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GROWTH AND SURVIVAL IN A NORTHERN POPULATION OF HISPID COTTON RATS

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Using data from a 28-month capture–mark–recapture study that included 3 winters, we compared rates of body growth and survival for a population of hispid cotton rats (*Sigmodon hispidus*) in eastern Virginia with another marginal population in eastern Kansas, and where possible, with southern populations in coastal Texas and central Florida. Patterns of seasonal growth were similar in Virginia and Kansas, being low, often near 0, in winter but moderate in other seasons, unlike the uniform seasonal growth rates in Texas. Survival rates were similar between the sexes in both Virginia and Kansas but the overall monthly survival rate in Kansas (0.75) was much higher than the means for Virginia (0.69 for females and 0.62 for males). In sum, despite mild and mostly snow-free winters in eastern Virginia, the patterns of body mass and rates of growth and survival were more similar to those of Kansas populations than to those of cotton rat populations from Texas or Florida.

Key words: cotton rat, growth rate, *Sigmodon hispidus*, survival rate

Mammals of tropical origin moving into temperate locations potentially have multiple problems, starting with shorter breeding seasons and the greater energy requirements for homeothermy in cooler environments. Small mammals, such as the hispid cotton rat (*Sigmodon hispidus*), have additional problems because their small bodies lose much heat due to high surface area-to-body-mass ratios. Further, cotton rats have poorly developed behaviors for dealing with winter, for although they sometimes build nests in burrows dug by other species (Dawson and Lang 1973; Shump 1978), they do not routinely build insulative underground nests or exhibit communal huddling in nests. Other evidence of poor ability to adapt is seen during harsh winters, when northern populations of cotton rats, such as those in eastern Kansas, exhibit decreased survival (Campbell and Slade 1993; Eifler and Slade 1998, 1999) and sometimes disappear (Sauer 1985). Even in less severe winters, tails or ears are lost to frostbite and adults lose body mass (Campbell and Slade 1993, 1995; Eifler and Slade 1998, 1999; Eifler et al. 2003; Slade et al. 1984), potentially decreasing survival and reducing population size.

The hispid cotton rat (hereafter, cotton rat) is the sole member of its genus that has extended its distribution broadly into north temperate locations. Most of the 12 species of *Sigmodon* are restricted to northern South America and Central America but 4 species range as far north as the United States (Hall 1981); 3 are restricted to locations in southern Arizona and New Mexico. Only *S. hispidus* is broadly distributed northward and eastward. During the 20th century, the distribution of cotton rats expanded into Kansas (Cockrum 1948), Nebraska (Farney 1975; Genoways and Schlitter 1966; Jones 1960), and Missouri (Easterla 1968). Its range extension northward on the East Coast is not as well documented as in the Midwest, but the cotton rat was 1st recorded in Virginia in 1940 (Patton 1941). Now widespread across southern Virginia, its movement farther northward presently is blocked by the Chesapeake Bay and its associated large rivers. Thus, the northern limit of distribution on the Atlantic Coast currently is in eastern Virginia, the location of our study.

Populations of cotton rats have been studied most extensively in the Texas coastal prairie near Houston by Cameron and his colleagues and in old fields in eastern Kansas by Slade and his colleagues. The populations in Texas probably more closely represent central populations, whereas those in Kansas are marginal. The latter location is most comparable to eastern Virginia, and both are at 37°N latitude and near or at the northern limit of distribution. However, the winters in eastern Kansas are more severe, being typical of continental climates, whereas those of eastern Virginia are moderated by close proximity to the Chesapeake Bay and the Atlantic Ocean.

The objectives of our study were to compare rates of body growth and survival of Virginia cotton rats with those of other populations, especially those from Kansas; and to learn

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whether populations in eastern Virginia more closely resemble marginal populations at the same latitude or central populations, where more moderate winters prevail.

Materials and Methods

Study location.—Our 1-ha study grid was placed in an 11.5-ha old field in southern Chesapeake, Virginia (37°50′N, 76°20′W), on property owned by The Nature Conservancy. At the start of the study in December 2002, the field was dominated by chest-high little bluestem (*Schizachyrium scoparium*), with asters (*Aster*) and softrushes (*Juncus effusus* and *J. tenuis*) common in the wettest parts of the grid. Rosettes of forb species, for example, dog fennel (*Eupatorium capillifolium*) and goldenrods (*Solidago*) and other grasses (*Pancium*), also were common, particularly in the winter. Also present were volunteer trees of loblolly pine (*Pinus taeda*), sweet gum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*). Initially, a few of the pines were taller than the little bluestem, but across the study period, pines came to dominate the grid.

Summers in the region typically are hot and winters are relatively mild. The highest monthly temperatures are in July (average 25.79°C), whereas January is the coldest month (average 4.21°C). In comparison to northeastern Kansas, monthly means are similar from April to October, but are 4–6°C warmer in winter in Virginia. In Virginia, monthly precipitation ranges from 80 mm in April and November to >140 mm in July and August, there being no identifiable dry season. In contrast, winters in Kansas are dry and summers are wet. The wettest periods are in July–September in Virginia and spring and early summer in Kansas.

Field techniques.—The 1-ha square trapping grid had 64 trap stations set at 12.5-m intervals. Fitch live traps (Rose 1994) were placed at each coordinate. Trapping was conducted for 3 consecutive days each month from December 2002 through March 2005, the period used in analysis here. In June 2003, trap disturbance briefly altered the schedule. Traps baited with a mixture of wild birdseed and sunflower seeds were checked early each morning. From April to October, it was necessary to lock the traps open in the mornings and reset them in the afternoons to prevent heat-induced mortality. Animal capture and handling procedures were followed in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Each small mammal was given a numbered ear tag, and its station of capture, body mass, sex, and reproductive information were recorded. Reproductive condition of males was assessed by testes position (descended for reproductives or abdominal for nonreproductives—McCravy and Rose 1992). For females, reproductive condition was based on 3 characteristics: perforate or nonperforate vaginal opening; size of nipples (small, medium, or large); and closed, slightly open, or open pubic symphyses. Pregnancy also was recorded when apparent.

Statistical analyses.—Model-I 2-factor analysis of variance (ANOVA) was used to detect significant differences in mean mass between the sexes and among months on log-transformed data. Ryan–Einot–Gabriel–Welsch multiple range (REGWF) tests were performed for each ANOVA in which factors were significant (SPSS, Inc. 2003). Juveniles (<50 g) were excluded from comparisons of mean masses of adults. Sample sizes were 15–20 for each sex even during periods of lowest density (35–40 during 2 brief periods) with the exception of 4 instances in which sample sizes were 5, 9, 12, and 14.

Daily growth rates were determined using the body masses of an individual from its 1st capture in 1 month to its 1st capture in the next month(s) and dividing by the number of intervening days. Juveniles and pregnant females were excluded from these analyses because of the large gains in body mass at these stages of life. Daily growth rates (g/day) were multiplied by 7 to compare with previously published weekly growth rates (e.g., Cameron and Spencer 1983; Eifler and Slade 1999; Slade et al. 1984). Mean growth rates were calculated for sex, month, season, and mass class, but small sample sizes prevented some comparisons.

Growth rates also were analyzed for sexes and seasons using a model-I 2-factor ANOVA, and a model-I 3-factor ANOVA on untransformed data examined the effects of sex, season, and mass class on growth rates. Winter was defined as December–February, spring as March–May, summer as June–August, and autumn as September–November. Further, each animal was placed into 1 of 7 mass classes based on its mass at time of capture. Mass classes were divided into 20-g intervals, except mass class 1 (<50 g). Increments of 20 g were used because of the smaller size of the Virginia subspecies in comparison to 30-g increments used in other studies of populations of cotton rats. When the factors of ANOVAs were significant, REGWF tests were performed to further evaluate the sources of significance. In addition, growth trajectories for animals with long capture histories were plotted to reveal patterns of growth among individuals.

Downloaded from the United States Geological Survey Web site, the software package *JOLLY* (Hines 1996), which uses the Jolly–Seber model, was used to determine survival rates. In addition, chi-square statistics were produced by *JOLLY* to assess estimates of survival as a suitable model for the data. The daily survival rates calculated by the Jolly–Seber model were raised to the 30th power to obtain monthly survival rates. Because 2-sample *t*-tests of monthly survival rates revealed no differences between the groups with and without juveniles, juveniles were included (SPSS, Inc. 2003). Two-sample *t*-tests evaluated monthly mean survival rates for males and females for the entire study.

For comparative analysis of survival and growth, monthly growth rates were calculated by multiplying daily growth rates by 30. Correlation analysis was conducted for months for both sexes.

Results

During the 28-month study period, 864 small mammals of 8 species were ear-tagged in 9,088 trap-nights; 513 (59.4%)
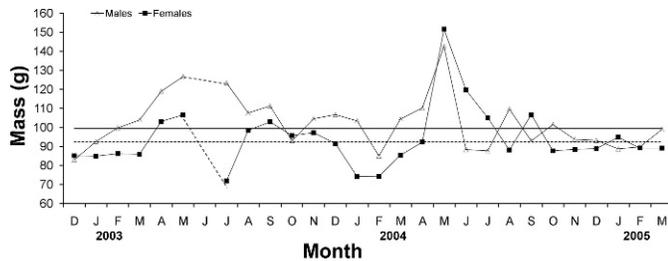
FIG. 1.—Monthly mean masses (g) for adult male and female hispid cotton rats (*Sigmodon hispidus*) for the study period. The upper solid horizontal line is the mean mass line for males and the lower line is for females. Dashed lines indicate no trapping was conducted in June 2003.

were cotton rats. For males, 248 were captured 694 times and 265 females were captured 874 times. Meadow voles (*Microtus pennsylvanicus*, 15.6%) and eastern harvest mice (*Reithrodontomys humulis*, 14.9%) were continuously present throughout the study and 45 house mice (*Mus musculus*, 5.2%) were tagged, but none after May 2003. Marsh rice rats (*Oryzomys palustris*), 2 shrew species (*Cryptotis parva* and *Blarina carolinensis*), and woodland voles (*Microtus pinetorum*) comprised the remainder.

Body mass.—Adult males (99.5 g $\pm$ 1.33 *SE*; $n = 466$) were significantly heavier ($F = 7.451$, *d.f.* = 1, 958, $P = 0.006$) than adult females (92.2 $\pm$ 1.13 g; $n = 522$). Mean masses increased steadily from January to May for males, but less quickly for females (Fig. 1). Mean mass of females changed little from October through March except for a slight decrease in mean mass from January to February 2004. Additional increases in mean mass for both sexes were observed during June and July and the highest mean masses were seen in May 2004 (142 g for males and 152 g for females).

Our analysis using a model-I 2-factor ANOVA produced a significant sex–month interaction for body mass ($F = 2.046$, *d.f.* = 22, 958, $P = 0.003$), indicating that mean body mass for each sex was not significantly different in all months. Despite no significant differences in mean mass for winter months, based on REGWF tests, slight graphical variations in mean masses were observed in all 3 winters (Fig. 1). Significant differences in mass also were observed in other months ($F = 4.975$, *d.f.* = 25, 958, $P = 0.001$).

Growth rates.—Mean growth rate per week for adult males, 3.2 g/week $\pm$ 0.262 *SE* ($n = 335$), was slightly greater than for nonpregnant females across the study (2.12 $\pm$ 0.21 g/week, $n = 396$; $F = 0.07$, *d.f.* = 1, 729, $P = 0.79$). Growth rates varied over the course of the year (Fig. 2), with those of males being greater than those of females in 15 months, compared to 7 months when rates were higher for females. Higher growth rates for females occurred mostly in spring.

Significant differences were found 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, $P = 0.001$) using a model-I 2-factor ANOVA because not all growth rates for each sex were significantly different in all seasons. REGWF tests on the sex–season interaction showed that growth rates of
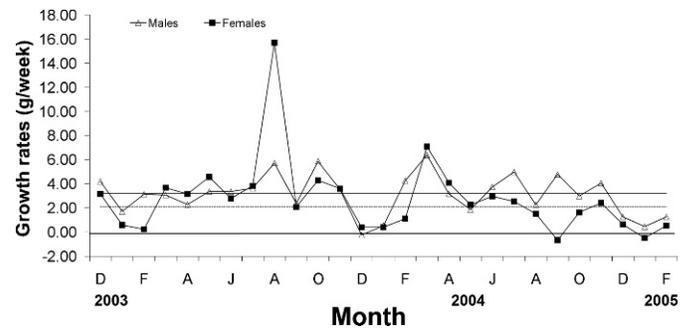
FIG. 2.—Monthly mean growth rates (g/week) for male and female hispid cotton rats (*Sigmodon hispidus*) for the study period. Juveniles and obviously pregnant females were excluded from this analysis. The horizontal solid and dashed lines represent mean growth rates for males and females, respectively.

males in both autumns were significantly higher than those of the last 2 winters. Growth rates of females in spring 2004 were significantly higher than those of all 3 winters and summer 2004; the highest growth rates were seen in summer of 2003.

A model-I 3-factor ANOVA also was performed and because of inadequate sample sizes for some mass classes, only growth rates for 281 males and 384 females were used. Significant differences were observed for the interaction among sex, season, and mass class ($F = 2.43$, *d.f.* = 7, 657, $P = 0.018$). REGWF tests, used to examine sex–season–mass class interactions, revealed autumn growth rates for mass class 1 males to be significantly lower than summer growth rates, but growth rates for males in mass class 2 in autumn were significantly higher than those in summer and winter. Growth rates for males in mass class 4 were significantly higher in both spring and autumn than in winter and summer. REGWF tests for females showed that growth rates in mass class 1 in summer and autumn were significantly higher than winter growth rates. For mass class 2, growth rates of females in summer were significantly higher than for any other mass class for either sex, whereas autumn growth rates were significantly higher than those of winter. Females in mass class 3 possessed the highest growth rates of the study, with significantly higher growth in spring and autumn than in winter. Similar growth patterns also were observed for heavier females. Females in mass class 4 exhibited spring and summer growth significantly higher than in winter and autumn, and growth rates for females in mass class 5 in spring and for mass class 6 in summer were significantly higher than those in autumn and winter. Overall, the highest seasonal growth rates for both sexes were observed in summer. Growth rates in other seasons never exceeded 10 g/week and negative growth often characterized the heaviest mass classes (Fig. 3).

Growth trajectories were produced for individual cotton rats with long capture histories, using mass values of successive months of capture. For months with gaps in the trapping record, mean mass was determined by interpolation. Growth trajectories of males confirmed positive winter growth trends for the winters of 2002–2003 and 2004–2005, but no or negative growth in 2003–2004 (Fig. 4). For females, growth
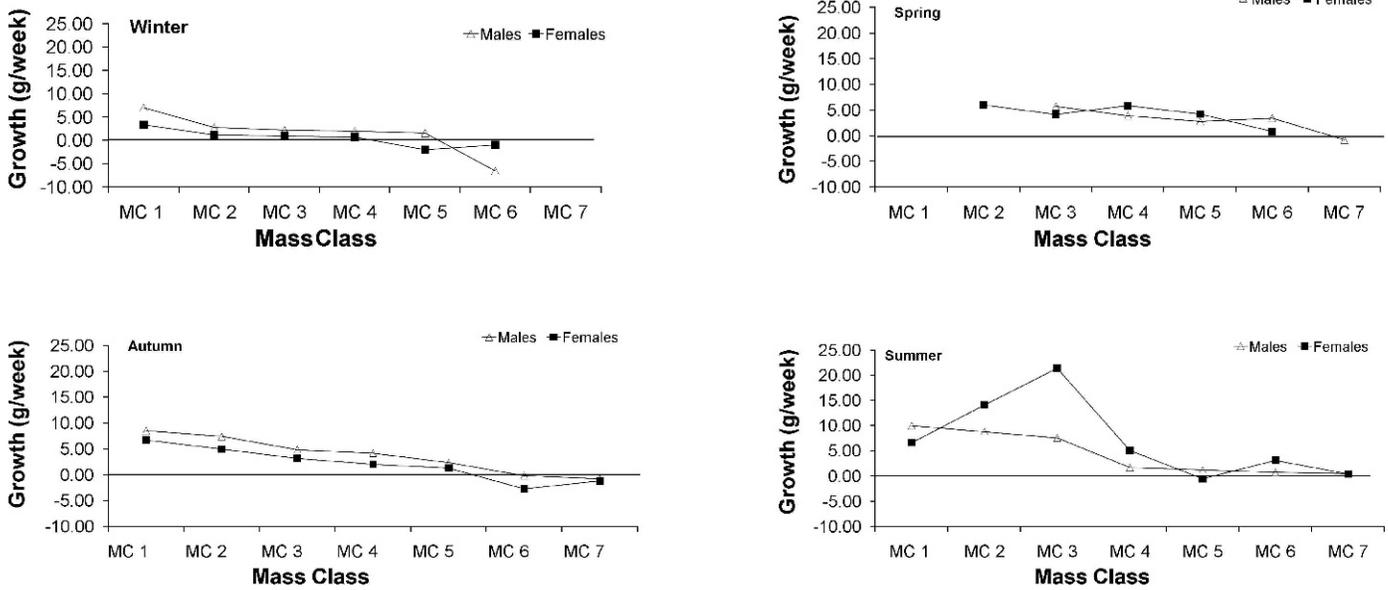
FIG. 3.—Mean growth rates (g/week) for all seasons and years combined for male and female hispid cotton rats (*Sigmodon hispidus*) per mass class (MC). The line at 0.00 represents 0 growth rate.

trajectories were consistent with the trend of no or negative growth in winter and autumn-born young animals generally had higher positive growth, especially in winter, than young born in the summer (Fig. 4).

Survival rates.—Monthly survival rates were calculated for both sexes (Fig. 5). Goodness-of-fit tests revealed that *JOLLY* results were good models for males ($\chi^2 = 24.10$, *d.f.* $= 14$, $P = 0.055$) and females ($\chi^2 = 19.61$, *d.f.* $= 16$, $P = 0.238$). Overall, females had similar rates of survival per month as males ($t = -1.133$, $P = 0.263$), 0.693 ± 0.044 *SE* and 0.624

± 0.054, respectively. Monthly survival rates fluctuated during the year, but males and females displayed similar patterns (Fig. 5). Decreases in survival rates were observed for both sexes near the ends of all 3 winters. Females had high survival rates in both autumns, when the population was expanding. Males had higher survival rates than females in 7 months, whereas females had higher rates in 15 months.

Correlation analysis showed no significant relationships between mean monthly growth rates and survival rates for males ($r = -0.080$, $n = 47$, $P > 0.05$) or for females ($r = 0.072$, $n = 47$, $P > 0.05$). We also examined the relationship between growth and survival by correlations of growth 1 month (or season) with survival the following month (or season). 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 ($r = -0.019$, $n = 46$, $P > 0.05$). Likewise, no significant relationship was

FIG. 4.—Growth trajectories showing change in mass (g) per month for A) male and B) female hispid cotton rats (*Sigmodon hispidus*) with long capture histories. Filled circles represent actual mass values and open circles and dashed lines represent interpolated mass values.
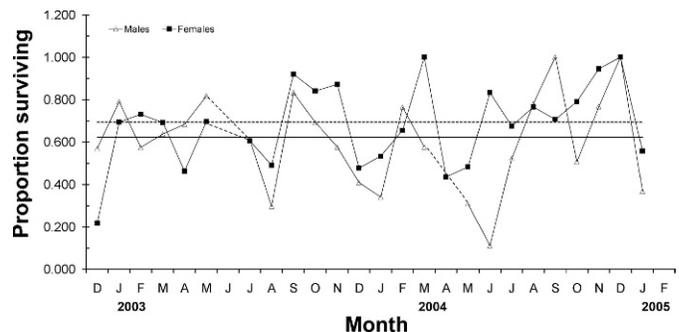
FIG. 5.—Monthly survival rates (including juveniles) for female and male hispid cotton rats (*Sigmodon hispidus*) for the study period. The upper solid horizontal line indicates the mean survival rate for females and the lower line indicates that for males. Dashed lines represent breaks in the survival data for both sexes in June 2003 and for males in April 2004, when no data were collected.

seen for seasons ($r = 0.222$, $n = 6$, $P > 0.05$ for males; $r = 0.494$, $n = 6$, $P > 0.05$ for females).

Correlation analysis also was performed on seasonal survival and proportions of transients to total density of animals in the population. Using log-transformed data among seasons, significant negative correlations for males ($r = -0.768$, $P < 0.05$) and females ($r = -0.715$, $P < 0.05$) were detected. Thus, seasonal survival was negatively affected by high proportions of transients present in the population.

Because the examination of winter survival in cotton rats was an important objective of our study, we followed cohorts from winter 2002–2003, autumn 2003, or autumn 2004. Only the persistence of these individuals in successive seasons was considered. Of the cotton rats of both sexes tagged the 1st winter, only some of the intermediate mass classes survived until autumn. All mass classes of both sexes were present in autumn of 2003, but only individuals in mass classes 1, 2, and 3 persisted into the next spring. All mass classes for both sexes also were present in the autumn of 2004, but only females and again those from classes 1–3 persisted into the 1st month of the next spring. Of these females, those from mass classes 1 and 2 were present with greater frequency. The average residency on the grid was 2.6 months for males and 3.0 months for females. The longest-resident cotton rat (rat 446) was tagged as an adult in September 2003 and last seen in January 2005; she was observed 16 months as an adult.

DISCUSSION

Previous studies of populations of cotton rats in Virginia have focused on aspects of life history (Bergstrom and Rose 2004; Rose and Mitchell 1990) other than body mass, growth, and survival. We have examined these features with the goal of comparing values from Virginia with those of another marginal population, eastern Kansas, and where possible with southern populations from coastal Texas or Florida.

We recognize that we are estimating apparent survival, as measured by repeatedly recapturing animals, and that dispersal confounds any accurate assessment of true survival. Studies of dispersal in small mammals, conducted mostly with arvicoline rodents, have produced equivocal results regarding the quality of dispersing animals. A further factor is that cotton rats are highly vagile, a feature known to investigators who have studied cotton rats on grid populations. In our study, 42.7% of tagged cotton rats were caught in only 1 month. However, 6.85% of tagged males and 5.66% of tagged females disappeared for 2–3 months and then returned to the grid, indicating that some apparent losses are due to animals moving off the grid and not attributable to mortality. We minimized predator losses of our trapped animals by occasionally removing gray foxes (*Urocyon cinereoargenteus*) and raccoons (*Procyon lotor*) from the grid.

Body mass.—Sexual dimorphism in mean body mass was evident in our study, a pattern seen in other geographic populations (Cameron and McClure 1988; Cameron and Spencer 1983; Derting 1997; Layne 1974; Petersen 1973).

Males (99.5 g) were significantly heavier than females (92.2 g), except in some autumn months (Fig. 1). Rose and Mitchell (1990) also reported the smallest sex differences in body mass for cotton rats in Virginia at the end of the breeding season.

In Kansas, decreases in mean mass, especially in the largest animals, are more common than increases in winter and cotton rats in an intermediate size class (60–119 g) prevailed by the end of winter (Campbell and Slade 1993; Slade et al. 1984). In our study, males had irregular patterns of mass change in winter (Fig. 1), with large gains in the 1st, losses in the 2nd, and static mass in the 3rd winter. Thus, males can gain mass in winter in Virginia, but decreases or static mass were just as likely. Females in Virginia lost mass in the 2nd winter, but in other winters mass was stable or nearly so. Therefore, both sexes lost mass the 2nd winter and had static mass in the 3rd, differing only in the 1st winter.

By contrast, males in Texas increased 25% in mass from 80.0 g to 100.0 g during the December–February period, whereas females increased 8% from 71.0 g to 77.0 g at that time (Cameron and Spencer 1983). The cotton rats in Florida (Layne 1974) averaged 114.0 g in February and March, and peaked in September (149.0 g), making them huge compared to those in Texas (94.7 g for males and 80.0 for females). Thus, in moderate winters, patterns of change in mass in populations in Virginia are more similar to those in Kansas than to populations in Texas or Florida. In harsh winters, populations in Kansas can go extinct (Sauer 1985), likely the result of loss of body mass before death.

Growth.—Growth rates of cotton rats are highly variable among populations, and often differ between the sexes (Cameron and Spencer 1983; Derting 1997; Eifler and Slade 1999; McClure and Randolph 1980; Meyer and Meyer 1944). In our study population, males had slightly faster growth rates (1.08 g/week) than females across the study. McClure and Randolph (1980) suggest that sexual differences in growth are the result of differences in energy allocation. In the laboratory, male cotton rats are larger and have higher total ingestion rates than females. Because they use less energy in reproduction than females, males can devote greater proportions of food energy to somatic growth than females can and this may explain growth rates of males exceeding those of females in most seasons and populations. However, in Texas, females grew slightly faster than males in all seasons (Cameron and Spencer 1983).

Overall, monthly growth rates were similar between the sexes in our study (Fig. 2), with rates just above 0 in winter months, increasing in early spring and maintaining +3–4 g/week in most other months. With 1 exception for males and 2 for females, monthly growth was positive (Fig. 2). Steady and mostly positive growth rates suggest that seasonal and environmental stressors as well as energy use were similar between the sexes. Eifler and Slade (1999) speculate that seasonal differences in growth, especially in winter, might not be observed in southerly populations due to a more moderate climate. A comparison of seasonal growth rates from coastal

TABLE 1.—Seasonal growth rates of hispid cotton rats (*Sigmodon hispidus*) for 3 distinct geographic locations in the United States: coastal Texas; Lawrence, Kansas; and Chesapeake, Virginia. Growth rates in Texas are uniform across the seasons, whereas seasonal variation in growth was present in both Kansas and Virginia.

Location	Winter growth rate (g/week)		Spring growth rate (g/week)		Summer growth rate (g/week)		Autumn growth rate (g/week)		Reference
	Males	Females	Males	Females	Males	Females	Males	Females	
Coastal Texas	4.17 ± 0.22	4.86 ± 0.26	4.36 ± 0.28	4.69 ± 0.26	4.06 ± 0.26	4.90 ± 0.30	4.08 ± 0.18	4.44 ± 0.20	Cameron and Spencer 1983
Eastern Kansas	0.30 ± 0.26	−0.44 ± 0.29	6.4 ± 0.51	6.27 ± 0.51	4.37 ± 0.41	5.02 ± 0.49	3.10 ± 0.18	1.98 ± 0.23	Eifler and Slade 1999
Eastern Virginia	2.29 ± 0.49	0.59 ± 0.18	3.21 ± 0.36	4.45 ± 0.41	3.96 ± 0.72	6.25 ± 1.39	4.08 ± 0.39	2.54 ± 0.33	Present study

Texas, eastern Kansas, and eastern Virginia (Table 1) supports this contention. The winter growth rates in Texas were the same as other seasons (all 4+ g/week), unlike in Kansas, where they hovered near 0 and were slightly positive in Virginia. Except for the faster growth rates of both sexes in spring in Kansas, the seasonal rates were remarkably similar in Kansas and Virginia, varying mostly by ±1 g/week for both sexes (Table 1). The higher spring rates in Kansas may be related to its continental climate and the high food quality in the more seasonal environment (Cameron and McClure 1988); our study site in eastern Virginia lies close to Chesapeake Bay and the Atlantic Ocean, resulting in long, cool springs after the mild winters associated with a maritime climate. In Virginia, males had higher growth rates than females overall and in autumn and winter (Table 1); the higher rates for females in spring and summer may be due in part to undetected pregnancies in these seasons.

Patterns of seasonal variation in growth also were observed at the mass-class level (Fig. 3), with substantial and mostly positive growth in all seasons except winter. In winter, the largest mass class disappeared, large cotton rats had negative growth rates, and other mass classes were just above the 0 growth line. As is typical for growth patterns in rodents and specifically in cotton rats (Meyer and Meyer 1944), growth was rapid in the lightest mass classes in all seasons and often near 0 in most seasons for the heaviest class, reflecting the rapid growth of young and the asymptotic growth of the largest, often oldest, cotton rats. Thus, the quality of animals in the population can affect the growth rate for that month or season: if the majority consists of young animals, growth rates will be high, perhaps unexpectedly high. The low growth rates in winter are likely due in part to the presence of mostly adult animals then, that is, animals whose growth rate, irrespective of food abundance or quality, is slowing or asymptotic. In eastern Virginia, because most litters are born before early October (Bergstrom and Rose 2004; Rose and Mitchell 1990), in most years young are approaching adult size by December and their growth rates are slowing. Nevertheless, some animals were in the lower mass classes even in winter (Fig. 3), the result of late litters or slow growth of some animals.

Growth trajectories of cotton rats with long capture histories (Fig. 4) supported the overall growth trends seen in the analyses of monthly and seasonal growth data. Although positive growth of cotton rats in mass classes 1–3 is possible,

others of similar size sometimes lost mass in the winter, as did heavy males in the last 2 winters. Growth trajectories also revealed that some males can attain masses >180 g, with the largest being 188 g. Males in the populations in Kansas attained even heavier masses (Slade et al. 1984). Growth trajectories showed that females were more conservative in their growth patterns than males, particularly in winter (Fig. 4). It is also clear from growth trajectories that summer-born animals have higher positive growth than autumn-born animals, reflecting that females born early can breed that autumn, whereas those born later survive the winter as lightweight animals before they breed in spring, as also happened in Kansas (Slade et al. 1984). Based on growth rates, comparisons of mass classes, and on growth trajectories, the populations in Virginia and Kansas are similar.

Survival rates.—Survival in cotton rats is not well documented except in Kansas (Campbell and Slade 1993; Reed and Slade 2006), although Layne (1974) presents information on survival rates for 3 age classes over a 1-year period in central Florida. Bergstrom and Rose (2004) speculated on survival based on monthly samples of necropsied animals from eastern Virginia, but our capture–mark–release study has allowed monthly and seasonal patterns of survival to be explored in greater depth. We observed similar monthly survival rates for females ($\bar{X}$ = 0.69) and males ($\bar{X}$ = 0.62) across our 28-month study that included 3 winters. Reed and Slade (2006) also report mean survival being similar between the sexes in Kansas, where the overall survival rate from 1973 to 1990 was 0.75 for both sexes combined (Campbell and Slade 1993), much higher than in Virginia.

Except in the 3rd winter, the seasonal pattern for females in Virginia was for survival rates to be lowest in winter and then progressively higher in later seasons. By contrast, in Kansas (Campbell and Slade 1993), survival rates were highest in winter among all mass classes. Seasonal survival rates were high in autumn in both Kansas and Virginia, especially for females in Virginia (Fig. 5). Summer survival rates usually are lower than in spring, causing some investigators (e.g., Fleharty et al. 1972; Kincaid and Cameron 1982; Slade et al. 1984) to suggest that the less nutritious vegetation of summer causes a shift in diet to meet energy demands. However, contrary to that notion, female cotton rats in eastern Virginia are consuming higher proportions of nutritious dicots in summer than in spring (R. K. Rose, pers. obs.). Low summer survival

rates may be due to the dispersal of maturing juveniles, disappearance of overwintered adults, or mortality associated with reproduction. Low rates of winter survival may be due in part to the December–March flooding on low-lying sections of our grid. Cotton rats clearly avoided the wettest parts of the grid (areas dominated by meadow voles), probably to escape the heat loss associated with wetting of their naked feet and fur.

In our study, monthly survival rates varied greatly and trends were seldom similar between the sexes (Fig. 5). Males had higher monthly survival than females in only 7 (mostly winter) of 27 months. The reasons probably relate to the reduced movements of males during the nonbreeding (winter) season, thus increasing the probabilities of being captured on the grid. In 2003, after low rates for both sexes in August, survival rates jumped to ≥0.80 in September, but then declined steadily together into early 2004. In 2004, survival rates for females were low in April, but increased steadily throughout the rest of the year. Survival rates of males often were increasing as well. The increasing survival rates for females in the last year of study, best seen in Fig. 5, contributed to the highest density of 124 individuals/ha in January 2005. Periods of lowest density (approximately 35 individuals/ha) were seen in May 2003 and February 2004; survival rates for both sexes were above average for both months.

We observed no significant correlations between rates of growth and either survival or subsequent survival, but residency pattern was important. Specifically, increases in the proportions of transients (animals caught in only 1 month) to total density were associated with decreases in seasonal survival. The significant negative correlations between seasonal proportions of transients and seasonal survival indicate that as the proportion of transients increases, survival decreases. Perhaps other investigators will evaluate the role of transients in their population studies.

The high survival rates of both sexes in the 3rd winter are puzzling. However, a contributing factor to this high winter survival may have been their consumption of pine bark in significant amounts, perhaps improving both their nutrition and survivorship. Of the >15,000 loblolly pines that invaded and came to dominate the grid in the old field, nearly two-thirds were partially girdled and 15% had been completely girdled. Not all bark eating was attributable to that winter, but we tallied >2,000 freshly (>300 completely and >1,700 partially) girdled pines during February and March 2005, the last 2 months of our study. About 9% of the winter diet consisted of pine bark (L. Walker, Old Dominion University, pers. comm.). Cotton rats start by removing the scales near the base of the tree and then eat the inner bark and cambium and often consume all bark to a height of 18 cm, as high as a cotton rat can reach.

The 3rd winter also was a season of concordance between the sexes in body mass (static), growth rates (low), and survival rates (high), conditions that led to the recruitment of a higher proportion of young animals than in the previous autumn, resulting in an estimate of density of 124 individuals/ha in January 2005. Thus, although the survival rates in Virginia were lower than those in Kansas (Campbell and Slade 1993), high densities were achieved in Virginia. Even the lowest densities in Virginia (approximately 35 individuals/ha) were much higher than the high densities achieved in coastal Texas (14 individuals/ha—Cameron 1977) or in Florida (≈20 individuals/ha—Layne 1974).

In conclusion, the patterns of body mass and rates of growth and survival of our study population in Virginia were more similar to the population studied by Slade and his colleagues in eastern Kansas than to those of southern populations, yet some differences were noted as well. In both states, cotton rats lost body mass over the winter with lower-mass animals growing slowly and those in the heaviest mass classes often disappearing. By contrast, cotton rats in Texas gained mass during the December–February period and those in Florida were very large ($\bar{X}$ = 114 g) in February and March. Growth rates were similar in Virginia and Kansas, except both sexes had higher rates in spring in Kansas. Cotton rats from both states had low growth rates compared to the seasonally uniform growth rates from Texas. Monthly survival rates were similar in both states, although Kansas had higher overall survival, 0.75 per month compared to 0.69 (females) and 0.62 (males) in Virginia. Perhaps most surprising are the high winter survival rates in eastern Kansas, with its continental winters, compared to eastern Virginia, with its maritime climate and generally mild and often snow-free winters.

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