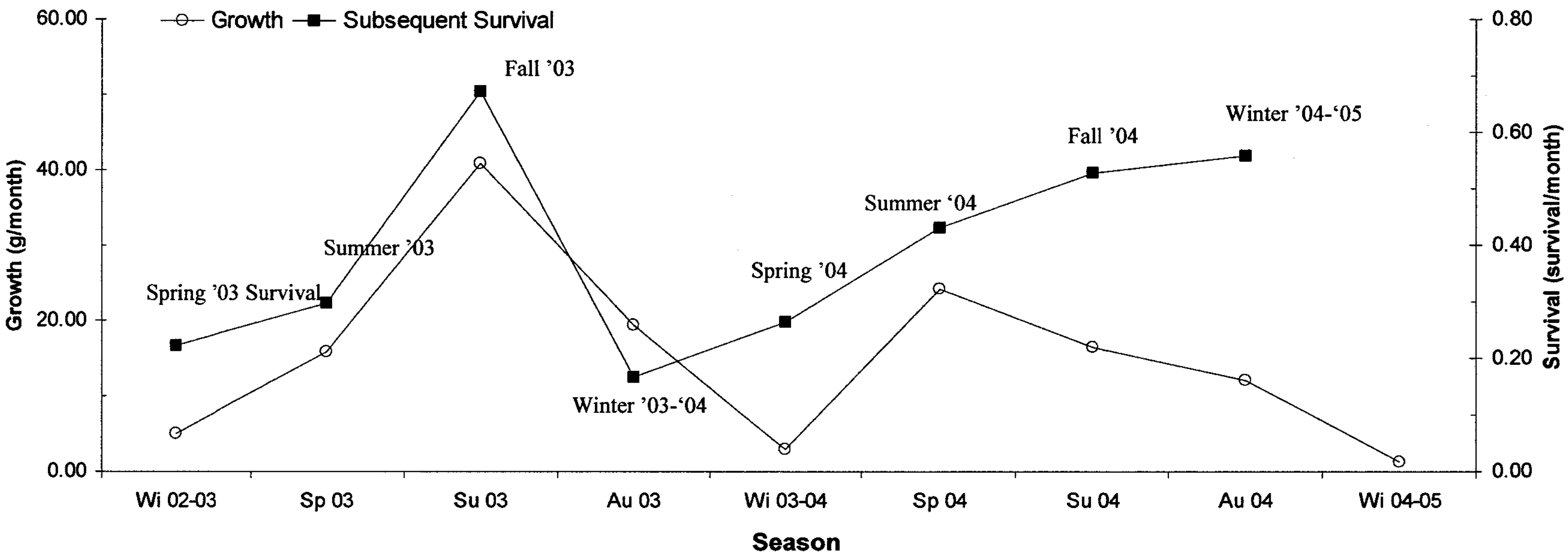

Fig. 38.—Female seasonal growth (g/month) versus subsequent survival for the study period. First survival data point is for spring 2003 survival. Patterns of seasonal growth and subsequent seasonal survival closely mimicked each other for the first half of the study. In the latter half of the study, as seasonal growth both increased and decreased, subsequent seasonal survival continued to increase.

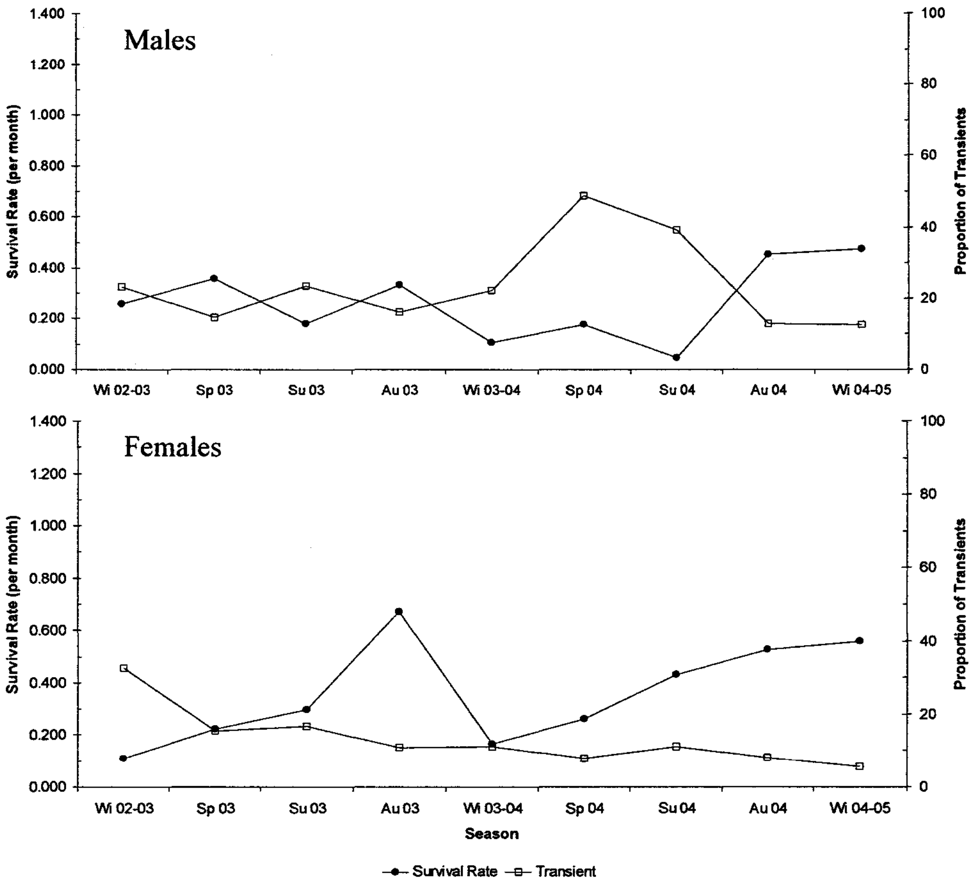

FIG. 39.—For males (top) and females (bottom), seasonal survival versus seasonal proportions of transients in the population for the study period. For males, periods of increased seasonal survival were associated with lower proportions of transients, while decreases in seasonal survival were associated with increased and higher number of transients. For females, stable and steady proportions of transients were associated with stable and increased patterns of seasonal survival.

survival rates were observed from spring of 2004 to the end of the study which coincided with a stable pattern in the proportions of transients.

No significant relationships were present for seasonal growth and the proportions of seasonal transients, using log-transformed seasonal growth and transient data ($r = 0.347$, $p > 0.05$ for males, $r = 0.230$, $p > 0.05$ for females). However, similar trends of the proportions of transients and seasonal growth were observed for males, but not for females (Figure 40). For males, increases and decreases in both seasonal growth and proportions of transients mimicked one another in the first half of the study. For the latter half of the study, no patterns were apparent. For females, the stable and steady percentage of transients did not follow patterns of seasonal growth (Figure 40).

Since winter survivorship in cotton rats was one of the most important objectives of the study, winter patterns of survival were plotted based on the same cohort of individuals of each mass class observed from the autumn into successive seasons. Mass class designations were based on the mass of individuals in the initial season of consideration: winter 2002-2003, autumn 2003 or autumn 2004. Growth of these individuals was not taken into account; instead, their presence or absence in successive seasons based on initial mass class was used.

As a result of no data having been collected prior to December 2002, survival data was used from this first month of collection. For males, every mass class with the exception of mass class 1 was observed in the winter of 2002-2003 and only the intermediate mass classes were seen in the spring, summer and autumn of the following year (Figure 41). For females, this same trend was observed (Figure 41). In the autumn of 2003, all mass classes of both sexes were present, but only the lightest mass classes

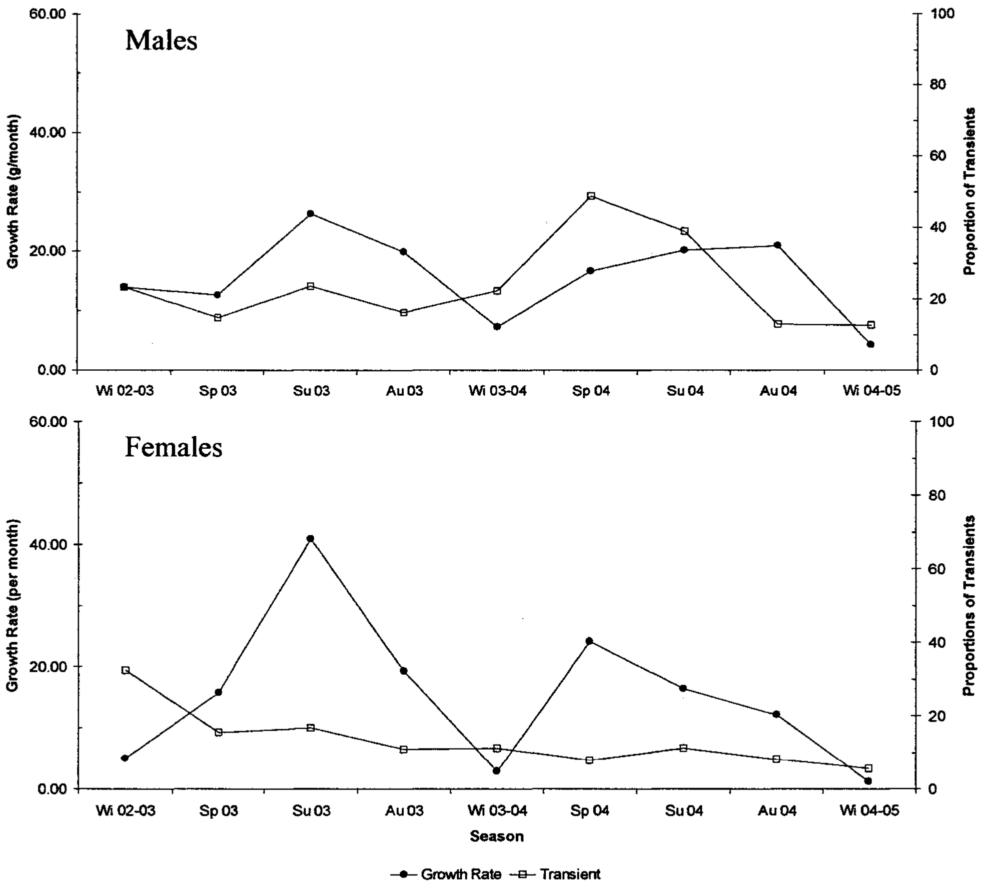

FIG. 40.—For males (top) and females (bottom), seasonal growth versus seasonal proportions of transients in the population during the study period. For both males and females, no significant relationships existed between these rates. Similar patterns of increase and decrease were observed for males only in the first half of the study, while no similar patterns were apparent for females.

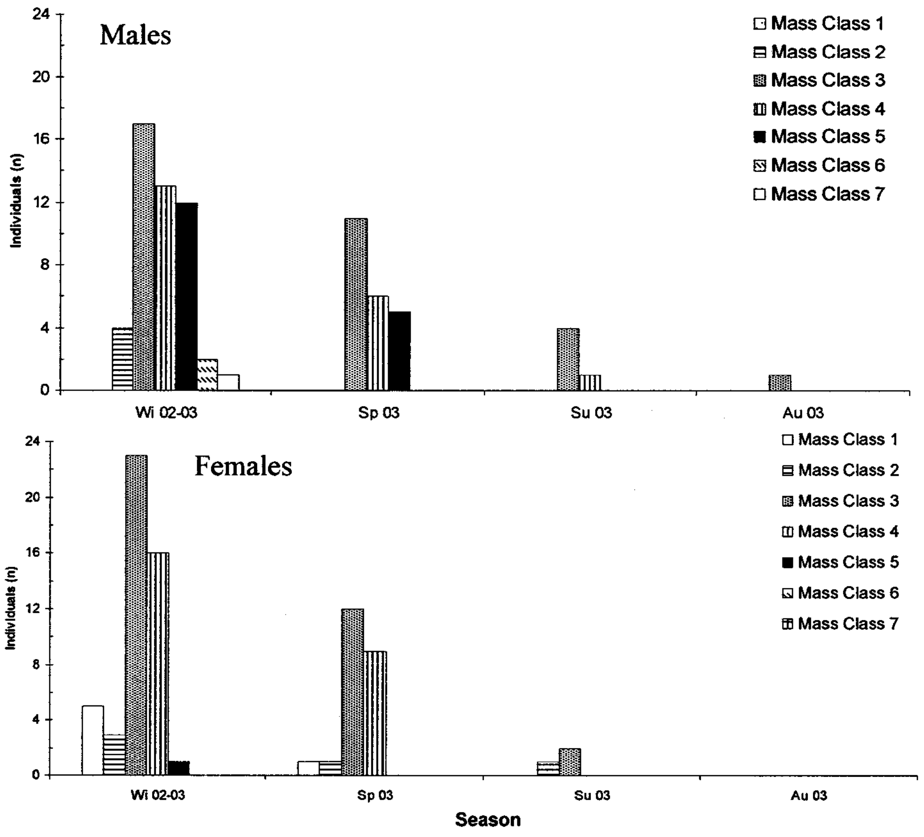

FIG. 41.—The distribution of survivors from the same cohort of males (top) and females (bottom) alive in winter 2002-2003 and their disappearance in the following seasons. Only initial mass of these individuals determined their assignment to a mass class into each season; therefore, growth was not taken into account. Males from mass class 3 and 4 were observed into summer 2003 and one individual from mass class 3 survived into autumn 2003. Females from mass classes 2 and 3 survived into summer 2003, but none into autumn 2003.

(mass classes 1, 2 and 3 for males; mass class 3 for females) persisted into the spring of 2004 (Figures 42). For females, only one individual (#446), which was first observed in the autumn of 2003 in mass class 3, survived until January of 2005, a total of 16 months as an adult. In this study, the average life span was 2.6 months for males and 3.0 months for females. All mass classes for both sexes were present in the autumn of 2004, but only females were seen into the first month of the spring of 2005 (Figures 43). Of these females, the lighter mass classes (mass classes 1 and 2) were present with greater frequency.

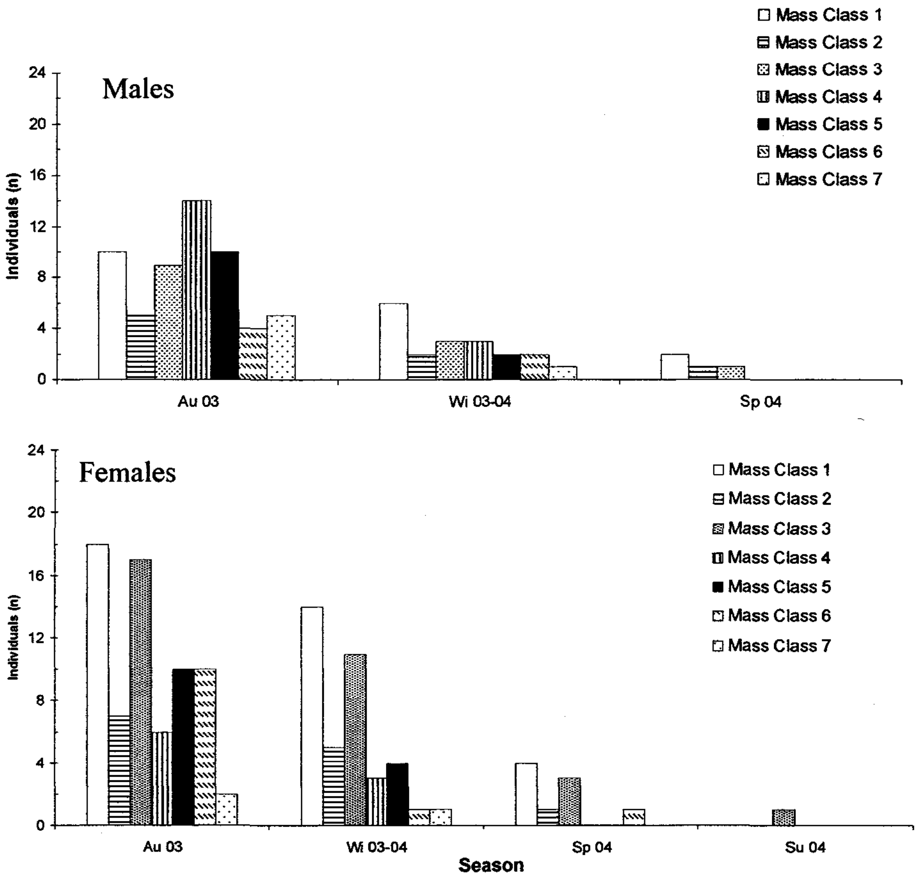

FIG. 42.—The distribution of males (top) and females (bottom) alive in autumn 2003 and their disappearance in the following seasons. Males from the lowest mass classes (1, 2, and 3) survived the autumn breeding season to the spring breeding season. Females from the lowest masses classes (1, 2, and 3) and mass class 6 survived from autumn 2003 to spring 2004. One female individual from mass class 3 survived into the winter of 2004-2005 (not shown).

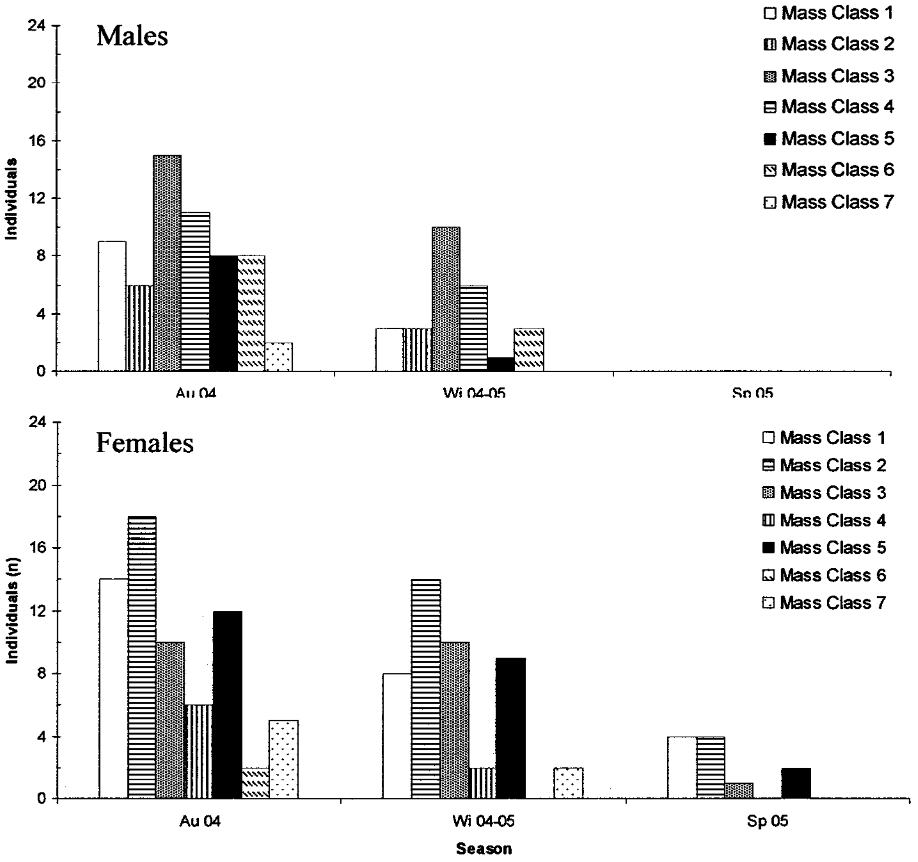

Fig. 43.—The distribution of males (top) and females (bottom) alive in autumn 2004 and their disappearance in the following seasons. No males survived into spring 2005. Females from the intermediate mass classes (2, 3, and 4) and mass class 6 survived into the spring 2005.

DISCUSSION

Previous studies of Virginia populations of *Sigmodon hispidus* have focused on several different aspects of its life history (Rose and Mitchell 1990; Bergstrom and Rose 2004), but not specifically on growth and survival. My study reaffirms previously reported population trends, as well as brings new insight regarding growth and survival in this geographic region using mark-and-recapture techniques. Patterns of winter growth and survival are particularly important for understanding the causes of localized extinctions during winter months at other geographic locations.

S. hispidus have been well documented in the midwestern and southern United States, particularly in Kansas and Texas (McClenaghan and Gaines 1978; Cameron and Spencer 1983; Sauer et al. 1984; Sauer 1985; Campbell and Slade 1993; Slade and Campbell 1995; Eifler and Slade 1998; Eifler and Slade 1999; Slade and Iskjaer 1999). Similarities and differences observed in the population dynamics of this study compared to other geographic populations serve to better understand overall population trends and the relationship between seasonal rates of body growth and survival in *S. hispidus* and perhaps for other seasonally breeding small mammal populations.

In this study, the available habitat allowed for a great variety of species to take up residency in this old field. *S. hispidus* remained the dominant species on the grid until the last several months of the study, when *Microtus pennsylvanicus* and *Reithrodontomys humulis* became the dominant species (Table 1). Changes to the plant community due to old field succession negatively affected *S. hispidus*. *S. hispidus* is dependent on dense herbaceous vegetation as a food resource and for cover, but the rapid influx of loblolly pines and other trees has excluded necessary herbaceous plant species. However, Rose and Birney (1985) noted that *M. pennsylvanicus* in small mammal communities has the ability to become the dominant small mammal and influence other populations. Interspecific interactions between *Sigmodon* and *Microtus* have been studied (Odum 1955; Wiegart 1972), but due its larger body size, *S. hispidus* typically has a competitive advantage over *Microtus* (Terman 1974). Therefore, the decline in *Sigmodon* was more likely due to vegetation changes on the grid rather than interspecific competition from increasing numbers of *M. pennsylvanicus*.

The other species were less abundant than the *S. hispidus, M. pennsylvanicus* and *R. humulis* (Table 1). *Mus musculus* disappeared within the first few months of trapping. *Mus*, an introduced species and a superb colonizer of new habitats, is often displaced when populations of native rodents become established (Pearson 1963; Lidicker 1965; Delong 1967). Changes in available habitat likely played a role, but interspecific competition may also have influenced their disappearance from the grid (DeLong 1967). *Oryzomys palustris* typically inhabits marshes and moist meadows, so their limited presence in wet areas of the grid was not unexpected (Kincaid et al. 1983). Both the occasional capture of shrews and the rare occurrence of *Microtus pinetorum* were due in part to proximity to its native forested habitat located west of the study grid (Miller and Getz 1969; Dueser and Shugart Jr. 1979). *M. pinetorum* and the shrews are elusive species that typically inhabit underground burrows (Dueser and Shugart, Jr. 1979; Schadler and Butterstein 1979). In addition, the presence of M. pinetorum was likely the result of seasonal timing associated with its above-ground activities (Miller and Getz 1969).

General Population Trends

The 1:1 sex ratio observed in the tagged population was similar to ratios in other populations of cotton rats (Goertz 1964; Goertz 1965; Cameron 1977; Stafford and Stout 1983; Cameron and McClure 1988; Langley and Shure 1988; Table 1). However, the overall significant female bias for animals captured and accounted for once per month in this study is different from results observed in other cotton rat population studies (Table 2; Figure 7). Kincaid and Cameron (1985) found a male-biased sex ratio (62.6% males:37.4% females) in a Texas coastal prairie. Other studies have demonstrated a male-biased sex ratio at certain times of the year at other geographic localities (McClenaghan and Gaines 1978; Cameron and Spencer 1983; Cameron and McClure 1988). In this study, the sex ratio is consistent with these patterns and favored males in the spring and summer seasons, while more females were observed in winter (Figure 8).

Males are known to increase their average daily movement and expand their ranges during the spring and the summer as they seek mates (Slade and Swihart 1983). Both sexes tend to restrict their movements during the winter (Slade and Swihart 1983). The overall female bias in captures may be due in part to the significantly higher numbers of male transients and female residents observed in this study. In general, larger home ranges and greater average daily movements have been documented for males (Goertz 1964; Petersen 1973; Cameron and Spencer 1981; Swihart and Slade 1983), but increased male transiency within a population could skew sex ratios to favor females.

Habitat quality may also play a role. Cotton rats consume a mixed diet of monocots and dicots to maintain their energy and nutrient requirements (Randolph and Cameron 2001). Cameron (1995) showed that males are more common in dicot and mixed habitats in the Texas coastal prairie, while females occupy mostly mixed habitats. Kincaid and Cameron (1985) demonstrated that males occurred equally in mixed and monocot habitats, but less in dicot habitats in the coastal prairies of Texas. Females exhibited similar distributions, but had stronger negative associations with dicot habitats than males (Kincaid and Cameron 1985). In-depth vegetative analysis was not conducted in my study, so the proportions of habitat compared to male and female occurrence could not be determined. However, it would be worthwhile to conduct this analysis in the future to explore the potential contribution of vegetation on the grid to the female-bias in the population.

The high incidence of adults observed in this study has been reported in other populations of cotton rats (Fleharty and Choate 1973; Drabek 1977; Eifler and Slade 1999; Table 3). Juveniles never exceeded the numbers of adults in any season, but were more abundant at some times than others (Figure 9). During the winter seasons, few or no juveniles were present on the grid and none were seen in the last winter season of the study. This pattern is most likely the result of high mortality of juveniles in winter and the rapid growth into adult size classes before the onset of winter (Campbell and Slade 1993). The presence of few juveniles in the spring suggests either low recruitment and potentially high rates of dispersal (Campbell and Slade 1993). Juvenile numbers increased in the summer and autumn, indicating greater survival and residency during these seasons. Fleharty and Choate (1973) and Drabek (1977) observed similar trends of juvenile recruitment in the summer and autumn seasons.

The proportions of transients, visitors and residents were similar to those seen in other populations of cotton rats (Slade and Swihart 1983; Doonan and Slade 1995; Table

4). Residents were most numerous, followed by transients, then visitors (Table 4). In this study, more female residents were present than males, which likely produced overall female bias of captured individuals (Figure 10). However, transient males were more prevalent than transient females (Figure 10). Slade and Swihart (1983) also report that males move more than females. This greater movement likely contributes to the larger proportions of male transients and female residents observed in this population.

Despite the fact that male transients did not display obvious seasonal patterns, seasons in which high proportions of transients were observed often corresponded to times of potential dispersal, particularly in the spring (Campbell and Slade 1995; Figure 11). In general, males begin to increase their movements at the start of their reproductive lives (Swihart and Slade 1983). Therefore, increases in the proportions of male transients during the spring and the fact that slightly more male transients than residents were observed in the spring of 2004 are to be expected. Even though males display increased mobility and demonstrate larger home ranges than females (Goertz 1964; Petersen 1973; Cameron and Spencer 1981; Swihart and Slade 1983), residents were still numerically dominant in the male segment of the population.

Females are more likely to take up residency than are males. Females had similar low proportions of transients and visitors and high proportions of female residents (Table 4). Increases in the proportions of female residents were observed in the autumn (Figure 11), periods of increased population density and a second pulse of reproductive activity. Increases in the proportions of resident females in the winters of 2003-2004 and 2004-2005 were likely due to the need to restrict movements and conserve energy during the winter months (Swihart and Slade 1983; Eifler and Slade 1998).

In this study, some exceptions to the expected seasonal trends in residency patterns were seen. A slight increase in the numbers of transient females in the autumn of 2003 and the winter of 2003-2004 were most likely associated with increased population density and recruitment during these seasons (Doonan and Slade 1995). Similar increases in the proportions of visitors during both autumns, as well as increases in the proportions of resident females compared to males in autumn of 2003 and winter 2003-2004, can also be attributed to increases in density and recruitment. The increase in the proportion of female residents in the spring of 2004 could be related to the increase in the proportion of male transients, which are seeking potential mates.

Population Density

Estimates of population density were obtained through two methods: the software package JOLLY and the minimum number alive (MNA) technique. Previous studies have reported that MNA techniques are conservative and often underestimate density (Doonan and Slade 1995). However, correlation analysis revealed the density estimates to be similar in my study.

Annual population densities were slightly bimodal in 2004, with large increases seen in autumn and smaller increases in the spring of 2004 (Figure 12). This pattern of density is primarily seen in southern cotton rat populations (Odum 1955; Cameron 1977; Cameron and Spencer 1981; Kincaid and Cameron 1985). Cotton rat populations in the northern portions of the species' range, most specifically in Kansas, exhibit one peak in abundance in autumn (Fleharty and Choate 1973; Glass and Slade 1980a; Doonan and Slade 1995; and Rehmeir et al. 2005). Population density trends in Virginia, then, are typical of southern populations, despite being at the same latitude as Kansas (37° N).

This may be due in part to the warmer oceanic climate observed in Virginia in winter compared to Kansas.

Overall, population density was not significantly different between the years of the study and similar patterns of change in density were observed both years. Maximum densities occurred in autumn with highest numbers in both Novembers (106/ha and 101/ha) and January 2005 (124/ha), while spring increases in density were not as dramatic (60/ha, May 2004) (Figure 12). Such high overall abundances and autumn abundances have not previously been reported for natural cotton rat populations. However, densities in the 100/ha range were found in Kansas populations supplied with supplemental food (Doonan and Slade 1995). Cameron (1977) reported maximum autumn densities of 14/ha in Texas, while Odum (1955) reported a ten-year autumn average high density of 69/ha in Georgia. Populations from the short-grass prairie of western Kansas had maximum density of 20/ha in autumn (Fleharty et al. 1972).

Minimum densities in my study were observed in the 30-40/ha range in early spring of 2003 and winter of 2003-2004 and densities never fell below 30/ha at any time. Minimum densities in other northern distributions were observed in the spring (0.02/ha; Fleharty et al. 1972) and zero (Fleharty et al. 1972; Glass and Slade 1980b). In southern populations of cotton rats, Odum (1955) and Cameron (1977) reported lowest densities in the winter and summer in Georgia (8/ha) and Texas (0.5/ha), respectively.

Small mammal densities are influenced by several different extrinsic and intrinsic factors. Climate can have a substantial impact on population density in cotton rat populations, particularly during the winter, when population declines often have been observed (Dunaway and Kaye 1961; Goertz 1964; Cameron 1977; Langley and Shure

1988). Low temperatures associated with winter weather likely cause population declines and even localized extinctions. These trends are typically observed in northern populations of cotton rats (Sauer 1985). In my study, density declined in the winter, but not to the same low levels seen in other northern populations. The milder winters observed in my site at the northern part of the species' range in Virginia likely have less impact on population density than do harsher winters found in Kansas (Figure 2). The warm autumns and mild winters can also extend the breeding season and lead to higher recruitment of animals into the winter (Rehmeir et al. 2005), which would explain the spike in population density in January 2005 (Figure 12).

The quality of the habitat is another factor influencing population density. The high levels of plant biomass characteristic of the early summer are tied to the reproductive cycle and thereby contribute to large increases in population density in the autumn (Cameron 1977; Langley and Shure 1988). During the winter and early spring, plant biomass is substantially lower than in other seasons. The decrease in the amount of vegetation cover will also affect population density by making animals more susceptible to predation (Goertz 1964). The loss of herbaceous plants due to old-field succession and decreased numbers of *S. hispidus* near the end of my study supports the negative effects that changes in vegetation can have on cotton rat population density.

Another factor affecting density is juvenile recruitment during the reproductive season. The entrance of juveniles into the population contributes to increases in density (Cameron 1977), seen in autumn and to a lesser extent in late spring. Dispersal of animals out of the population can have the opposite effect on population density (Stafford and Stout 1983), which may also explain decreased population density in the early spring.

Patterns of Reproduction

Due to the energy constraints, as a result of their small size, small mammals are adapted to carefully regulate their energy budgets. Because energy constraints are most profound over the winter months, small mammals typically suspend such high-energy cost activities, as growth and reproduction. At northern locations, the effects of winter are more extreme and periods of growth and reproduction are even more contracted than in southern locations. Cotton rats in my study reproduced in accord with the energy-conserving tendencies of small mammals in general and exhibited the reproductive trends observed in other cotton rat populations (McClenaghan and Gaines 1978; Rose 1986; Rose and Mitchell 1990; Bergstrom and Rose 2004). The patterns of reproductive cessation observed in this population were also similar to those seen in previous Virginia cotton rat studies (Rose 1986; Rose and Mitchell 1990; Bergstrom and Rose 2004). In these studies, females were reproductively active from March to October and males became reproductively active one month earlier and ended one month later. Because males do not pay the costs of pregnancy and lactation, they can stay reproductive longer and still survive the winter. By increasing testes size in February, mature males also are fertile as soon as the first females come into estrus (Rose 1986).

In my study, males of adult size with descended testes were not observed until March and reproductive adult females were not observed until April in both years (Figures 13 and 15). McCravy and Rose (1992), using data from several species of small mammals, including *Sigmodon hispidus*, examined both externally and internally for reproduction, found descended (scrotal) testes to predict reproductive competency with 86.7-93.8% success, whereas three female features were less useful (vaginal orifice

69.7%; medium-to-large nipples 73.7%; and slightly open to open pubic symphysis 67.5%). However, significant correlations between the external character used in my study and percent of convoluted epididymides of Virginia cotton rats from the Bergstrom and Rose (2004) study demonstrate that the use of descended testes is an adequate method of determining reproductive activity in males. A comparison between my study and the Bergstrom and Rose (2004) study shows that there were several instances when no reproductive (only non-scrotal) males were present, but increasing percentages of convoluted epididymides were seen during these months, especially in February (Figure 14). These instances were observed either at the beginning of the breeding season and towards the end (February and November). However, the percentages of convoluted epididymides during these times were lower than 40% and not as high as percentages observed at the peak of the breeding season (Bergstrom and Rose 2004). In the Bergstrom and Rose (2004) study, the percentage of convoluted epididymides remained at zero in February and November 1987, demonstrating that males were not always reproductively active one month earlier or one month later than females. This observation was also seen in my study (November 2004) when no reproductive males were observed.

McClenaghan and Gaines (1978) also used percentages of convoluted epididymides as indicators of male reproductive activity in Kansas populations at the same latitude as this study. In their study, males never reached 100% breeding levels during the reproductive season and the highest percentages were documented during the summer. In contrast to McClenaghan and Gaines (1978), both the current study and the Bergstrom and Rose (2004) study showed lower proportions of reproductive males over the summer (Figure 14). These decreases in reproductive activity are associated with mid-summer lulls in reproduction, which have been suggested to be the result of high summer temperatures (Cameron 1977). Decreases in mid-summer reproduction may also be associated with spring recruitment and non-reproductive cotton rats entering the population. The fact that there are fewer breeding cotton rats in the population at this time may contribute to these mid-summer lulls.

Similar shortened breeding seasons with males demonstrating the same one month advantage over females were seen in Kansas (McClenaghan and Gaines 1978). However, the breeding season started one month later in Kansas and males are reproductively active from March to November (Campbell and Slade 1995). This shorter breeding season is comparable to the breeding season observed in my study based on only external characteristics, which confirms that reproduction during the winter months is not advantageous in northern populations of cotton rats.

The small percentages of reproductive males observed in January 2003 and 2005 are due to the survival of a few large males that failed to regress their testes (Figure 13). Cameron (1977) observed that cotton rats in Texas are reproductive all year with reduced activity in the winter. Bergstrom and Rose (2004) also noted this trend in populations of cotton rats in Georgia. However, despite the relatively milder winter conditions in Virginia, this strategy is not energetically possible in northern parts of the species' range. The energetic costs of pregnancy and lactation during the spring and summer are greater than or equal to energetic costs experienced in the winter (Fournier et al. 1999). In addition, no reproductive males were present in the months preceding or following January in either year. The few males that remained reproductively active throughout the winter found no cycling females and thus no winter breeding was detected. Therefore, overall patterns of reproductive activity for males in my study concur with previous Virginia investigations of cotton rats demonstrating a cessation in breeding (October-March) and earlier onset of reproductive activity in males than in females. These results are also similar to those observed in Kansas populations at the same latitude.

Female cotton rats are at even more of an energetic disadvantage than males. The combined costs of pregnancy and lactation are energetically demanding throughout the entire breeding season. It would be detrimental for females to remain reproductively active over the winter months, especially in the northern portions of the species' range. In my study, a small proportion of females continued to display reproductive competence during the winter, but none became pregnant (Figure 15). In all instances, these females did not survive to the following springs. In other Virginia studies, investigators have reported that the breeding season spans from March to October, but females are not at their maximal reproductive potential during the first month of the breeding season (Rose 1986; Rose and Mitchell 1990; Bergstrom and Rose 2004). Despite slight differences, overall reproductive trends from my study compared well to those found in Virginia females in the Bergstrom and Rose (2004) study. A significant correlation between my results and those of Bergstrom and Rose (2004) demonstrated that our findings were similar. A cessation of breeding over the winter months was observed for both studies, with maximal reproductive output in the spring and autumn months.

The suspension of breeding during the winter is also observed in Kansas populations at the same latitude (McClenaghan and Gaines 1978). However, the compressed breeding seasons for females in Kansas starts one month later than for

Virginia females (Rose and Mitchell 1990). The more compressed breeding season in Kansas compared to Virginia may be the result of colder and harsher winters. The mild and moderating ocean climate of eastern Virginia may allow for a longer breeding season. In addition, any differences in seasonal variation on the quality and availability of food resources due to environmental factors may also impact the length of the breeding season in northern populations (Derting 1997). In contrast, females in southern populations, such as those in Texas and Georgia, have the potential to remain reproductively active all year round (Cameron 1977; Bergstrom and Rose 2004). These southern geographic regions are also less seasonal than at northern locations, contributing to differences in litter sizes, as well as to breeding patterns in general (Derting 1997).

In my study, between 60-70% of females were reproductively competent during April 2003 and March 2004, while higher percentages were achieved later in spring and persisted into the summer and autumn months. Bergstrom and Rose (2004) also reported similar trends in that maximum reproductive potential was attained by mid-spring and again during the mid-autumn months. This trend for gradual increase in reproductive potential is also reported in other northern populations of cotton rats (McClenaghan and Gaines 1978). Pregnancy rates observed in this study (20.65%) were much lower than previously reported for Virginia cotton rats based on necropsied females (68.7%; Rose and Mitchell 1990). This is most likely due to undetected pregnancy in the population of cotton rats in the current study, when only females in the third trimester can be judged as pregnant with certainty.

The current study also shows that females were reproductively competent longer compared to females in previous Virginia studies (Rose 1986; Rose and Mitchell 1990).

Bergstrom and Rose (2004) reported that a few reproductively competent females were pregnant as late as November. In my study, females remain reproductively active through November and a small number of these females were pregnant during this month (Figure 16). The three pregnant females observed in November 2003 did not survive the winter. However, one pregnant female seen in November 2004 did survive until March 2005. This observation is unusual in that Bergstrom and Rose (2004) speculated that in order for females to survive the winter, it is necessary to suspend breeding early in the autumn.

Bergstrom and Rose (2004) speculated that females that reproduce during the summer and autumn do not survive the winter in Virginia. In my study, the majority of pregnant females were observed in autumn months, with the next greatest frequency in the late summer (Figure 16). From the capture histories recorded of these pregnant females, the speculations of Bergstrom and Rose (2004) are partially supported. No females that were pregnant in either the summer or autumn of 2003 survived to the following spring. However, three pregnant females from the summer and autumn of 2004 survived to the spring, which included the November pregnant female previously mentioned. The persistence of these females does not support the speculations of Bergstrom and Rose (2004). However, of these surviving females, one was pregnant in August 2004, which might have been early enough in the breeding season to recoup energies diverted to pregnancy and lactation before winter. The other two females that survived to spring 2005 were pregnant in October and November of 2004. This is extremely late in the breeding season to have the opportunity to recoup reproductive energies; thus, these females appear to be exceptions.

In all three instances, these females were light (56, 62 and 80 g). This might have been a factor to their continued survival over the winter because less energy is required to support small body sizes. If so, perhaps Bergstrom and Rose (2004) are correct that fully adult females that breed in summer and autumn do not survive to the spring. Cotton rats of intermediate size have better overwinter survival than heavier cotton rats (Campbell and Slade 1993); similar trends seen in the current study. In addition, the slightly, but not significantly, warmer average temperatures in Virginia experienced in the winter of 2004-2005 (5.82 °C) compared to the winter of 2003-2004 (4.54 °C) may also have contributed to the survival of these females.

Of the three females recorded as being pregnant multiple times in their trapping history, two did not survive over the winter. These females were pregnant in the late summer and again in the mid-autumn. As a result of the higher energy demands of multiple pregnancies, the energies and resources of these females are reduced and multiple pregnancies are just as detrimental to winter survival as breeding later in the season, as predicted by Bergstrom and Rose (2004). The surviving female was pregnant twice in its lifetime (May and October of 2004) and persisted multiple seasons, including one winter season. This female was first observed as an adult in October 2003 and last seen in January 2005. It was the longest living animal in my study and most certainly the exception to the energetic and survival constraints imposed on other cotton rats.

Bergstrom and Rose (2004) also speculated that all breeding females in Virginia in the spring were comprised of first-time mothers that were born no later than September or October. These speculations were based on reproductive data from necropsied animals and confirmed in the current study. In the spring of 2004, the large majority (80%) of breeding females were overwintering animals born in October and November of 2003. In fact, one juvenile from late summer also survived to become reproductively competent, but was not seen again after April 2004. Some previously untagged intermediate weight females were also recruited into this first pulse of breeding. Females in March 2005 also comprised autumn-born animals that survived the winter after recruitment in September, October and November of 2004.

A mid-summer lull in breeding activity was present for females in my study in 2003, but not 2004. Female reproductive rates dropped below 70% in July of 2003 and rebounded to nearly 80% in September (Figure 17). In 2004, female reproductive rates were 75% in August of 2004 and almost 95% in September of 2004. Bergstrom and Rose (2004) also reported no mid-summer lull in the summer of 1989. The decrease in reproductive activity in 2003 is likely the result of the recruitment of young adults into the population (Bergstrom and Rose 2004). The later onset of spring recruitment in 2003 may have increased the number of non-reproductive females into the population during the summer of 2003, but this was not the case in the spring of 2004. However, the higher temperatures of summer could have depressed both diurnal activity and breeding (Cameron 1977), which was observed to a much lesser extent in 2004.

Bergstrom and Rose (2004) believed that June-July breeders, the early phase of the second pulse of breeding lasting from June-September, would be composed of early spring breeders reproducing for the second time and progeny from the spring pulse reproducing once or perhaps twice. Unfortunately, this speculation cannot be confirmed because of an insufficient amount of data available for the early stages of the second pulse. There was a relatively low number of April and May female breeders observed and this translated into even fewer numbers of reproductive females surviving into summer and autumn. These females either had low spring survivorship or simply went undetected in the summer and autumn months. However, in 2003, summer breeders consisted mainly of older females surviving the winter months. Pregnancy could not be confirmed for these individuals in the spring, but they were judged to be reproductively competent with monthly trapping. Pregnancy is only confirmable in the third trimester and many pregnancies go undetected, even when all females are breeding. The remainder of the reproductive population was newly tagged females of intermediate weight, likely second-time breeders that contributed to the first birth pulse, which, if true, confirms the speculations of Bergstrom and Rose (2004). Only a few second-time breeders were transient reproductive females, which may have contributed to the population but were never seen again.

In 2004, trends in summer breeders were similar to those observed in summer 2003. In both years, the autumn breeders consisted mainly of summer-born females, as well as mid-summer recruits from the first birth pulse. The majority of these mid-summer recruits were of intermediate mass and only one or two of these recruits were transient individuals. Despite the fact that low numbers of pregnant females were present in both April and May in my study, the overall structure of breeding females closely follows patterns predicted by Bergstrom and Rose (2004).

Body Mass

In this population of cotton rats, sexual dimorphism in mean body mass was evident, a pattern seen in other populations of cotton rats, irrespective of geographic location (Petersen 1973; Cameron and Spencer 1983; Cameron and McClure 1988; Rose and Mitchell 1990; Derting 1997; Bergstrom and Rose 2004). Males were significantly larger than females; however, there were a few autumn months (October 2003 and September 2004) when females had slightly higher mean masses than males (Figure 18). These differences are most likely the result of gains in body mass due to undetected pregnancy. Sexual dimorphism was also present between the two years of my study. Differences in body mass between males and females, as previously reported by Rose and Mitchell (1990) for Virginia cotton rats, were smallest at the end of the breeding season.

Mean masses observed in my study are the same as those reported by Rose and Mitchell (1990) and significantly higher than those reported by Bergstrom and Rose (2004). The two prior Virginia studies were based on necropsy data rather than the mark-and-recapture techniques used in my study. This difference in collecting method could affect results because the random sample of animals collected for necropsy may consist of more animals that were either smaller or larger in size. These size effects are minimized in all studies by excluding juveniles (<50 g) and pregnant females. The exclusion of pregnant females is more accurately done in the necropsy studies because reproductive organs are removed to give total somatic body mass. Juveniles could be excluded with confidence in my study, but it is possible that undetected pregnancy in these females might contribute to the significantly higher mean mass for these females compared to females observed in Bergstrom and Rose (2004).

Despite the differences in collection techniques, overall differences in mean mass were likely due to the larger number of individuals captured in my study compared to previous Virginia studies. Rose and Mitchell (1990) and Bergstrom and Rose (2004) were limited in the number of animals captured, never taking more than 30 out of the field per month. Mark-and-recapture techniques allow more flexibility and greater numbers of animals to be captured per month because none of these animals are being permanently removed from the grid. The Bergstrom and Rose (2004) study was just as long as my study (28 months), but produced half the number of animals and had an overall significantly lower mean mass for both sexes. However, the Rose and Mitchell (1990) study was the shortest (12 months) and had even less animals, but exhibited slightly higher mean masses. Therefore, the higher numbers of animals in this population of cotton rats had a more moderating effect on mean mass, as evidenced by a mean mass intermediate to the current study and the Bergstrom and Rose (2004) study. The larger number of animals was also overall a more random sample of the population contributing to the variation in mean mass between these Virginia populations of cotton rats.

When comparing mean mass between years of study, it became evident that it was not just the quantity of animals, but the quality of the population that can affect mean mass. Mean mass of females was similar between the years, but males had a significantly higher mean mass in 2003 than in 2004. Furthermore, more males were present in 2003 compared to 2004. Of these males, the numbers of male transients were similar in 2003 and 2004 (Table 4); however, average mean mass of transients was almost ten grams higher in 2003 than on 2004. In addition, not only were more resident males observed in 2003 than 2004, but mean mass for these male residents in 2003 was also higher. A larger quantity of heavier transients and residents in 2003 helps to explain the mean mass differences for males between years of the study.

Similar mean masses were observed for females between both years, which suggested that residency trends did not affect female mean mass. Although the numbers of transients and residents differed between 2003 and 2004, the mean mass of females remained similar between years. Overall, any effects to mean mass due to residency patterns would undoubtedly go undetected in necropsy studies, as residency status cannot be determined in these animals.

In addition to intrinsic factors affecting mean mass, extrinsic factors, such as the weather, could also potentially affect mean masses. However, I do not believe that weather played a role in the observed differences in mean mass for these Virginia cotton rat populations. Lower annual temperatures and higher precipitation totals could have the potential to adversely affect mean mass, as is evident in other populations of cotton rats (Goertz 1965; Cameron 1977; Campbell and Slade 1993; Derting 1997). However, monthly mean temperatures and monthly precipitation totals for each of the previous Virginia studies (1983-1984 and 1987-1989) and my study were not significantly different from 50-year means for these geographic locations in Virginia (Table 6). In addition, no significant differences were present when temperature and precipitation totals for each study were compared (Table 6).

Although annual temperature and precipitation patterns did not differ from the 50-year means, isolated events may have negatively affected mass at certain times throughout the study. In mid-September 2003, a hurricane passed through eastern Virginia and the total rainfall for the month of September was higher than normal (Figure 4). Mean mass was seemingly unaffected in this month, but it is possible that subsequent months could have been affected. The summer of 2004 was also wetter compared to the previous summer and any potential negative effects in body mass may not be seen until later in the year, e.g., winter months.

In addition, snowfall was observed during each of these studies with the highest amount of snowfall seen in February 1989 (23.5 inches) in the Bergstrom and Rose study. This potentially harsher winter may have contributed to some of the observed difference in mean mass; however, significant snowfall (12 inches) was also present in December 2004 of the current study (Figure 5). Trapping was not conducted while snow covered the ground in order to avoid the direct effect of snowfall on mean mass. Despite high snowfall events in the Bergstrom and Rose (2004) study and based on no detected influence of snowfall on mean mass in my study, it is likely that snow does not contribute to the lower overall mean masses in the Bergstrom and Rose study and other Virginia studies of cotton rats (Rose and Mitchell 1990).

Variation in climate between the Virginia and Kansas sites at the same latitude may explain geographic differences in mean mass. The previously reported mean masses for Kansas populations at the same latitude were 110 g for males and 106.2 g for females (Derting 1997). Kansas and Virginia experience similar seasonal weather conditions; however, Kansas winters are colder and harsher than those observed in Virginia, which likely contributes to the large size of Kansas cotton rats at these northerly locations (Bergmann's rule). Higher mean masses in these Kansas populations are thought to be the result of winter selection for larger animals (Campbell and Slade 1993). In more seasonal, northern environments, such as those found in Kansas and Virginia, larger animals may have larger reserves of energy and may be better equipped to survive during times of stress, such as the cold temperatures associated with winter (Campbell and Slade 1995). The higher accumulation of fat observed in Kansas populations of cotton rats is a factor in their larger overall size (Cameron et al. 1979; Campbell and Slade 1993; Eifler and Slade 1998). Although it could be argued that the milder winters of Virginia could in theory lead to increase in body mass during the winter, this does not happen (Figures 18 and 19). In fact, the Virginia subspecies, *virginianus*, is the smallest of the four most recognized subspecies of *Sigmodon hispidus*.

In most instances, mean mass in southern populations is lower than mean masses seen in northern populations of cotton rats. In southeastern Texas, the reported mean mass for males is 94.7 g for males and 80.0 g for females (Cameron and Spencer 1983). The mean mass documented for Georgia populations is 102.2 g for males and 96.2 g for females (Bergstrom and Rose 2004). In Arkansas populations, males are 74.8 g and females are 80.7 g and males and females found in Mexico are 87.7 g and 72.7 g, respectively (Petersen 1973; Cameron and McClure 1988). With the exception of Georgia cotton rats, Virginia cotton rats have larger mean mass than other southern populations of cotton rats. This trend conforms to Bergmann's rule, which states animals of the same species tend to be larger in colder climates, e.g., larger body size at northerly geographic locations. Cotton rats in the southern portions of their range do not have to cope with the stress of winter; therefore, larger body size is not adaptive in these populations and energy can be devoted to reproduction rather than to increases in somatic mass. These southern locations are also less seasonal in available habitat quality than northern locations, where differences in the amount of available annual protein from plants can contribute to lower mean masses (Campbell and Slade 1995).

Cotton rats in Georgia were heavier than their Virginia counterparts, which contradicts Bergmann's rule. Bergstrom and Rose (2004) attributed these differences to higher overwinter survival and especially to younger age distributions in Virginia cotton rats. In seasonal environments, cotton rats will allocate more energy to thermoregulation than to mass gain, which increases the chances of survival, but would lead to overall smaller body mass. Because breeding patterns are constrained in northern locations, shorter-lived cotton rats become reproductively competent at a younger age in order to promote greater reproductive success, which also leads lower the mean mass of the population. Since patterns of reproduction in my study are similar to those reported by Bergstrom and Rose (2004), it is likely that comparable younger age distributions and overwinter survival also contribute to these observed differences in mean mass between my Virginia population and the Georgia population of cotton rats.

In my study, monthly mean mass varies over the year (Figure 18). Mass was the highest for both males and females in the spring months, particularly in May of 2003 and 2004. Increases in mass from the winter into the spring are expected due to warming temperatures and a greater availability of food resources. Similar increases in spring mass were also observed in previous Virginia populations (Rose and Mitchell 1990; Bergstrom and Rose 2004), as well as other geographic populations of cotton rats (Fleharty and Choate 1973; Slade et al. 1984). However, males gain mass more steadily than females from January to May because, unlike females, males can divert more of their energy to somatic growth (Fleharty and Choate 1973). Slade and Sauer (1985) also believed that heavier animals would be favored in early spring, due in part to their larger size buffering against the adverse effects of the environment. Increases in mass for both sexes were also associated with preparation for the breeding season, as mean mass for females in my study remained relatively flat from October to March, the period of suspended breeding. Higher mean masses were also observed in June and July, periods of high reproduction in females (Figure 15).

Increases in spring mass may also be due in part to fluctuations in population density. Weights of individuals increased when the weather was mild and the population was low, while decreases in weights occurred when population density was high and when the weather conditions were poor (Odum 1955; Goertz 1965; Joule and Cameron 1974; Cameron 1977). The spring months in this study exhibited some of the lowest population densities (Figure 12) and may have affected body mass in these months. However, because no significant correlations were found between mass and population density for either sex, my population shows no depressing or releasing effect of population density on body mass.

Seasonal patterns of mean mass confirm the overall monthly mean mass trends observed in my study. The heaviest males and females, seen in spring, were significantly heavier than in winter. Mean masses of females were similar between spring seasons, which demonstrate similarities in the timing and impact of the spring breeding season. Increases in mean mass in the spring were similar to those reported in other populations of Virginia cotton rats (Slade et al. 1984; Rose and Mitchell 1990; Bergstrom and Rose 2004), although Cameron and Spencer (1983) found decreases in spring mean masses attributable to recruitment of smaller animals into the population. In my study, young were not recruited until later in the breeding season, especially in 2003.

Despite the fact that high mean masses were observed in June and July, spring-to-summer decreases in mean mass were present for both sexes. The decline in mean mass was clearly evident for males in the summer of 2004, but was not significantly different from mean mass in the summer of 2003. These decreases in mean mass are most likely linked to changes in the plant community. Slade et al. (1984) reported that during the summer above-ground plants become dry and cotton rats are forced to find more nutritious alternative food sources and in contrast Kansas cotton rat populations will exhibit increases in body mass during the summer. Bergstrom and Rose (2004) also reported heavier animals in the summer for both Georgia and previous Virginia studies. Despite these population differences in summer mean mass, it is possible that changes in cotton rat diet have the potential to positively affect mean masses due to increased availability of food resources, as seen in the spring. Summer decreases may also be attributable to recruitment of smaller animals from the first breeding pulse of the late spring. The later onset of full reproduction in my population results in later entry of recruits into the population. These lower mean masses reduce the overall mean mass in summer, rather than in the spring (Cameron and Spencer 1983).

In my study, mean mass rebounded into the autumn and these increases were steadier for males than for females. Due to reproductive demands associated with autumnal breeding, females must manage their energy budgets more carefully than males, patterns also seen before spring. It is adaptive for males to divert more energy to somatic growth, while females build fat reserves in anticipation of the breeding season (McClure and Randolph 1980). Despite the summer-to-autumn increases in mean mass observed in both sexes, autumn mean masses did not significantly differ in 2003 or 2004. This suggests that both autumns had similar available food resources and that reproductive efforts did not have a significant impact on mean mass. Cameron and Spencer (1983) observed lower overall mean mass in the autumn due to the breeding season and recruitment. Campbell and Slade (1993) also reported loss of body mass in heavier cotton rats in autumn, but these losses were interpreted as being associated with the imminent winter season. Differences in body mass between the sexes were smallest at the end of the breeding season; mean masses were not significantly different in the autumn of 2003. Rose and Mitchell (1990) also observed smaller differences in body mass during this time of the year.

In order to better understand observed changes for both monthly and seasonal mean mass, distributions of mean mass among mass classes were used to obtain a clearer picture of the overall effects of body mass (Figures 20 and 21; Table 10). These distributions show the entry of juveniles into the population, animals previously excluded from calculations of mean masses. Mass class 1 consisted solely of juveniles, first observed in May as part of the first breeding pulse. Juveniles were generally not present during the winter months; however, a few juveniles from the autumnal breeding pulse were seen into December due to the breeding season extending into November. Three juvenile females were seen in January 2003, but none in other winter months (Table 10). As the breeding season continued, lightweight animals in mass classes 1 and 2 became more prevalent. In Kansas populations, cotton rats of lighter masses also come to dominate during April and May, when reproduction begins to occur, and their presence continues to persist through June to November (Slade and Sauer 1985). Other smaller mass classes also had more animals in the late summer and autumn months, which further demonstrates the recruitment of young animals into the population during these times.

Despite their small numbers in comparison to other mass classes, males in mass class 7 were generally observed all year round. Females in these higher mass classes were only observed in the warmer months (May-September). Males with fewer energetic constraints associated with reproduction can achieve heavier body mass as they continue to grow, if slowly (Figures 25 and 26). Although females often attain these high masses during pregnancy, they quickly lose this weight after giving birth. Heavy body mass does not ensure survival in every season. Campbell and Slade (1993) found that heavy cotton rats had lower survivorship compared to lighter cotton rats, most likely due to difficulties in maintaining their energetic needs.

Cotton rats in the intermediate mass classes (mass classes 3 and 4) were the most common throughout the study (Table 10). Joule and Cameron (1974) also reported twice as many animals in the intermediate mass classes during warmer months in Texas when food resources were most abundant. Intermediate mass classes were also most prevalent in winter, when the lightest and heaviest mass classes were typically underrepresented. It is more energetically practical for cotton rats to maintain these intermediate masses, especially during the winter, in accordance with fulfilling their higher energetic demands. The costs of sustaining the lightest and heaviest masses are even more difficult when energy demands are at their limits in the winter. A convergence of body mass into these intermediate mass classes would be achieved by smaller cotton rats gaining body mass and larger cotton rats losing mass over the winter months. These trends of winter mass gains and losses producing animals of similar body mass were also observed in Kansas (Slade et al. 1984).

In my study, winter mass was of specific interest because previous studies of Virginia populations had suggested mass gains in males over the winter (Rose and Mitchell 1990). Cameron and Spencer (1983) also found that males steadily gained weight throughout the winter in Texas. This trend is opposite to that observed in Kansas cotton rats, where mass losses were more common than gains during the winter (Campbell and Slade, 1993). In my study, males had irregular patterns in mass change over the winter months (Figure 18). Males did gain mass during the first winter (2002-2003), but displayed mass losses over the second winter (2003-2004). In the last winter (2004-2005), mass remained relatively unchanged. It is evident that males do have the ability to gain mass over the winter months in Virginia, but decreases in mass or nil growth over the winter months are just as common. In most instances, it may be more beneficial to allocate energy toward thermoregulation than to mass gain and maintain stable masses to better ensure survival.

A similar decrease in mean mass was also observed for females in the winter of 2003-2004, which indicates that similar forces were adversely affecting the population then. A combination of lower temperatures and population density may have negatively impacted cotton rats in this season then. Despite this decrease in mass for females in winter 2003-2004, females in the two other winter seasons remained stable in mass and no extreme changes in mass were observed. In both Virginia and Kansas, similar trends in female mass were present over the winter (Rose and Mitchell 1990; and Campbell and Slade 1993), i.e., nil or negative growth.

In Texas populations of cotton rats, females steadily gained mass throughout the winter (Cameron and Spencer 1983). This is likely the result of temperature and climate differences, which allows for this continual gain in mass over the winter. In addition, larger animals in the north have proportionately more fat during the winter than do smaller animals in the south (Cameron et al. 1979). Northern cotton rats are subject to more extensive draining of fat stores during the winter than southern cotton rats (Cameron et al. 1979; Campbell and Slade 1993). This is due in part for the need of northern populations of cotton rats to allocate more energy toward thermoregulation in colder winter climates than do their southern counterparts in locations with milder winters. The more stable mass observed in females compared to males over the winter months is likely the result of more careful maintenance and regeneration of these fat reserves after the breeding season. Any allocation of energy toward body growth during the winter, particularly after recouping energies associated with pregnancy and lactation, could compromise survival. In general, larger masses are not necessarily better in northern parts of the species' range, as observed in this study and other populations of cotton rats during the winter. The concentration of cotton rats at more intermediate masses suggests that animals of this size have the highest survival potential, as their masses are more easily energetically maintained.

Growth Rates

Growth rates are highly variable among different populations of cotton rats (Cameron and Spencer 1983; Slade et al. 1984; Eifler and Slade 1999). Differences in growth can be attributed to effects of the environment on cotton rats, as well as the ways in which energy is allocated by these animals in these locations (Slade et al. 1984; Derting 1997; Eifler and Slade 1999). Growth rate differences are also reflected between the sexes, and in some populations of cotton rats, these differences are solely observed at the seasonal levels (Slade et al. 1984; Eifler and Slade 1999). Animals in more seasonal, northern environments display more annual variability and faster growth than those in less seasonal and more southerly environments (Cameron and Spencer 1983; Slade et al. 1984; Eifler and Slade 1999).

In my population of cotton rats, males overall exhibited slightly, but not significantly, faster growth rates than females. Similar greater male growth rates have been reported in other studies (Meyer and Meyer 1944; McClure and Randolph 1980; Eifler and Slade 1999). Some of these observations are more apparent at the seasonal and mass class level (Slade et al. 1984). McClure and Randolph (1980) suggested that sexual differences in growth are the result of differences in energy allocation. Males have higher total ingestion rates and consume more energy because they are larger, but males use less in reproduction and can devote greater amounts of energy toward somatic growth (McClure and Randolph 1980). Since males have more available energy to allocate to growth than females, males usually have higher rates of growth. However, Cameron and Spencer (1983) reported that females grew faster than males; they could not account for the small but significant difference between the sexes. These differences were not the result of pregnancy because like many growth rate studies, including my study, pregnant females were excluded from the analysis of growth (Cameron and Spencer 1983; Slade et al. 1984; Eifler and Slade 1999).

When individual years of the study were compared, males had faster rates of growth at the yearly level, except for females in 2003. Mean growth rate for females in 2003 was higher than males in 2003 and 2004, as well as females in 2004. This is the direct result of a significantly higher rate of growth of female cotton rats in August 2003 (14.08 g/week). The large peak in female growth is the highest growth rate of the study and it is unusual when compared to growth rates observed in August 2004. It is likely that this higher rate of growth is not only confounded by undetected pregnancy, but also in this instance higher growth rates are attributed to an increase in the growth of lighter weight cotton rats being recruited into the population during this month. Although this higher rate of female growth is atypical, Slade et al. (1984) reported an even higher rate of growth for cotton rats (20.1 g/week), which also occurred over the summer.

Throughout the study, both sexes generally had positive growth, but negative and nil growth were observed in some instances (Figure 22). Positive growth was more pronounced for females, especially in the spring and early summer, as well as in late autumn. Faster rates of growth during these times are attributed to growth in association with reproduction (Eifler et al. 2003) and would likely be higher for pregnant females. In addition, increased growth could be the result of lighter weight cotton rats entering the population at these times. In the spring, warmer temperatures and an increase in the availability of food resources help to expedite the growth of young cotton rats that are coming into reproductive condition for the first time (Eifler and Slade 1999). Recently recruited, light-weight cotton rats in late autumn also contributed to increases in growth then. However, the slight negative growth of females in the month of September is also likely related to changes in body mass due to undetected pregnancy. Females will undoubtedly experience decreases in growth after parturition and they may continue to lose mass due to the high costs of lactation, which are approximately three times greater than pregnancy (Migula 1969).

Eifler and Slade (1999) also reported that weather affected growth at various times of the year. Rain was positively associated with growth in males in most seasons, but female growth was adversely affected by rain in all seasons except spring (Eifler and

Slade 1999). Spring rains trigger the growth of plants, increasing resources and in turn body growth. However, the negative and nil growth of males and females in the winters of my study were most likely the result of lower temperatures in the winter months. In populations of cotton rats in Kansas, snow cover and low winter temperatures negatively affected growth (Eifler and Slade 1998; and Eifler and Slade 1999). Especially in winter, increased energy costs associated with both thermoregulation and growth are detrimental for cotton rats. Even in warmer winters, cotton rats are susceptible to decreases in growth as a result of increased activity in order to forage for food of poor quality (Eifler and Slade 1999).

Seasonal differences in growth are more common in northern populations of cotton rats (Fleharty and Choate 1973; Layne 1974; McClure and Randolph 1980; Slade et al. 1984; Derting 1997; Eifler and Slade 1999) than in southern cotton rat populations (Cameron and Spencer 1983). In Texas, the mild climate allows for a continuous food supply all year round. Cotton rats in these locations lose a small amount of body fat during the summer and none in the winter (Cameron et al. 1979). The average growth rate in Texas populations of cotton rats is 4.1 g/week for males and 4.7 g/week for females and ranged between 0.6–6.33 g/week (Cameron and Spencer 1983). In comparison, seasonal growth in northern populations varies annually and growth is often negative or depressed in winter (Dunaway and Kaye 1961; Fleharty and Choate 1973; Swihart and Slade 1980; Slade et al. 1984; Eifler and Slade 1999). Cotton rats in northern locations are subject to more variation in temperature and resource availability (McClure and Randolph 1980), whereas southern locations do not exhibit this same variation. Slade et al. (1984) reported growth rates in Kansas populations of cotton rats ranging between -6.7–+20.1 g/week, while Eifler and Slade (1999) found growth rates to range between -0.44–+15.77 g/week. Despite its southern location, Layne (1974) also observed seasonal variation in Florida populations of cotton rats, but at a smaller magnitude compared to Kansas cotton rats (3–4 g/week). Florida cotton rats exhibited reduced growth in winter due to dry conditions, which affected plant productivity and the quality of food resources available for consumption.

Due to the more mild and moderate climate in Virginia, especially in winter, Eifler and Slade (1999) speculate that seasonal differences in growth might not be observed in such populations. However, some seasonality in growth rates was observed in my study, particularly during the winter months. Positive growth was observed during the warm seasons and decreases in growth were seen in winter (Figure 23). Overall, winter growth rates for both sexes were lower than in all other seasons. Males exhibited similar positive growth rates among the three winters, despite a somewhat higher rate in the first winter (2002-2003). Females also demonstrated similarities among growth rates in all three winters, but unlike males, positive growth was not detected in any winter season. These lower winter rates of growth are likely the result of a combination of lower temperatures and poorer quality food resources. Cotton rats are forced to allocate energies for their basic maintenance requirements, most importantly towards thermoregulation, in order to survive the winter (Eifler and Slade 1999). The lack of positive growth of overwintering females serves to further demonstrate the constraints on female energetics. Females must carefully balance their energy allocation during the breeding season and seemingly cannot contribute as much energy to body growth as males do. After the energetically demanding breeding season, females cannot afford to allocate energy to growth, but immediately begin paying the higher costs of thermoregulation at a time when food is diminishing in availability and quality.

Steady and increased growth rates in both spring and autumn for both males and females demonstrate that similar seasonal trends in environmental effects and energy use exist in this population of cotton rats. Spring females had faster rates of growth than males; however, in autumn, growth rate patterns were reversed and males had faster growth rates. In spring, positive growth reflects warming trends and increased resource availability, resulting in females resuming somatic growth as well as the increased mass of undetected pregnancies. Increases in growth may also be associated with overwintering cotton rats replenishing diminished fat reserves (Fleharty et al. 1973). Similar patterns of increased growth, as well as higher female growth, are also present in Kansas cotton rat populations in the spring (Slade et al. 1984). However, more variation in growth rate is observed in Kansas compared to Virginia populations (3.1–14.5 g/week) of cotton rats (Slade et al. 1984). In addition to warmer temperatures and greater food availability, this increase in spring growth is also the result of recruitment of light weight individuals, which have the highest rates of growth. Slade et al. (1984) suggest the rapid growth of young cotton rats is linked to increased plant productivity. Therefore, these younger cotton rats will likely attain sexual maturity more quickly and might contribute better reproductive success in the cohorts of my study.

Another large portion of growth can be attributed to gains in mass as a result of reproduction. These gains would be more pronounced for females due to increases in growth related to pregnancy. Since food resources are becoming less abundant during the autumn season, any increases in growth are likely the result of continued recruitment of lighter weight animals and the growth associated with reproduction in the second breeding pulse. The rapid growth of these individuals enables them to achieve the intermediate mass needed in order to survive the winter. Males might display faster rates of growth because more energy can be allocated to somatic body growth at the end of the breeding season, while females must recoup energy losses diverted to reproduction before the onset of winter. Hence, the lower rates of female growth during the autumn seasons in my study were likely due to the combination of mass loss as a result of parturition and the energetic stability found at more intermediate masses (Figures 23 and 24). In general, smaller cotton rats will continue to grow, if slowly, while larger animals will lose body mass and thus survivors converge on an intermediate mass to better survive the winter (Slade et al. 1984; Campbell and Slade 1993; Eifler and Slade 1999).

In comparison to the positive growth observed in both spring and autumn, both sexes had variable summer growth (Figure 23). Higher summer temperatures adversely affect growth rates in populations of cotton rats in Kansas (Eifler and Slade 1999). Similar summer temperatures are observed in Virginia (Figure 2) and most likely have the same impact on growth in this cotton rat population. At the same time, the available vegetation is changing and may be less nutritious than in the spring. Most often cotton rats alter their diets and are forced to find other food sources or deplete stored energy reserves, which might also adversely affect growth in the short-term (Fleharty and Olsen 1969; Slade et al. 1984). Despite the slight spring-to-summer decreases in growth rate for the summer of 2004, positive growth was still observed.

The extreme increase in female growth observed in the summer of 2003 is not consistent with the lower and decreased growth rates for summer females in 2004 or males in either summer season. However, the highest rates of growth for other populations of cotton rats have been observed in the summer (Slade et al. 1984). The higher rate of female growth in the summer of 2003 is likely partially confounded by undetected pregnancy, as well as the rapid growth of light weight cotton rats entering the population from the first breeding pulse of the year.

Growth rate was also analyzed seasonally at the mass class level in order to examine the contribution of growth rates from individual classes to the overall scope of growth in this population of cotton rats. Previous growth rate studies on cotton rats (Cameron and Spencer 1983; Slade et al. 1984; Eifler and Slade 1999) used slightly larger mass class intervals than those used in this study. Cameron and Spencer (1983) and Slade et al. (1984) categorized mass classes based on 30 g intervals and did not designate a mass class only for juveniles. In my study, smaller intervals (20 g) were used to account for the overall smaller size of the Virginia subspecies. Mass class 1 was composed strictly of juveniles weighing <50 grams.

In general, growth rates in the lighter mass classes (mass classes 1 and 2) were significantly faster than in the intermediate (mass classes 3-5) and heaviest mass classes (mass classes 6-7). Rapid growth of lighter and presumably younger cotton rats is also seen in other populations of cotton rats (Fleharty and Choate 1973; Cameron and Spencer 1983; Slade et al. 1984). Juvenile cotton rats are extremely precocial at birth and attain independence in 14 days (McClure and Randolph 1980). Juvenile cotton rats have high assimilation efficiencies in the early stages of life, enabling Virginia females to become fertile by 3-4 weeks of age and males by 5-6 weeks (McClure and Randolph 1980; Rose and Mitchell 1990).

Growth was similar among the intermediate mass classes, but was significantly slower than growth in the lighter mass classes. In these intermediate mass classes of slower growing animals, less variation among the seasons was observed. This trend is also present in other northern populations of cotton rats (Slade et al. 1984). Male and female cotton rats that maintain intermediate masses and growth rates have the ability to allocate energies differently because their energy budgets have costs associated with sexual behavior. For overwintering cotton rats, intermediate masses mean lower energetic costs for maintenance (on a per gram basis) than lightweight animals, despite higher costs for thermoregulation then. In my study, as well as in Kansas populations of cotton rats (Slade et al. 1984), smaller individuals typically gain mass and larger individuals lose body mass and converge into these intermediate mass classes, which presumably are more energetically efficient.

Although growth rates in mass classes 6 and 7 were similar to each other, they were significantly lower than all other mass classes and were often negative or near negative in these heavier cotton rats. Larger cotton rats have more energetic challenges supporting the costs associated with excess mass than smaller cotton rats and as a result will often lose mass in the face of environmental stresses. Nil and negative growth are likely associated with the energetic difficulties in maintaining heavier mass and the need to attain a smaller mass with its reduced energetic costs. As evident in this study, as well as other cotton rat studies (Cameron and Spencer 1983; Slade et al. 1984), the heaviest individuals were few in most seasons.

In my study, both male and female growth rates showed seasonal variation at the mass class level, particularly in the lightest and heaviest mass classes (Table 14).

Juvenile males (mass class 1) had faster rates of growth in the summer than in the autumn, while female juveniles displayed similar growth between the summer and autumn seasons. Summer and autumn growth of juvenile females were also faster than for juvenile males. Slade et al. (1984) found that male cotton rats compared to females of similar mass exhibited higher rates of growth throughout the autumn. Light females in Kansas also possessed high rates of growth during the summer, which are likely attributable to growth associated with reproduction (Eifler et al. 2003). Slade et al. (1984) also observed somewhat (but not significantly) higher rates of summer growth in lighter females than in lighter males.

During the spring and winter seasons in my study, few or no juveniles at all were observed. These small numbers and absences can be attributed to the later recruitment of juveniles from the first breeding pulse, which did not occur until in the early summer months, especially in 2003. Juveniles became more prevalent in this population in late spring and early summer rather than earlier in the spring. Therefore, no growth rates could be calculated for males in mass class 1 for spring and winter or for females in spring. Of the few juvenile females observed in the winter, growth rates were at their lowest, but still positive. This positive growth in juvenile females suggests that they are continuing to grow during the early winter in an effort to attain a higher and more survivable mass.

Among growth rates for males in mass class 2, patterns of growth were reversed in autumn and summer compared to those in mass class 1 (Table 14). Autumn growth rates were significantly higher than summer growth, which conforms to trends for lighter male cotton rats previously reported by Slade et al. (1984) during these seasons. Higher growth rates might reflect that males in mass class 2 are more actively recruited into the population in autumn than males of mass class 1. As previously mentioned, slight decreases in seasonal growth for the summer of 2004 were observed for both sexes. Increases in mass throughout the summer adversely affect growth at the mass class 2 level (Table 14). This further demonstrates that as animals gain mass there is increased difficulty in the summer maintaining higher rates of growth, which is most likely due to higher summer temperatures depressing diurnal activity and decreasing plant productivity (Slade et. al 1984; Eifler and Slade 1999). No growth rates could be calculated for spring males of mass class 2, which can be attributed to both poor and delayed recruitment of these lighter males.

Females in mass class 2 had significantly higher summer growth rates than females in any other mass class (Table 14). These growth rates were higher than those of any other mass class and confirm that the source of increased growth described in the summer of 2003 is mainly due to increased growth of lightweight cotton rats being recruited in the population and to a lesser extent growth due to undetected pregnancy. Continued growth of these females may also be attributed to the regeneration of fat reserves in preparation for the upcoming litters (McClure and Randolph 1980). Autumn growth rates were significantly higher for females in mass class 2 than winter growth rates. However, male growth in mass class 2 was higher than females for both autumn and winter. These trends correspond to patterns previously reported for lighter individuals in Kansas populations of cotton rats (Slade et al. 1984).

The lower rates of female growth found in winter for mass class 2 suggests that less energy is being expended on growth and more is being allocated to fulfill the more important energy needs of these cotton rats during the energetically demanding winters, including thermoregulation. Because of their small body size, cotton rats are already at an energetic disadvantage due to proportionately higher surface-to-volume ratios, hence, the necessity for cotton rats to devote more of their energy, particularly during the winter, in order to properly meet their thermoregulatory demands. Like males, too few females were observed during the spring to calculate growth rates, which confirms a delay in recruitment, likely due to the fact that maximum reproductive potential was not achieved by either sex until later in the spring and early summer, especially in 2003.

For growth rates of males in the intermediate mass classes (3-5), seasonal variation was present, but the finding of no significant differences among the seasons in some mass classes indicates a convergence towards similar rates of growth (Table 14). Growth rates for males in mass class 3 did not exhibit significant differences among winter, summer or autumn seasons, which supports the possibility of similar growth in animals of intermediate mass. Although no seasonal differences in growth were observed in this mass class, growth rates for males in autumn and winter were higher than summer growth rates. These growth trends were similar to those seen for males in the lighter mass classes in my study, as well as in the lighter mass classes for males in Kansas populations of cotton rats (Slade et al. 1984). Growth rates in mass class 3 could not be calculated for the spring due to small sample sizes, which coincided with the lower overall densities in this season (Table 14).

For mass class 4, males displayed significantly lower rates of growth in the winter and summer than in spring and autumn (Table 14). Similar but not significant trends were seen in mass class 3. The lower but not significantly different growth rates between winter and summer seasons suggest that extremes in environmental conditions impose similar stresses on cotton rats at these masses. Extremes in temperatures have the ability to depress growth at any mass (Slade et al. 1984; Eifler and Slade 1999) and energies in both seasons are allocated to more effectively maintain thermoregulation at both higher and lower temperatures. Spring and autumn growth was higher in mass class 4 and these higher rates of growth were likely associated with overwintering and spring-born males that are already established in the population. Males were also gaining weight in the spring as a result of improved nutrition and the growth in the autumn was associated with reproduction.

In males of mass classes 5 and 6, no overall differences in seasonal growth between these mass classes were observed (Table 14). Slade et al. (1984) also reported no distinct seasonal variation in growth rates of cotton rats at these masses. Although, in my study, slightly higher growth rates in the spring and autumn were observed in mass class 5, a higher rate of growth for mass class 6 was only seen in the spring. Any positive and higher growth in spring and autumn compared to other seasons for these mass classes was indicative of older and more established males gaining mass, as seen for males in mass class 4. However, males in these higher masses classes more often displayed almost zero and negative growth during all seasons. This becomes evident for summer and autumn males in mass class 6, for which growth is near zero or negative (Table 14). Negative rates of growth in larger animals are also observed in Kansas populations of cotton rats (Slade et al. 1984; and Eifler and Slade 1999). Negative growth in the summer is likely due to depressed diurnal activity to avoid thermal stresses during the hot and dry days. The higher summer temperatures may decrease growth because larger animals have more difficulty dumping excess heat than smaller animals (Eifler and Slade 1999) and lower masses would be less energetically demanding. This could also account for some of the nil and negative growth of larger cotton rats observed in the winter in that nocturnal activities are suppressed in order to avoid the stress of cold nights. In addition, and to a lesser extent, negative growth may also reflect decreases in nutritious plant foods during these seasons, which are not sufficient to support the daily energy requirements of these larger animals. However, this cannot be confirmed in my study without the use of vegetative and diet analysis.

Of the seasonal growth rates available for analysis in mass class 7 (Table 14), rates of growth in the summer and autumn continue the trend for heavier masses to experience both asymptotic and negative growth. Due to their larger body size, heavier cotton rats often have difficulty simultaneously supporting such high masses and supporting their daily energetic needs, which results in this nil and negative growth. Cotton rats of this heaviest mass class were not observed in winter and only one growth rate could be calculated in the spring. Therefore, based on the overall low numbers of individuals in mass classes 6 and 7, the attainment of higher masses does not lead to longer lives.

Female growth of the intermediate mass classes also exhibited seasonal variation in growth, but unlike males, similar rates of growth among mass classes were only present in certain seasons (Table 14). For mass class 3, positive growth rates for females were similar between spring and autumn, while winter growth was significantly lower. These positive rates of growth in spring are likely the result of increased growth of females that have survived the winter and are gaining mass due to increased availability of resources and increased fat reserves associated with reproduction (Fleharty et al. 1973; Eifler and Slade 1999). In the autumn, positive growth might be a consequence of animals in mass class 3 allocating energy to a second bout of reproduction before winter and the cessation of reproduction (Eifler et al. 2003). However, as seen in my study, any attempt to reproduce in the autumn months severely compromises chances of overwinter survival. Therefore, females may exhibit positive growth to reach more intermediate masses, which presumably are more energetically efficient and contribute to their survival over the winter.

Female cotton rats in mass classes 4-6 had slightly different growth trends than those in mass class 3 (Table 14). Spring and summer growth rates were significantly higher than growth in the autumn and winter, which were either nil or negative in these mass classes. In spring and summer, not only are overwintering females growing at a rapid rate in combination with improved nutrition, but lightweight recruits entering the population are also growing at a fast pace. These smaller animals are expending huge amounts of energy on growth to mostly likely quickly achieve reproductive maturity and increase their chances for reproductive success (Eifler et al. 2003). The much slower and negative growth observed in autumn and winter indicates that females in mass classes 4-6 are allocating relatively less energy to growth during these times. Females do not have positive growth over the winter months, when the costs of thermoregulation are exceedingly high. The lack of available resources during winter makes the promotion of growth energetically almost impossible, especially when females are recouping energies from reproduction in the autumn. It would seem that lower overall autumnal growth in these larger individuals is consistent with trends that less energy is being used for growth.

Growth associated with reproduction in these higher mass classes is also becoming less prevalent.

However, in contrast to female growth, males in mass classes 4-6 maintain relatively higher rates of growth during the winter. The necessity to conserve and replenish energies from autumnal reproduction is less severe in males than in females. Males might be able to divert small amounts of energy toward growth in the early winter. In my study, male growth was positive in mass classes 4-6, but began to decrease with increasing body mass, trends also observed in females. These patterns suggest that the lighter mass classes have the ability to continue to grow in the late autumn and early winter in order to reach more energetically efficient masses, which potentially facilitate higher rates of overwinter survival. Kansas populations of cotton rats show similar trends in growth in that smaller individuals continue to grow, while larger individuals lose mass during the winter (Slade et al. 1984; Campbell and Slade 1993; Eifler and Slade 1999). These animals will typically converge on a more intermediate mass throughout the winter, which is a more energetically adaptive mass to maintain. The fact that no female growth rates could be calculated in mass class 7 for any season shows that the necessary energies in these higher masses are extremely difficult to sustain and are often associated with heavier pregnant females excluded from this analysis. The few female cotton rats in this mass class perhaps indicate that these masses are not energetically adaptive, or females with their low rates of growth in the heavier mass classes simply do not live long enough to enter mass class 7 in large numbers.

Seasonal growth rates per mass class further illustrate that seasonal as well as sexual differences in growth were present in this Virginia population of cotton rats

(Figure 24). The mean growth per week for the entire study (-6.5–+21.33 g/week) was comparable to growth rates observed in other northern populations of cotton rats (-6.7–+20.1 g/week, Slade et al. 1984; and -0.44–+15.77 g/week, Eifler and Slade 1999). In my study, the highest rates of growth were detected in the summer for both sexes, and as previously mentioned, were associated with increased growth of lighter mass class recruits entering the population and into reproduction. These individuals are growing a rapid rate to ensure greater reproductive success by attaining reproductive maturity at a much younger age (Eifler et al. 2003) and in Virginia at a lower body mass (Rose and Mitchell 1990). Slade et al. (1984) also reported that growth rates were highest during the summer season. With the exception of summer in the current study, seasonal growth rates never exceeded 10 g/week and negative growth was typical in the heavier mass classes.

Males exhibited higher rates of growth in the autumn and winter than females, which is likely due to the fact that males can allocate their energies differently than females during these seasons (Figure 24). One way males reduce metabolic costs is by regressing their testes to 1% of summer mass. Accessory organs (seminal vesicles and perineal gland) shrink similar amounts, resulting in greatly lower metabolic costs among non-breeding males in winter (Rose and Mitchell 1990). After the energetically stressful summer and autumn breeding seasons, females need to concentrate on conserving energy and replenishing depleted fat reserves before the onset of winter. Energies diverted toward maintaining growth may compromise chances of overwinter survival in females. In contrast, males do not have to manage their budgets in the same way and can afford to maintain higher rates of positive growth over the winter. However, positive and the highest rates of winter growth were observed in mass class 1, where the last of the lightest weight recruits were rapidly growing in early December (Figure 24). Overall, winter patterns of growth were unchanged, perhaps to compensate for increased environmental stress and the higher energetic demands of winter. Despite the slight decrease in autumn growth compared to the spring and summer, the lightest and intermediate mass classes maintained positive growth. However, for the heaviest mass classes of both sexes (6-7), nil and negative growth was observed during both the autumn and winter, which is likely due to the inability of these larger cotton rats to meet the energetic demands associated with these higher masses (Figure 24). These heaviest animals are also losing mass and thereby dropping into lower mass classes in order to maintain the lower energetic demands of animals at intermediate body sizes, and others are disappearing as their numbers are diminished.

Female growth had the opposite seasonal trends to males, exhibiting slightly higher growth in spring and summer than males (Figure 24). Higher female growth in these seasons was likely the result of increased growth due to reproduction. Not only were overwintering females (mass classes 3-4) growing in response to increased resource availability in the spring in preparation for the first birth pulse, but lightweight cotton rats (mass classes 1-2) were also growing at a rapid rate to attain reproductive maturity and to promote their greater reproductive success (Eifler et al. 2003). Positive and stable rates of growth for both sexes were observed in both spring and summer in the lightest and intermediate mass classes (1-4). However, near nil growth was observed in the heaviest mass classes (6-7), which is likely the result of these larger animals not being able to effectively maintain their body temperatures during times of excessive heat (Eifler and

Slade 1999) and would be potentially detrimental to survival. Consequently, larger cotton rats will have nil growth or losses in body mass to achieve smaller and more energetically manageable masses. In addition, these slower and negative growth rates indicate a reallocation of energies away from growth and more towards thermoregulation.

Growth trajectories of select cotton rat individuals with long capture histories serve to strengthen overall growth trends seen in the analyses of monthly and seasonal data. Male growth trajectories confirm that positive growth of lighter weight individuals is possible over the winter months (Figure 25). However, male cotton rats in these same mass classes also can lose mass during the winter. Negative growth of some individuals with heavier masses was also visible in both winters of 2003-2004 and 2004-2005. Some males had positive growth at all times of the year. Growth trajectories also showed that males can attain masses in the 180+ g range, with the largest male being 188 g. Males in Kansas populations of cotton rats attained even heavier masses (Slade et al. 1984).

Growth trajectories for females showed that females were more conservative in their growth patterns compared to males, particularly over the winter months (Figure 25). In contrast to the more pronounced positive growth of male individuals during the winter, females had either nil or negative growth for all masses in each winter season. These trends confirm seasonal patterns of growth previously seen for overwintering females. In general, females maintained masses in the intermediate mass class range (mass classes 3-4), but the occasional increase into higher mass classes was probably the result of pregnancy. At least 20 pregnant females attained masses in excess of >150 g; the maximum weight at pregnancy was recorded at 188 g, which was comparable to the heaviest scrotal male observed in my study. Females quickly lose mass associated with pregnancy and return to pre-pregnancy masses. Due to the higher energetic demands experienced in the heavy mass classes, it is unlikely that females are able to sustain such high masses for extended periods of time without consequence. Like males in my study, female mass never surpassed 200 g, which has been observed in pregnant females in Kansas populations of cotton rats (Slade et al. 1984). This is not surprising, considering that Virginia females have much lower overall mean mass than females in Kansas (Derting 1997).

It is also evident from these individual growth trajectories that summer-born individuals have higher positive growth than autumn-born individuals (Figure 27). Slade et al., (1984) found that individuals born in summer grew rapidly enough to reach sexual maturity in less than 2 months (ca. 60 g) in Kansas populations. Kansas cotton rats born in the autumn grew more slowly than summer cotton rats, resulting in these 60-80 g individuals overwintering without the opportunity to reproduce (Slade et al. 1984). Virginia juveniles had similar growth trends and were most likely the result of similar seasonal environmental and energetic stresses in both Kansas and Virginia due to their northern locations.

In addition, autumn-born animals had better overwinter survival than those individuals born in summer (Figure 27). Summer-born individuals in both sexes were generally not seen at the end of winter. This corresponds with the trend that summer-born individuals, particularly females that reproduce before the end of the breeding season, are not likely to survive the winter in Virginia. However, one female born in August of 2003 survived into the spring, but based on its continuous stable winter mass, this female did not reproduce in the autumn. On the other hand, autumn-born cotton rats that forego reproducing before the onset of winter maintain lower masses and have a higher probability of surviving until spring. These autumn-born survivors rapidly gain mass in spring due to somatic growth and increases in gonadal and accessory gland masses in males and pregnancy in females. Therefore, not only is it beneficial to maintain an intermediate mass over the winter months, but overwinter survival is dependent on whether or not additional energies are expended on reproduction at the end of the breeding season.

Survival

Survivorship in cotton rats is not as well documented as other aspects of life history, such as mean mass and growth. While many have speculated on the possible factors that affect survival in cotton rats (Sauer 1985; Swihart and Slade 1985; Langley and Shure 1988; Doonan and Slade 1995; Eifler and Slade 1999), very few have conducted survival studies on this species. Of the survival studies reported for populations of cotton rats, the majority have been for northern portions of the species range (Campbell and Slade 1993; Reed and Slade 2006). In Virginia, speculations regarding overwinter survival of reproductive females has been reported (Bergstrom and Rose 2004), but monthly and seasonal survivorship in this region had not been previously investigated. The mark-and-recapture efforts in my study have allowed for seasonal patterns and overall survivorship in Virginia populations of cotton rats to be explored.

Since cotton rats of juvenile mass (< 50 g) might be more susceptible to environmental pressures and energy stresses than larger cotton rats (Campbell and Slade 1993), the possibility for decreased survival of these animals was examined. Juvenile cotton rats have been known to influence the outcome of growth rate studies, hence their exclusion from growth analysis in the current study and other studies (Cameron and Spencer 1983; Slade et al. 1984; Eifler and Slade 1999). However in regards to survival in my study, juveniles and adults of both sexes did not exhibit any significant differences (Figure 28). Thus, for further analyses these age classes were combined to strengthen the survival rate results.

Even though transients were only observed once, these animals were included in the survival analyses. Although it is not known whether these transients die or emigrate off the grid, they were still an important factor to survival because they can potentially affect the dynamics of the population. The Jolly-Seber approach accounts for both of these possibilities and is a good estimator of survival probabilities in this regard (Williams et al. 2002). The exclusion of transient animals from these analyses failed to produce any meaningful results. Previous survival studies on Kansas cotton rats have used both transients and residents in their analyses (Sauer and Slade 1985; Campbell and Slade 1995). However, Doonan and Slade (1995) conducted survival analyses using only residents and found lower rates of winter survival. Therefore, to obtain an accurate picture of survival, particularly in the winter, the inclusion of all animals in the calculations of survival in my study was necessary.

No significant differences were detected in male and female survival throughout the study. Mean rates of survival were slightly higher for females than males, but both sexes displayed similar patterns of monthly survival (Figure 29). Reed and Slade (2006) also reported that survival between the sexes in Kansas populations of cotton rats was similar throughout most of the year. However, survival of males and females has the potential to differ as a result of sex-specific mortality factors, such as mass-related sexual dimorphism and the reproductive efforts of females (Reed and Slade 2006). Female survival might also be higher than males due to the greater mobility and larger home ranges observed in males (Goertz 1964; Petersen 1973; Cameron and Spencer 1981; Swihart and Slade 1983), which could lead to decreased survival at certain times of the year.

In my study, both sexes had occasional differences in monthly survival, but similar trends for their survival rates were more common. Males and females exhibited the lowest rates of survival during the winter and summer months, months with extreme temperature and weather conditions, which have the potential to adversely affect survival. Cotton rats may experience difficulties with thermoregulation and balancing their energy budgets in times of extreme heat and cold. The increased energy demands during severe winters can lead to low winter survivorship (Campbell and Slade 1993). Over the winter months, reduced food availability and suitable cover may directly reduce overwinter survival (Swihart and Slade 1985; Langley and Shure 1988). The decreases in survival observed during the summer were likely associated with increased metabolic costs due to reproduction, as well as changes in available food resources in these months. The vegetation is less nutritious during the summer than in the spring and cotton rats often have to alter their diets in order to meet their energy demands (Fleharty and Olsen 1969; Kincaid and Cameron 1982; Slade et al. 1984). However, the changes in cotton rat diets might not be enough to support the higher metabolic demands of reproductive cotton rats, particularly for females, and the consequence is lower summer survivorship. Lower rates of summer survival may also be the result of the later entrance of juveniles into the Virginia population, as well as the disappearance of older overwintering animals.

In contrast, increased rates of survival for both sexes were observed in the spring and autumn months. The higher rates of survival in spring coincide with warmer temperatures and increased food availability. However, increases in survival in the autumn months are likely the result of recruitment of lighter, non-juvenile cotton rats entering and establishing themselves in the population. The fast life history of cotton rats allows lightweight individuals to reach reproductive maturity at a more rapid rate and most likely acts as an adaptive feature for survival. The largest influx of these lightweight cotton rats was also observed during the late spring, which had the potential to positively contribute to survival in summer.

Despite the relatively stable patterns of survival in this study, some rates of monthly survival greater than 1.00 were observed for females in March 2004 and for males in September and December 2004 (Figure 29). These abnormally high rates of survival are not an accurate representation of survival for either sex and represent small sample sizes of cotton rats in these particular months. In addition, survival estimates will tend to be less accurate towards the end of the study because the future capture histories and potential survival of these animals are not known. Although errors in survival are present in a few months, this is not enough to compromise the accuracy of survival rates for the entire study. These few discrepancies can be explained and do not negatively influence these survival rates; otherwise, significant differences would have been observed for both males and females in 2003 and 2004.

Seasonal survival patterns for both sexes confirm trends seen in monthly patterns of survival (Figure 30). Overall, females continue to have slightly higher and more stable rates of survival than males, which may be the result of smaller home ranges and the decreased mobility of females. These males may be at somewhat of a greater disadvantage than females because they expend more energy associated with increased movement (Eifler and Slade 1998). At times of high energy demands, animals are also at an increased risk of exposing themselves to predation while meeting their energetic needs (Eifler and Slade 1998). These lower rates of male survival occur in the summer and winter seasons when energy demands are high in conjunction with temperature extremes and changes in plant productivity. Despite the relatively stable rates of survival seen in females, a pronounced decrease in survival was observed in the winter of 2003-2004 at a time when environmental and energetic stresses, such as colder weather and increased energy demands for thermoregulation, were very high. In contrast to winter survival, increases in autumnal survival for both sexes were likely the result of the recruitment of lightweight cotton rats into the population, as well as reduced energetic demands in preparation for the onset of winter. Overall, it would seem that the higher energetic stress associated with pregnancy and lactation experienced by females would lead to lower rates of seasonal survival than males, but the opposite trends were observed. In this case, the increased activity and more transient tendencies exhibited by males could contribute to their overall lower rates of survival.

Since balancing energetics is a crucial element to cotton rat survival, results of my study suggest that imprudent allocation of energies at certain times of the year has the potential to adversely affect survival. The energy necessary for growth is extremely high and consumes a steadily increasing proportion of energy as cotton rats get older (McClure and Randolph 1980), even as their growth rate becomes asymptotic. In northern populations of cotton rats, growth is influenced by seasonal climate conditions and is often depressed over the winter months (Dunaway and Kaye 1961; Fleharty and Choate 1973; Swihart and Slade 1980; Slade et al. 1984; Cameron and McClure 1988; Eifler and Slade 1999). These already higher energetic demands in the northern limits of the species' range may be more influential in preventing growth in times of extreme environmental and energetic stress. In this Virginia population of cotton rats, correlation analysis did not detect significant relationships between either monthly or seasonal growth and the corresponding rates of survival for males or females. In addition, no significant correlations were found for the sexes between both monthly and seasonal growth and subsequent survival (Figures 35, 36, 37 and 38). However, comparisons of monthly growth and survival rates for both sexes showed that growth may have influenced survival at different times throughout the study (Figures 31 and 32).

Males experienced increases in survival during times of decreased growth (January and September 2003), indicative of less energy being allocated to growth, which positively contributes to survival (Figure 31). This would be particularly important over the winter months. It is evident that increased growth in the summer months had a negative impact on survival. The warmer temperatures and altered behavior during these months did not deter summer growth, but as a result, survival was lower for cotton rats. When stable rates of male growth were observed, survival also remained stable or increased, perhaps indicating that energy budgets were well-balanced at these times. Despite the fact that in most instances growth rates have some effect on survival, there was a period in the study (late autumn 2003 to mid-spring 2004) in which patterns of male growth and survival closely followed each other rather than exhibiting inverse relationships. In addition to slightly, but not significantly, lower winter temperatures in the winter of 2003-2004 compared to the other winter seasons, it is likely that some factor other than growth influenced survival during this time. In order to properly thermoregulate in response to these colder temperatures, cotton rats might expend more energy in searching for food and consequently increase their risk to predation (Eifler and Slade 1998). Thus, any additional energy allocated for basic maintenance might negatively affect survival.

Females exhibited similar but more stable patterns of survival compared to males (Figure 32). Stable periods of survival for females were more common throughout the study and coincided with both decreased and steady rates of growth. However, decreased growth in the winters of 2002-2003 and 2004-2005 seemed to influence increases in overwinter survival. Females must carefully manage their energy budgets after the energetically demanding breeding season. It is evident that females in these instances are more conservative than males in their expenditure of energy to growth during the winter months, which positively affects survival. Similar to males, increased growth in the summer months results in a slight decrease in survival. This increase in growth in August 2003 was previously attributed to the higher rates of growth associated with lightweight cotton rats entering the population at this time. Campbell and Slade (1993) also observed lower survivorship in the summer months as a result of the entry of juveniles into the population. In combination with extreme hot or cold temperatures, increased growth during times of high energetic demands may contribute to decreased survival as a result of an inability to successfully balance their energy needs, hence, the lower survivorship in the winter and summer months compared to other seasons. In addition, females are also expending more energy than males towards reproduction throughout the entire breeding season. Both the higher temperatures of summer and the additional energies needed to support pregnancy and lactation likely contribute to the decreased survival in these months. Females, like males in the winter of 2003-2004, showed parallel patterns of decreased growth and survival, but these trends persisted longer in females and were observed into the mid-summer of 2004. Thus, growth has little impact on female survival during this time and other environmental and energetic factors seemingly play a role in influencing survival.

Seasonal patterns of growth and survival rates for both males and females confirm the observed monthly trends in this population of cotton rats. Comparisons of these rates in males revealed a more definitive effect of growth on survival and continue to suggest an inverse relationship between growth and survival (Figure 33). Energies allocated to growth in the summer months may have a negative effect on survival, while reduced rates of growth seemingly result in stable and increased survival in other seasons. This trend was absent during the winter of 2003-2004 and spring of 2004 and was most likely the result of additional environmental and energetic stress associated with these specific seasons. Energies normally allocated towards growth are likely being used to overcome extra energetic stress during the winter, which would prevent increases in survival.

Females exhibited more stability in seasonal rates of growth than males and the impact on seasonal survival was less variable (Figure 34). Stable and decreased growth has a positive effect on survival in most seasons. The fact that female survival was relatively steady throughout most of the study shows that despite the additional energetic demands experienced during the breeding season, these female cotton rats appeared to be very well-adapted in this geographic region. Positive and stable rates of survival were also observed in the summer of 2003, despite the large increases in growth of female cotton rats in August 2003 (Figure 34). This trend was indicative of a moderating effect of positive survival from the other summer months of 2003. Like males, the similar patterns of seasonal growth and survival in the winter of 2003-2004 and spring 2004 showed that both sexes were being equally impacted by some factor other than growth. These cotton rats were most likely responding to some environmental factors that elicit similar energetic responses, such as a harsher winter resulting in decreased survival.

Monthly patterns of growth and subsequent survival support the inference that growth can influence survival, but in this respect a more short-term influence of growth on future survival was seen. The stable and decreased growth seen in males often results in increased rates of subsequent survival, while increased growth negatively affects survival in most instances (Figure 35). However, in contrast to comparisons of growth and survival, stable and decreased growth, particularly in the winter of 2003-2004, had a positive effect on survival in subsequent months. The cessation of growth, as well as decreased growth, during the winter months might not have an immediate impact on survival, but it is evident that longer term survival is dependent on careful allocation of energy at these times. Any energy-saving strategy over the winter months will positively contribute to overwinter survival. Similar to previous comparisons of male growth and survival, increases in male growth in early summer have negative effects on late summer survival. Although growth is not hindered in the summer months, it is evident that the high energy demands associated with the combination of growth, reproduction, and basic somatic maintenance, e.g., thermoregulation, was particularly costly during this time.

For females, comparisons of growth and subsequent survival were similar to those of males, but were more pronounced in terms of effects on future survival (Figure 36). As for males, the positive effect of stable and decreased growth on subsequent survival is likely due to the proper allocation of energies toward the more important metabolic functions. In addition to decreased subsequent survival in some summer months, these comparisons also show that rates of subsequent survival in the spring were adversely affected by increased growth rates. In these instances, decreased spring survival can be attributed to increased and higher rates of growth in the prior months. As with males, decreased rates of growth observed as early as autumn 2003 and extending into the winter of 2003-2004 have a positive effect on survival in subsequent spring months. This trend confirms the benefit of cessation of growth to increased overwinter survival, the effects of which are not immediately observed. It may also be a strong indication that individual cotton rats are losing mass and converging on an intermediate mass during the winter in order to better conserve their energies and survive the winter.

Seasonal patterns of growth and subsequent survival for both males and females closely mimicked one another throughout the first half of the study (Figures 37 and 38). Perhaps seasonal growth has less of an effect on subsequent survival at this broader scale. In this instance, growth at the seasonal level for both sexes had less impact on future survival and perhaps these larger units of time were less accurate in revealing the relationship between growth and subsequent survival. However, inverse patterns between these rates for males and females began to emerge in the latter half of the study, indicating that seasonal growth can have a lasting impact on future survival rather than no impact at all (Figures 37 and 38).

Of most interest is the positive effect of winter growth in 2003-2004 on survival in spring 2004, which was also observed at the monthly level. This trend may show that cotton rats do not allocate large amounts of energy in the winter toward growth as a necessary strategy to maintain overwinter survival. In males, it was also evident that summer continues to remain an extremely energetically stressful season for this geographic population of cotton rats. As a consequence of sustaining multiple high energy maintenance activities and dealing with warmer temperatures, males had decreased survival in the summer of 2004, perhaps in response to increased growth rates in spring 2004 (Figure 37).

Females did not exhibit this same inverse of relationship between seasonal growth and survival, which might suggest that some other factor was influencing the decreased summer survival in males. Females experience similar and high energetic demands during the breeding season, as a result of the high energetic costs associated with pregnancy and lactation. If growth were the only intrinsic factor affecting future survival, then females would show similar patterns during this summer season. The increased seasonal survival in the last two seasons of the study is the result of stability in male seasonal growth and decreased seasonal growth for females during both the summer and autumn of 2004. In contrast to males, seasonal growth in females during this latter half of the study demonstrated a more pronounced effect on subsequent seasonal survival (Figure 38). In these seasons, more moderate and decreasing rates of growth allow for reduced demand on the energetic budget of cotton rats and energies can be better allocated in order to maintain higher rates of survival.

In addition to environmental and energetic stresses influencing survival, the residency status of individual cotton rats in the population may also contribute to the observed patterns of survival. Increases in proportions of transients can account for some of the decreased rates of seasonal survival not fully explained by relationships associated with growth, particularly in males. The significant negative correlations found between seasonal proportions of transients and seasonal survival suggests that as the proportion of transients increases, seasonal survival decreases. Transients negatively contribute to survival as a result of their single observation in the study, which is either due to death or emigration. The times of the year when large numbers of transients entered the population as juveniles or older migrating adults and were never seen again perhaps coincided with times of increased movement or decreased survival. Thus, the seasons with the lowest rates of survival were influenced either directly or indirectly by increased proportions of transients. This trend was most apparent in males because males had higher numbers of transients than females (Table 4). Males had high proportions of transients in spring and summer of 2004 (49% and 39%, respectively), seasons with the lowest rates of seasonal survival (Figure 39). Hence, the spring and summer had higher numbers of transients at times when new recruits also were entering the population. Therefore, not only is survival in these seasons influenced by environmental and energetic stresses, but also by the residency status of individual cotton rats.

In contrast to the comparisons between proportions of transients and seasonal survival, no significant correlations between proportions of transients and seasonal growth were detected. Despite the fact that similar patterns of growth and the proportions of transients were observed for males (Figure 40), it is not likely that these rates influenced one another. It is more of coincidence that these patterns resemble each other because growth of individuals is based on more than one observation between successive captures. The fact that transient individuals are only observed once suggests that there would not be an effect on seasonal growth. Since male transients were more prevalent than females (Table 4), it would not be unusual for the proportions of female transients to have no impact on seasonal growth (Figure 40). Therefore, for the reasons associated with the calculation of growth rates based on multiple captures, proportions of female transients do not have any influence on seasonal growth.

Since one of the most important objectives of the study was winter survivorship, winter patterns of survival were investigated in more depth. Previous cotton rat studies have suggested that intermediate mass classes have better overwinter survival in northern populations of the species' range (Campbell and Slade 1993; Eifler and Slade 1999). These studies of seasonal survival were based on mass class (Campbell and Slade 1993; Reed and Slade 2006). However, there were not enough individuals to conduct survival analysis at the mass class level in my study. Instead, individual cotton rats from each mass class were observed from autumn into successive seasons in order to gain perspective on winter survival based on initial mass before the onset of winter (Figures 41, 42, and 43). It has been suggested that during the winter, small individuals continue to grow, medium-sized individuals remained constant in mass and larger cotton rats sometimes lose mass (Campbell and Slade 1993; Slade et al. 1984). In addition, Campbell and Slade (1993) report that cotton rats of intermediate mass (60-119 g) are better able to survive over the winter than smaller or larger individuals.

Therefore, in my study cotton rats from the autumn surviving into successive seasons can reveal better survival for individuals in certain mass classes. The higher numbers of male and female cotton rats in the lightest and intermediate mass classes that survived over the winter showed that these body masses were best adaptive to winter in Virginia (Figures 41, 42, and 43). Males and females had no distinct patterns of overwinter survival in these distributions of survival, only the fact that intermediate mass classes had better winter survival than other mass classes. However, one female individual cotton rat showed exceptional overall survival. This individual (#446, female) was present on the study grid for a total of 16 months as an adult and persisted through two winter seasons. In comparison to other populations of cotton rats, this is one of the longest periods of residence reported for this species (Odum 1955; Dunaway and Kaye 1961; Goertz 1964; Joule and Cameron 1974; Cameron 1977; Campbell and Slade 1995). Southern cotton rats have been suggested to have longer life spans than their northern counterparts (Campbell and Slade 1995). Joule and Cameron (1974) did not observe cotton rats in Texas surviving beyond 6-7 months, while Cameron (1977) later reported the longest periods of residence as 9-10 months in these same study sites. Dunaway and Kaye (1961) also observed some individuals to living 10 months in populations of cotton rats in Tennessee. Although maximum life expectancies are not specifically reported in Kansas cotton rats, average life expectancy is approximately 2 months (Campbell and Slade 1995), which is similar to average the average life spans in this study (2.6 months for males; 3.0 months for females).

In addition, in my study some surviving cotton rats were found in mass class 1 (Figure 42 and 43), but no individuals are observed in mass classes higher than mass class 3 into the spring of 2004 and 2005 or summer of 2004. Based on the results of seasonal mass class growth rates in my study, it is known that individuals in mass class 1 continued to grow over the winter months, while individuals in the larger mass classes exhibited nil and negative growth (Figure 24). Hence, it is reasonable to suggest that cotton rats in this population were also converging on intermediate mass over the winter months and it is these individuals that possess the best chances of overwinter survival. Trends of the intermediate mass classes persisting over the winter are similar to those observed in Kansas populations of cotton rats (Campbell and Slade 1993; Eifler and Slade 1999; Reed and Slade 2006). Despite the moderating oceanic climate and warmer winter weather conditions in Virginia compared to Kansas, it is interesting to observe the continued similarity in overall survival trends in the northern parts of the species' range.

CONCLUSIONS

Sigmodon hispidus remained the dominant species on the study grid throughout the study. General population trends were similar to those reported in other populations of cotton rats. The sex ratio in the tagged population was 1:1, but female bias was observed in the number of captures. The sex ratio was also season-specific, favoring higher numbers of males in the spring and summer and more females in the winter. The largest proportion of this population of cotton rats was adults, while juveniles increased in abundance in the summer and autumn months as a result of recruitment. Juveniles were almost non-existent over the winter seasons due to higher juvenile mortality and continued growth of smaller animals to attain an energetically efficient mass during these times. Patterns of residence also contributed to the dynamics of the population. Residents were more numerous than visitors and transients in both sexes. Overall, males had higher numbers of transients than females, but female residents were numerically dominant to male residents. In addition, these residency trends also fluctuated at different times of the year.

Population density in this population was similar to those observed in other northern populations of cotton rats with one single peak in increased abundance. Maximum densities (>100/ha) occurred in the autumn months and a smaller population increase was seen in the spring of 2004. This bimodality in density is more prevalent in southern distributions of the species. Densities declined in the winter months (to >30/ha), but not to the same low numbers observed in other northern populations of cotton rats. The milder Virginia winter climate might allow for more animals to persist over the winter months compared to other cotton rat populations in northern locations.

Patterns of reproduction were comparable to those of previous studies of Virginia cotton rats based on necropsied animals. Cessation of reproduction was generally observed for both males and females from October to March, which is similar to breeding patterns for other cotton rat populations in the northern limits of the species' range. However, some females remained reproductively active and were pregnant into November. Reproductive potential was not maximal until the late spring and mid-summer lulls in reproductive activity were also present. Speculations that females in Virginia that reproduce in the summer and autumn months did not survive over the winter was not confirmed because some females persisted into the spring. Other speculations about the composition of breeding females during the reproductive season were confirmed.

Slight differences observed for mean masses between Virginia populations of cotton rats, compared to other populations, were influenced more by intrinsic rather than extrinsic factors. Body masses were smaller in comparison to those reported for northern populations of cotton rats. Monthly and seasonal mean masses in this study showed that males were typically heavier than females. Increases in mean mass occurred during the spring, while lowest mean masses were observed over the winter months. Most males had positive growth in the winter, but similar to females, some had nil and negative growth. Cotton rats of more intermediate mass were dominant during the winter as a result of a convergence of smaller animals continuing to gain mass, intermediate individuals remaining the same mass and larger individuals losing mass or disappearing.

Rates of growth and survival were previously unreported for an Atlantic coast population of cotton rats. Like mean mass, males demonstrated slightly faster rates of growth than females. Seasonal variation in growth was evident in this Virginia population and the highest rates of growth were found in the spring and summer, while the lowest rates of growth were seen in the winter. Winter growth rates were typically nil and negative in both males and females, but positive growth was observed in one winter season. Rates of growth at the mass class level continued to support the trend for the adaptive value of intermediate mass. In general, lighter cotton rats typically gained mass and heavier cotton rats experienced depressed and negative growth. Growth is closely related to the annual quality of vegetation, as well as to energetic and environmental pressures imposed on populations of cotton rats. Fluctuations in growth are also influenced by recruitment of lightweight individuals and gains in mass were associated with reproduction.

Females exhibited slightly higher rates of survival than males. Seasonal differences in survival rates were also evident. Although rates of survival and growth were not correlated, decreased rates of survival were seen in winter, while stable and increased growth was observed in all other seasons. The influences on survival were similar to those thought to influence growth and a seemingly inverse relationship between the growth and survival was present. In addition, the proportions of transients in the population also had an impact on survival. Winter survival was of specific interest in this study and survival trends were similar to Kansas populations of cotton rats in that animals with more intermediate masses had better winter survival than those of smaller and larger masses.

Despite the milder and moderating oceanic climate in Virginia compared to Kansas, it is clear that these populations of cotton rats were more similar to other northern populations of cotton rats and have less in common with southern populations. The more seasonal environment at these northern limits seemingly imposes similar restrictions on these animals. However, in comparison to some other cotton rat studies, this was a relatively short term study. Therefore, it would be interesting to continue to monitor the effects of growth and survival in this area in order to see if this species continues to push farther north with global warming trends and more seasonable environmental conditions.

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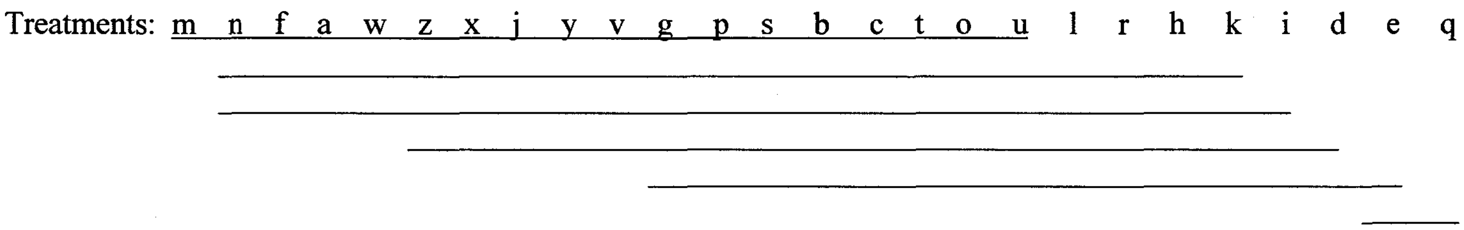
APPENDIX A

REWGF RESULTS – MEAN MASS MONTH

REGWF results on log-transformed data for the month factor from a model-I 2-factor ANOVA for mean mass (g). Significance between treatments represented by shared underlines. Mean mass values listed in table with appropriate treatment variable.


Treatments: m n f a w z x j y v g p s b c t o u l r h k i d e q

Treatments	*Means*	*Treatments*	*Means*
a – Jan ’03	1.925	n – Feb ‘04	1.885
b – Feb ’03	1.965	o –Mar ’04	1.971
c – Mar ’03	1.966	p – Apr ‘04	1.962
d – Apr ’03	2.037	q – May ’04	2.165
e – May ’03	2.109	r – Jun ’04	1.980
f – Dec ’02	1.912	s – Jul ‘ 04	1.964
g – Jul ’03	1.960	t – Aug ’04	1.970
h – Aug ’03	1.981	u – Sept ’04	1.973
i – Sept ’03	1.995	v – Oct ‘ 04	1.957
j – Oct ’03	1.953	w – Nov ’04	1.939
k – Nov ’03	1.986	x – Dec ’04	1.943
l – Dec ’03	1.975	y – Jan ’05	1.955
m – Jan ’04	1.864	z – Feb ’05	1.941

APPENDIX B

REWGF RESULTS – MEAN MASS SEX-MONTH

REGWF results on log-transformed for the sex-month interaction factor from a model-I 2-factor ANOVA for mean mass (g). Significance between treatments represented by shared underlines. Mean mass values listed in table with corresponding treatment variable.

Treatments: <u>2g 2n 2m 1r 1f 1s 2a 2v 1n 2o 2t 2f 2w 2c 2b 2x 2z 1y 1z 1a 1j 2l 1x 1w 2j 2p 2y 2h 2k 1u 1v 1h</u> 1b 1i 1k 2s 1c 2d 1l 1o 1t 2r 1g 1d 1e 1q 2q

Treatments – Males	*Means*	*Treatments – Males*	*Means*	*Treatments – Females*	*Means*	*Treatments – Females*	*Means*
1a – Jan '03	1.947	1n – Feb '04	1.917	2a – Jan '03	1.912	2o –Mar '04	1.923
1b – Feb '03	1.993	1o –Mar '04	2.014	2b – Feb '03	1.931	2p – Apr '04	1.962
1c – Mar '03	2.007	1q – May '04	2.151	2c – Mar '03	1.929	2q – May '04	2.176
1d – Apr '03	2.072	1r – Jun '04	1.887	2d – Apr '03	2.009	2r – Jun '04	2.047
1e – May '03	2.109	1s – Jul ' 04	1.906	2f – Dec '02	1.925	2s – Jul ' 04	2.005
1f – Dec '02	1.903	1t – Aug '04	2.033	2g – Jul '03	1.835	2t – Aug '04	1.924
1g – Jul '03	2.049	1u – Sept '04	1.973	2h – Aug '03	1.968	2v – Oct ' 04	1.914
1h – Aug '03	1.990	1v – Oct ' 04	1.985	2j – Oct '03	1.957	2w – Nov '04	1.926
1i – Sept '03	1.995	1w – Nov '04	1.955	2k – Nov '03	1.969	2x – Dec '04	1.934
1j – Oct '03	1.948	1x – Dec '04	1.953	2l – Dec '03	1.951	2y – Jan '05	1.968
1k – Nov '03	2.003	1y – Jan '05	1.938	2m – Jan '04	1.864	2z – b '05	1.937
1l – Dec '03	2.013	1z – Feb '05	1.946	2n – Feb '04	1.858		

APPENDIX C

REWGF RESULTS – MEAN MASS SEASON

REGWF results on the log-transformed data for the season factor from a model-I 2-factor ANOVA for mean mass (g). Significance between treatments represented by shared underlines. Mean mass values listed in table with corresponding treatment variable. Winter consisted of months (Dec-Feb), spring (Mar-May), summer (Jun-Aug) and autumn (Sept-Nov).

Treatments: a e i j g c d b f

Treatments	*Means*
a – Winter '02-'03	1.937
b – Spring '03	2.008
c – Summer '03	1.975
d – Autumn '03	1.975
e – Winter '03-'04	1.940
f – Spring '04	2.031
g – Summer '04	1.970
h – Autumn '04	1.953
i – Winter '04-'05	1.946

APPENDIX D

REWGF RESULTS – MEAN MASS SEX-SEASON

REGWF results on log-transformed data for the sex-season interaction factor from a model-I 2-factor ANOVA for mean mass (g). Significance between treatments represented by shared underlines. Mean mass values listed in table with corresponding treatment variable.

Treatments: 2e 2a 2c 2h 2i 1i 1g 1a 1h 2d 2b 1d 2g 1e 1c 2f 1b 1f

Treatments	*Means*	*Treatments*	*Means*
1a – Winter '02-'03 Males	1.952	2a – Winter '02-'03 Females	1.922
1b – Spring '03 Males	2.048	2b – Spring '03 Females	1.970
1c – Summer '03 Males	2.005	2c – Summer '03 Females	1.935
1d – Autumn '03 Males	1.982	2d – Autumn '03 Females	1.970
1e – Winter '03-'04 Males	1.986	2e – Winter '03-'04 Females	1.914
1f – Spring '04 Males	2.055	2f – Spring '04 Females	2.011
1g – Summer '04 Males	1.952	2g – Summer '04 Females	1.984
1h – Autumn '04 Males	1.956	2h – Autumn '04 Females	1.937
1i – Winter '04-'05 Males	1.947	2i – Winter '04-'05 Females	1.946

APPENDIX E

REWGF RESULTS – MEAN MASS SEX-SEASON-MASS CLASS

REGWF results on untransformed data for the sex-season-mass class interaction factor from a model-I 3-factor ANOVA for mean mass (g). Significance between treatments represented by shared underlines. Mean mass values listed in table with corresponding treatment variable. Mass class (MC) designations found in the legend of Table 10.

Treatments: 1c1 1d1 2c1 2d1 1c2 1d2 2c2 2d2 1d3 2c3 2a3 1a3 2d3 1c3 1b3 2b3 2c4 2a4 2d4 1d4 2b4 1a4 1b4 1c4 …

Treatments, continued: 2b5 2c5 1a5 1b5 2d5 1d5 2a5 1c5 1c6 1d6 2a6 2b6 1a6 1c6 1b6 2d6 2d7 2c7 1b7 1d7 1c7 2b7

Treatments – Males	*Means*	*Treatments – Males*	*Means*	*Treatments – Females*	*Means*	*Treatments – Females*	*Means*
1c1 – Summer MC 1	28.29	1a5 – Winter MC 5	118.16	2c1 – Summer MC 1	32.73	2a5 – Winter MC 5	118.81
1d1 – Autumn MC 1	31.16	1b5 – Spring MC 5	118.58	2d1 – Autumn MC 1	34.22	2b5 – Spring MC 5	115.88
1c2 – Summer MC 2	58.62	1c5 – Summer MC 5	119.40	2c2 – Summer MC 2	59.33	2c5 – Summer MC 5	118.00
1d2 – Autumn MC 2	58.63	1d5 – Autumn MC 5	118.81	2d2 – Autumn MC 2	59.34	2d5 – Autumn MC 5	118.66
1a3 – Winter MC 3	80.25	1a6 – Winter MC 6	138.58	2a3 – Winter MC 3	79.20	2a6 – Winter MC 6	135.38
1b3 – Spring MC 3	81.50	1b6 – Spring MC 6	138.50	2b3 – Spring MC 3	81.78	2b6 – Spring MC 6	136.40
1c3 – Summer MC 3	81.22	1c6 – Summer MC 6	133.25	2c3 – Summer MC 3	79.00	2c6 – Summer MC 6	137.50
1d3 – Autumn MC 3	77.33	1d6 – Autumn MC 6	135.38	2d3 – Autumn MC 3	80.60	2d6 – Autumn MC 6	140.25
1a4 – Winter MC 4	99.33	1b7 – Spring MC 7	158.43	2a4 – Winter MC 4	97.27	2b7 – Spring MC 7	167.60
1b4 – Spring MC 4	100.18	1c7 – Summer MC 7	167.30	2b4 – Spring MC 4	99.23	2c7 – Summer MC 7	157.60
1c4 – Summer MC 4	102.57	1d7 – Autumn MC 7	163.17	2c4 – Summer MC 4	97.00	2d7 – Autumn MC 7	154.57
1d4 – Autumn MC 4	99.22			2d4 – Autumn MC 4	98.73		

APPENDIX F

REWGF RESULTS – GROWTH RATE MONTH

REGWF results on untransformed data for the season factor from a model-I 2-factor ANOVA for growth rate (g/week). Significance between treatments represented by shared underlines. Mean growth rate values listed in table with corresponding treatment variable.

```
Treatments: i  e  a  g  h  b  d  f  c
            _______  _____________
               _______           ____
                  _____________
                     _____________
```

Treatments	*Means*
a – Winter ’02-’03	2.154
b – Spring ‘03	3.307
c – Summer ‘03	6.986
d – Autumn ‘03	3.772
e – Winter ’03-‘04	0.980
f – Spring ‘04	4.901
g – Summer ‘04	2.497
h – Autumn ‘04	2.931
i – Winter ’04-‘05	0.840

APPENDIX G

REWGF RESULTS – GROWTH RATE SEX-SEASON

REGWF results on untransformed data for the sex-season factor from a model-I 2-factor ANOVA for growth rate (g/week). Significance between treatments represented by shared underlines. Mean growth rate values listed in table with corresponding treatment variable.

Treatments: 2i 2e 2a 1e 1i 2h 2g 1b 1g 1a 2d 2b 1f 1d 1h 1c 2f 2c

Treatments	*Means*	*Treatments*	*Means*
1a – Winter '02-'03 Males	3.175	2a – Winter '02-'03 Females	1.171
1b – Spring '03 Males	2.925	2b – Spring '03 Females	3.728
1c – Summer '03 Males	4.441	2c – Summer '03 Females	11.121
1d – Autumn '03 Males	4.071	2d – Autumn '03 Females	3.472
1e – Winter '03-'04 Males	1.698	2e – Winter '03-'04 Females	0.620
1f – Spring '04 Males	3.899	2f – Spring '04 Females	5.624
1g – Summer '04 Males	2.997	2g – Summer '04 Females	2.155
1h – Autumn '04 Males	4.090	2h – Autumn '04 Females	1.791
1i – Winter '04-'05 Males	1.776	2i – Winter '04-'05 Females	0.252

APPENDIX H

REWGF RESULTS – GROWTH RATE MASS CLASS

REGWF results on untransformed data for the mass class factor from a model-I 3-factor ANOVA for growth rate (g/week). Significance between treatments represented by shared underlines. Mean growth rate values listed in table with corresponding treatment variable. Mass class designations are in the legend of Table 10. Bolded values signify negative growth rates.

Treatments: 7 6 5 4 3 2 1

Treatments	***Means***
1 – Mass Class 1	6.137
2 – Mass Class 2	4.631
3 – Mass Class 3	2.344
4 – Mass Class 4	2.580
5 – Mass Class 5	1.661
6 – Mass Class 6	0.039
7 – Mass Class 7	**-0.408**

APPENDIX I

REWGF RESULTS – GROWTH RATE SEX-SEASON-MASS CLASS

REGWF results on untransformed data for the sex-season-mass class interaction factor from a model-I 3-factor ANOVA for growth rate (g/week). Significance between treatments represented by shared underlines. Mean growth rate values listed in table with corresponding treatment variable. Mass class (MC) designations found in the legend of Table 10. Bolded values signify negative growth rates.

Treatments:
2d6 2a5 2a6 1d7 1d6 1c6 1c7 1c5 1c4 2a4 2a3 2a2* 2d5 1c3 1a5 1c2 2d4 1a3 1d5 1c1 1b5 1a2 2c6 2d3 2a1 1b6

*2a2 2d5 1c3 1a5 1c2 2d4 1a3 1d5 1c1 1b5 1a2 2c6 2d3 2a1 1b6 1b4 2b3 1d4 2b5 1d3 2d2 2c4 2b4 2c1 2d1 1d2 1d1 2c2

Treatments – Males	***Means***	***Treatments – Males***	***Means***	***Treatments – Females***	***Means***	***Treatments – Females***	***Means***
1a2 – Winter MC 2	2.77	1c5 – Summer MC 5	0.18	2a1 – Winter MC 1	3.30	2c4 – Summer MC 4	5.07
1a3 – Winter MC 3	2.17	1c6 – Summer MC 6	0.03	2a2 – Winter MC 2	1.16	2c6 – Summer MC 6	3.12
1a4 – Winter MC 4	1.95	1c7 – Summer MC 7	0.06	2a3 – Winter MC 3	0.95	2d1 – Autumn MC 1	6.67
1a5 – Winter MC 5	1.57	1d1 – Autumn MC 1	8.49	2a4 – Winter MC 4	0.70	2d2 – Autumn MC 2	4.89
1b4 – Spring MC 4	3.86	1d2 – Autumn MC 1	7.40	2a5 – Winter MC 5	**-2.03**	2d3 – Autumn MC 3	3.14
1b5 – Spring MC 5	2.73	1d3 – Autumn MC 1	4.85	2a6 – Winter MC 6	**-1.02**	2d4 – Autumn MC 4	1.96
1b6 – Spring MC 6	3.39	1d4 – Autumn MC 1	4.17	2b3 – Spring MC 3	4.16	2d5 – Autumn MC 5	1.23
1c1 – Summer MC 1	2.36	1d5 – Autumn MC 1	2.33	2b4 – Spring MC 4	5.82	2d6 – Autumn MC 6	**-2.77**
1c2 – Summer MC 2	1.95	1d6 – Autumn MC 1	**-0.17**	2b5 – Spring MC 5	4.19		
1c3 – Summer MC 3	1.43	1d7 – Autumn MC 1	**-0.79**	2c1 – Summer MC 1	6.63		
1c4 – Summer MC 4	0.36			2c2 – Summer MC 2	14.05		

VITA

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Relevant Experience:

Ecological field research, December 2002-July 2004; monthly field work in thesis study of the population ecology of a small mammal, *Sigmodon hispidus,* at Old Dominion University.

Graduate Research Assistant, Old Dominion University Phytoplankton Laboratory, two years.

Graduate Intern at GeoMarine, Inc., an environmental consulting firm, 6 months.

Research and lab assistant as undergraduate; Fairfield University, three years.

Published Abstracts:

Rose, R. K., and H. A. Green. 2006. An examination of seasonal growth and survival of the hispid cotton rat (*Sigmodon hispidus*) in southeastern Virginia, USA. **Hystrix,** the publication of the Italian Mammal Society.

Green, H. A., and R. K. Rose. 2005. An examination of seasonal growth and survivorship of the hispid cotton rat in southeastern Virginia. **Virginia Journal of Science.**

Green, H. A., and R. K. Rose. 2004. Temperate-zone small mammals: an examination of the hispid cotton rat in southeastern Virginia. **Virginia Journal of Science.**

Green, H. A., S. L. Ballard, D. J. Ross, and J. J. Mitnick. 2000. Methylation of homocysteine to methioine by 5-methyltetrahydrofolate. **Chemical Engineering & News Magazine.**

Presentations:

Rose, R. K., and H. A. Green. 2006. An examination of seasonal growth and survival of the hispid cotton rat (*Sigmodon hispidus*) in southeastern Virginia, USA. 10th Rodens et Spatium, International Conference of Rodent Biology, University of Parma, Parma, Italy.

Green, H. A., and R. K. Rose. 2005. An examination of seasonal growth and survivorship of the hispid cotton rat in southeastern Virginia. 83rd annual meeting of the Virginia Academy of Science, Harrisonburg.

Green, H. A., and R. K. Rose. 2004. Temperate-zone small mammals: an examination of the hispid cotton rat in southeastern Virginia. 82nd annual meeting of the Virginia Academy of Science, Virginia Commonwealth University, Richmond.

Green, H. A., S. L. Ballard, D. J. Ross, and J. J. Mitnick. 2000. Methylation of homocysteine to methionine by 5-methytetrahydrofolate. 220th meeting of the American Chemical Society, Washington (DC) Convention Center.

Green, H. A., S. L. Ballard, D. J. Ross, and J. J. Mitnick. 2000. Methylation of homocysteine to methionine by 5-methyltetrahydrofolate. Fairfield University Sigma Xi poster exposition, Fairfield, Ct.

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