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## COMPARATIVE LIFE HISTORIES OF GEORGIA AND VIRGINIA COTTON RATS

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Adult hispid cotton rats (*Sigmodon hispidus*) were collected from the field monthly for >2 years from populations near the northern edge of their range in Virginia and contemporaneously from south-central Georgia. Body measurements and weights were taken at capture, and after dissection embryos, corpora lutea, and placental scars were counted and measured; testes and seminal vesicles were dissected out, measured, and weighed. This allowed comparison of several life-history parameters between the populations and tests of several life-history hypotheses. The breeding season was up to 2 months longer in Georgia than in Virginia, where there was typically a 3-month or longer winter inactive period. Some reproductive activity was observed among Georgia females in all 12 calendar months, whereas pregnancies were never observed in Virginia during November–February. Average litter sizes were significantly higher in Virginia ( $5.91 \pm 1.41$ , up to 13) than in Georgia ( $5.16 \pm 1.79$ , up to 9); this difference may partly result from a higher incidence of embryo resorption and prenatal mortality in the Georgia population, primarily in the cooler 6 months of the year. Virginia rats averaged significantly smaller for both sexes, but this was likely the result of a younger age distribution. Among reproductive males and females, no body-size differences were found between populations except that pregnant females from Virginia averaged significantly longer. Fifty percent and 75% of the random sample of adult females and males, respectively, were reproductively active in Georgia, whereas only 35% and 40% were reproductively active in Virginia. Spermatogenically active males in Virginia had significantly greater relative gonadal mass than their Georgia counterparts. Overwinter survival of parous females was lower in Virginia. Virginia populations, in a more seasonal environment, displayed a more *r*-selected life history, with greater reproductive allocation, faster growth (except over winter), higher mortality, and less iteroparity.

Key words: age distribution, body size, cotton rat, latitude, life history, litter size, mortality, reproductive allocation, *Sigmodon hispidus*, survival

The hispid cotton rat (*Sigmodon hispidus*) is an abundant rodent of grassy-understory habitats throughout southeastern and south-central United States and extending southward through Panama (Hall 1981). During the late Pleistocene, its distribution was reduced southward to refugia in southern Florida and Mexico. Holocene expansion northward continues to the present day, with the frontiers currently in northern Kansas (*S. h. texianus*; Benedict et al. [2000] discuss apparent extirpation after expansion into southern Nebraska), Tennessee (*S. h. hispidus*), and southern Virginia (*S. h. virginianus*). Populations of *S. h. hispidus* from southern Georgia and northern Florida have been long established, whereas *S. h. virginianus* was 1st recorded in Virginia only in 1940 (Patton 1941; although Audubon and Bachman [1854] claimed it was present) and has

rapidly become abundant throughout the southern half of the state (Rose and Mitchell 1990; J. Cranford, pers. comm.).

Semiprecocial at birth, hispid cotton rats are fast-growing and short-lived. Gestation lasts about 27 days (Randolph et al. 1977), young leave the nest at 4–7 days, weaning occurs at 10–15 days, and they may breed at 2 months of age or less (Meyer and Meyer 1944). Average lifespans of 6 months in Georgia (where 55–76% of the population were “juveniles” weighing  $\leq 60$  g—Odum 1955) and 2–3 months in Texas, with only 2% of the females breeding more than once in Texas (Cameron and McClure 1988; although 7 of 8 females in Florida were multiparous over 1 summer [Layne 1974]), indicate that some populations of *S. hispidus* may be effectively semelparous.

Average litter sizes in *S. hispidus* range from <3 in Central America (Bowdre 1971) to 9 in northeastern Kansas (McCle-naghan and Gaines 1978) and were significantly correlated with both latitude and body length in a survey by Cameron and McClure (1988; although much of the former correlation may be explained by among-subspecies variation). Presumably, greater winter mortality farther north would select for larger

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litters as compensation, but it is not clear that interpopulational differences are genetically based. The substantially larger body size and litter size in Kansas populations of *S. hispidus*, compared to all others, is interesting, in that the litter-size differences disappear in captivity; however, neonate size of laboratory-born litters remained larger in Kansas rats, and mass and age at 1st estrus were higher (hence, longer maturation time) than in the 3 other subspecies (Derting 1997).

Field studies in Kansas have shown that larger rats have lower winter survivorship than medium-sized rats (Campbell and Slade 1993, 1995). Although some studies of laboratory-raised litters have found persistent and significant interpopulational differences in litter sizes paralleling those seen in field studies (Cameron and McClure 1988; Mattingly and McClure 1985), Derting (1997) found that the differences were insignificant in the laboratory, primarily because females descended from smaller-littered field populations produced larger litters in the laboratory. Other laboratory studies have found that maternal body size influences survival and recruitment of young when food is limited (Mattingly and McClure 1985); Campbell and Slade (1995) found no such body-size effect in the field and concluded that the overall higher recruitment in Kansas compared to Texas populations resulted from larger Kansas females weaning larger litters. Therefore, the direct effects of maternal body size or individual growth rates on litter size and recruitment are probably a more important component of selection than are attributes that might affect individual survivorship (Sauer and Slade 1985).

This study addresses whether the different lengths of habitation of *S. hispidus* in these 2 regions as well as the climatic differences across 6 degrees of latitude have led to interpopulational differences in mortality, natality, reproductive allocation, and body size. Few comparative field studies of small mammals have followed populations from 2 different regions concurrently over 1 or more years to examine seasonal trends in body size and reproductive variables. Contemporaneous long-term sampling may eliminate some of the confounding effects of weather-induced temporal variation in forage qualities or rat population densities in the 2 areas, such as El Niño–La Niña patterns (Hjelle and Glass 2000; Lima et al. 1999). Because temperatures in southeastern Virginia vary more with season than in southern Georgia (National Oceanic and Atmospheric Administration 1974; Web data Graph 1 [see “Materials and Methods”]) and colder winters mean less food is available then, we hypothesize that the breeding season is somewhat shorter in Virginia (Porter and McClure 1984) and that overwinter survivorship is somewhat lower. Both of these factors should select for a more semelparous strategy; therefore, we predict larger litters in the Virginia populations. Enhanced forage quality during the breeding season in the more seasonal environment would also argue that the Virginia rats should have larger litters, but simply as an environmental effect (Cameron and McClure 1988).

It is often hypothesized that body size should be larger in higher-latitude populations based on Bergmann’s rule (Mayr 1970) or the similar notion that increased seasonality leads to increased density-independent mortality against which larger body size is a better hedge (Zaveloff and Boyce 1988); or the

enhanced ability of larger females to bear and wean larger litters (Campbell and Slade 1995; Ralls 1976); or the hypothesis (assuming age distributions are equal) that growth rates should be faster in the area with the shorter growing season (Harvey and Read 1988). However, we hypothesize that body size in our field sample of Virginia rats will be smaller, either because, as more “*r*-strategists” (Pianka 1970) they reach reproductive maturity at a younger age and a smaller body size (Derting 1997) or because lower survivorship yields a younger age distribution.

We also hypothesize that relative gonadal mass in males will be greater in Virginia because of the shorter breeding season and enhanced sperm competition (Kenagy and Trombulak 1986). Finally, we hypothesize that accumulation of body-fat stores will be greater, especially during autumn (Cameron et al. 1979), and depletion of body-fat stores from winter through spring will be more pronounced in Virginia rats because of higher thermoregulatory and reproductive demands.

## MATERIALS AND METHODS

From October (September in Virginia) 1987 through November (December in Virginia) 1989, monthly samples of adult *S. h. hispidus* and *S. h. virginianus*, respectively, were collected in the field at numerous sites within a 30-km radius each of Valdosta, Georgia (approximately 31°N) and Norfolk, Virginia (approximately 37°N). Based on previous experience with the populations, only rats weighing  $\geq 50$  g were considered to be adults (B. J. Bergstrom, in litt.; Rose and Mitchell 1990). A goal was established of collecting 10–15 animals of each sex per month per location; actual sample sizes varied (Appendix I). Additionally, a sample of live-captured females in December 1989 in Georgia provided pregnancy data only. Collapsible Sherman (Georgia: 23 × 9 × 8 cm; H. B. Sherman Trap Co., Tallahassee, Florida) and Fitch-type (Virginia: 33 × 6 × 6 cm with 12-ounce can; laboratory made) live traps baited with sunflower seeds and grain were placed in a wide variety of grassy habitats. Livetrapped rats were quickly euthanized by overanesthetization with chloroform, weighed ( $\pm 1$  g), measured (total length, tail length, and hindfoot length,  $\pm 1$  mm), and immediately frozen for necropsy at a later time.

All reproductive organs were carefully dissected out, measured (length and width  $\pm 1$  mm) and weighed to  $\pm 0.01$  g. For males, organs weighed and measured included testes and seminal vesicles; for females, they included uteri and embryos. Total mass of these tissues for each rat was subtracted from total body mass to determine somatic body mass. To ensure consistency, both authors together performed necropsies on all animals collected during the first 2 months and cross-checked each other’s results.

If the tubules of the cauda epididymis were determined to be convoluted, it was concluded that spermatogenesis was active and the male was reproductive, regardless of whether testes were abdominal or scrotal (Jameson 1950; McCravy and Rose 1992). A female whose uterus was threadlike ( $\leq 1$  mm in breadth) and whose ovarian follicles showed no sign of corpora lutea was judged nulliparous. A female with corpora lutea and with discernible embryos but no placental scars, or only 1 set of placental scars and no embryos, was judged primiparous. One whose uterus contained recent and older placental scars or older scars plus corpora lutea in the ovaries (and embryos) was judged multiparous. Numbers of embryos and recent and old scars were recorded for each horn of the uterus. Numbers of corpora lutea were recorded for each ovary. Recent parturition was determined if the uterus was flaccid (and usually  $> 5$  mm in width) or if the pubic

**TABLE 1.**—Body-size data and 1-way ANOVA results for all adult females and males and for reproductive females and males from Georgia and Virginia populations of cotton rats. Values are mean  $\pm$  *SD* with sample size (*n*) in parentheses. Shared superscripts within columns indicate significant *F*-tests comparing like sex and reproductive status between localities; underlined superscripts indicate significance at  $P < 0.001$  and nonboldface at  $P \leq 0.02$ .

Locality, sex, status	Somatic mass (g)	Body length (mm)	Mass/length (g/mm)
Georgia			
Female: all adult	96.2 $\pm$ 24.2 (220) <sup>A</sup>	143.6 $\pm$ 18.4 (217) <sup>A</sup>	0.67 $\pm$ 0.14 (210) <sup>A</sup>
Female: pregnant	101.8 $\pm$ 23.0 (110)	142.7 $\pm$ 13.8 (108) <sup>B</sup>	0.71 $\pm$ 0.13 (108)
Male: all adult	102.2 $\pm$ 29.5 (222) <sup>C</sup>	148.0 $\pm$ 16.8 (223) <sup>C</sup>	0.69 $\pm$ 0.14 (222) <sup>C</sup>
Male: reproductive	108.8 $\pm$ 28.9 (167)	151.6 $\pm$ 16.5 (167)	0.71 $\pm$ 0.14 (166)
Virginia			
Female: all adult	87.8 $\pm$ 24.0 (234) <sup>A</sup>	139.2 $\pm$ 17.1 (236) <sup>A</sup>	0.63 $\pm$ 0.15 (214) <sup>A</sup>
Female: pregnant	101.6 $\pm$ 22.2 (82)	147.8 $\pm$ 15.8 (82) <sup>B</sup>	0.69 $\pm$ 0.18 (82)
Male: all adult	92.4 $\pm$ 26.1 (239) <sup>C</sup>	141.8 $\pm$ 16.6 (241) <sup>C</sup>	0.65 $\pm$ 0.15 (241) <sup>C</sup>
Male: reproductive	104.0 $\pm$ 26.3 (97)	150.9 $\pm$ 14.1 (97)	0.68 $\pm$ 0.14 (97)

symphysis was open. Degree of mammary development and prominence of the nipples also were recorded, as was perforation of the vagina.

The amount of subcutaneous fat, which is deposited in sequence, was recorded on a scale of 0 to 4, as follows: 0 = no fat; 1 = gonadal fat only; 2 = gonadal, axillary, and scapular fat; 3 = all the foregoing plus mesenteric fat; 4 = all the foregoing plus cutaneous fat, or obese.

In addition to performing standard *F*- and *t*-tests and simple linear correlations, we used MINITAB, Version 11.21 software (Minitab, Inc. 1996) to perform an analysis of covariance (ANCOVA, general-linear model), comparing litter sizes between Georgia and Virginia females, with somatic body mass as a covariate. After the locality–body mass interaction was found to be nonsignificant, indicating homogeneity of litter size–body mass slopes between the 2 localities, we tested for independent effects of locality and body mass and determined if there was a significant mass-specific difference in litter size between the localities (see Slade et al. 1996).

Figures displaying additional data from this study not included in this paper can be found online at <http://www.valdosta.edu/~bergstrm/sigmondon.doc>; this Web page will hereinafter be cited as “Web data.”

## RESULTS

*Climatic variability.*—South-central Georgia and southeastern Virginia have similar precipitation patterns, with peak rainy months being June and July and driest months being October–January (National Oceanic and Atmospheric Administration 1974; Web data Graph 1). However, Georgia’s pattern of seasonality of rainfall is more distinct, with greater extremes, greater overall precipitation, and an additional minor peak in March. Georgia averages 6–7°C warmer in the winter than Virginia, whereas summer temperatures are less different between the 2 regions (National Oceanic and Atmospheric Administration 1974; Web data Graph 1). Weather anomalies or departures from average temperature and precipitation for the actual 28-month period of sampling showed highly concordant patterns between the Quitman, Georgia (24 km E of Valdosta), and Norfolk, Virginia, reporting stations; in other words, unseasonable temperatures and unusual rainy or dry periods tended to occur simultaneously in both areas (monthly summaries from United States Department of Commerce, National

Oceanic and Atmospheric Administration Weekly Weather and Crop Bulletins, 1987–1989; Web data Graphs 2 and 3).

*Body size comparisons.*—As verification that our body-size threshold of 50 g constituting “adult” (contrary to Odum 1955) was appropriate, pregnant rats were captured weighing as little as 50 g (total live body mass) in Virginia and 56 g in Georgia. Males weighing as little as 53 g from both Georgia and Virginia had highly convoluted tubules of the cauda epididymes (indicating fully developed spermatogenesis—Jameson 1950).

For all adult females, Georgia rats were highly significantly heavier in somatic body mass, longer, and stockier (more mass per unit of body length) than Virginia females (Table 1). For the subsample of pregnant females, no differences were found in somatic mass or mass/length, but pregnant females from Virginia (34.7% of total) were significantly longer than pregnant females from Georgia (50% of total; Table 1). Results for all adult males mirrored those for females, with Georgia rats being highly significantly heavier in somatic mass, longer, and stockier than Virginia males (Table 1). Paralleling the trend among females, reproductive males constituted a much higher percentage of the total sample for Georgia (74.9%) than for Virginia (40.2%). For the subsample of reproductive males, no differences were found in body-size variables between the populations (Table 1).

Monthly variation in somatic body mass (Fig. 1) and head and body length (Web data Graphs 4 and 5) showed roughly parallel trends between the populations for both males and females, with longer and heavier rats appearing in the summer months and smaller rats in the winter months; this seasonal trend was more pronounced for both sexes in both populations during the 2nd year of the study than during the 1st.

*Pregnancy rates and litter sizes.*—During the 1st year of the study, both populations displayed a 5-month winter cessation of pregnancies (November–March), whereas, during the 2nd year of the study, the Georgia population displayed only a 3-month cessation of pregnancy (December–February), whereas the Virginia population showed 0% pregnancy for the same 5-month winter period as the 1st year (Fig. 2). Both populations showed a near-100% pregnancy rate in spring and early summer of both years and a 60–80% pregnancy rate in late

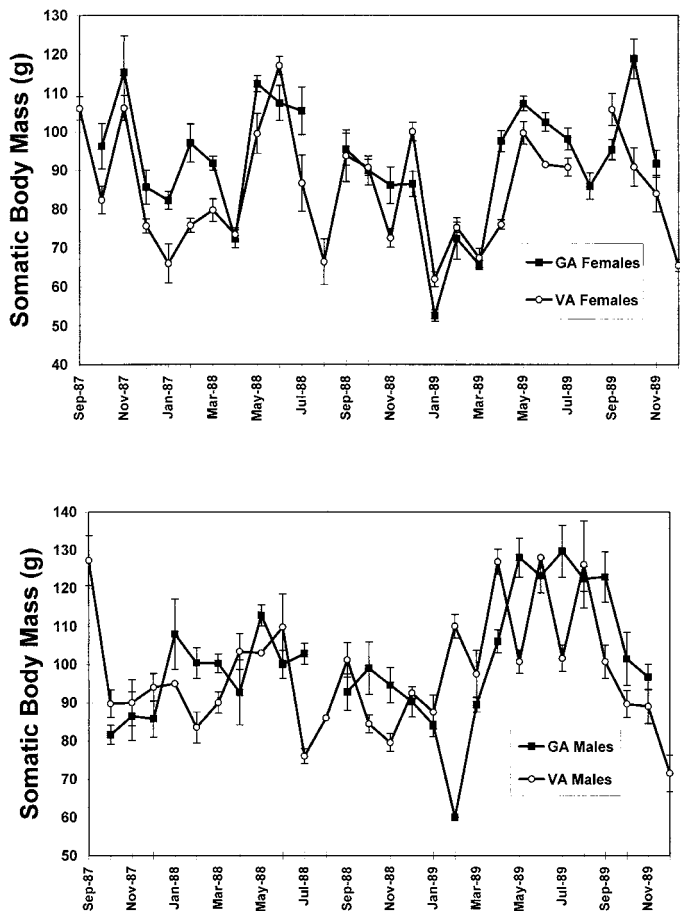


FIG. 1.—Mean somatic body mass per monthly sample of female cotton rats from Georgia (GA) and Virginia (VA) (= total live mass minus mass of uterus and ovaries; above) and mean somatic body mass per monthly sample of male cotton rats from Georgia and Virginia (= total live mass minus mass of testes and seminal vesicles; below). Bars indicate standard errors; lack of bar indicates sample size < 4.

summer and early autumn, with a conspicuous midsummer lull, when pregnancy rates were 50% or less (Fig. 2). However, during the last autumn of the study, the Virginia population showed a precipitous decline from 60% to 10% between September and November before reaching 0% in December, whereas the Georgia population remained about 80% pregnant from September to November, dropping only to 60% in December (Fig. 2).

Mean litter size (Fig. 3), as assessed by embryo counts of 110 pregnant females from Georgia, was 5.155 ( $SD \pm 1.41$ ; range 1–9), compared to 5.963 ( $\pm 1.79$ ; range 2–13) for 82 pregnant females from Virginia; this difference was highly significant ( $F = 12.24, df. = 1, 190, P = 0.001$ ). Mean numbers of corpora lutea counted within that same sample of pregnant females were 5.86 for Georgia females and 6.35 for Virginia females ( $n = 108$  and 80, respectively; some counts were inconclusive and so were not included; also, there was 1 probable case of twinning in a Georgia female and 1–3 such cases in Virginia). In fact, the between-population difference in this index of primary litter size was not significant ( $F = 3.38, df. = 1, 186, P = 0.071$ ). This implies a higher rate of prenatal mortality or embryo resorption

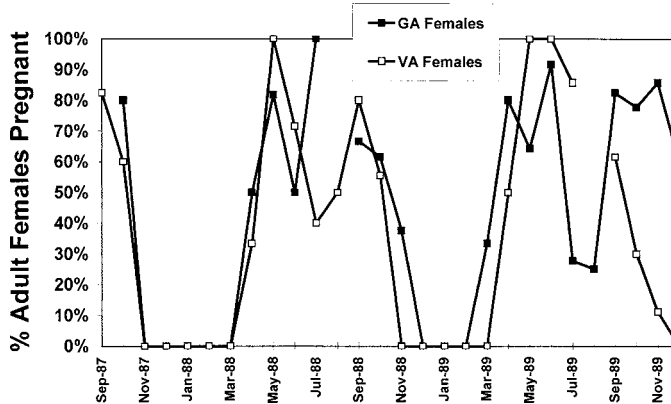


FIG. 2.—Percentage of adult female cotton rats per monthly sample in Georgia (GA) and Virginia (VA) that were pregnant (includes those with open pubic symphyses and flaccid uteri; see text).

in the Georgia population (11.8% of all corpora lutea, compared to 5.5% for Virginia). In the Georgia population—the only one with a significant proportion of pregnant females in the October–March period of both years—significantly more embryos were lost or resorbed per litter in these 6 winter months ( $\bar{X} = 1.26, n = 31$ ) than in the summer months of April–September ( $\bar{X} = 0.47, n = 77; t = 2.78, df. = 106, P = 0.0078$ ).

Nonsignificant trends of increasing litter size with increasing reproductive experience of the mother (primiparous compared to multiparous) were found in Georgia ( $F = 3.22, df. = 1, 108, P = 0.076$ ) and Virginia ( $F = 2.54, df. = 1, 80, P = 0.115$ ). ANCOVA revealed homogeneity of slopes in the relationship between litter size and somatic body mass for each of the populations (no interaction between locality and body mass; estimated common slope =  $0.0017 \pm 0.005; P = 0.741$ ); ANCOVA, including the interaction term, showed a nonsignificant locality effect ( $F = 0.19, df. = 1, 188, P = 0.660$ ) and a significant body-mass effect ( $F = 6.16, df. = 1, 188, P = 0.014$ ). Pregnant females from Virginia had larger mass-specific litter size than pregnant females from Georgia, as evidenced by the fact that subsequent independent analyses of variance (ANOVAs) (without the interaction term) found significant locality ( $F = 12.67, df. = 1, 189, P < 0.001$ ) and body-mass ( $F = 6.09, df. = 1, 189, P = 0.014$ ) effects on litter size.

Average litter sizes from April to July were somewhat higher for the Virginia population than the Georgia population (Fig. 3); in year 1 litter sizes tended to decrease throughout the breeding season in Virginia, whereas they remained high through November in the 2nd year. No particular seasonal trend in litter sizes was apparent among Georgia females.

*Male reproductive phenology and allocation.*—Males in Virginia displayed a total cessation of spermatogenesis for 4 months in the winter of the 1st year and 3 months in the winter of the 2nd year of the study, whereas Georgia males never displayed 2 consecutive months of 0% spermatogenic activity (although spermatogenic activity reached 0% in 2 nonconsecutive months and 1 month, respectively, in each of the 2 full years of the study; Fig. 4). The Georgia population remained 90–100% spermatogenically active continuously from February to

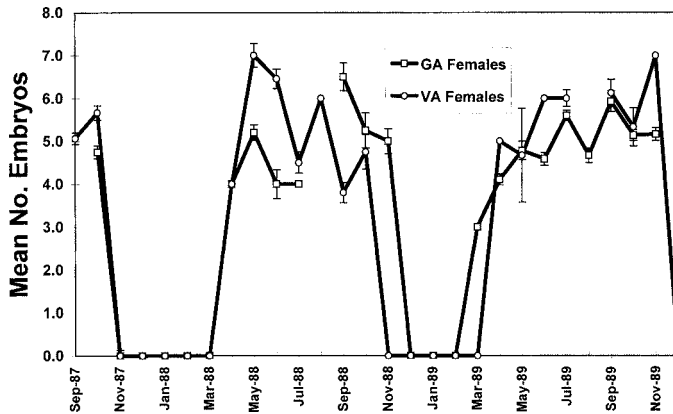


FIG. 3.—Mean number of embryos implanted in both uterine horns per monthly sample of pregnant female cotton rats from Georgia (GA) and Virginia (VA). Bars indicate standard errors; lack of bar indicates sample size < 4.

September in the 1st year and from April to September in the 2nd year, whereas the Virginia population stayed at 90–100% spermatogenic activity for shorter summer periods and less consistently, with an obvious midsummer lull in year 1 and an early autumn decline in year 2 (Fig. 4).

For all male rats, summed masses of testes and seminal vesicles as a percentage of total body mass were not significantly different (ANCOVA of summed gonadal masses with somatic body mass as a covariate;  $F = 1.38$ ,  $d.f. = 1$ , 459,  $P = 0.241$ ) between Georgia ( $1.50 \pm 1.12\%$ ,  $n = 222$ ) and Virginia ( $1.18 \pm 1.26\%$ ,  $n = 239$ ). However, for the subsample of only reproductive males (those with convoluted epididymides), Virginia males had highly and significantly greater relative gonadal mass ( $2.45 \pm 0.85\%$ ,  $n = 102$ ) than Georgia males ( $1.90 \pm 0.99\%$ ,  $n = 167$ ;  $F = 21.63$ ,  $d.f. = 1$ , 267,  $P < 0.001$ ).

*Seasonal pattern of reproductive experience in females.*—In the Georgia population, there were some multiparous females in the samples of each of the 12 calendar months, and nulliparous females composed the majority of the samples only in the months of January and February; also, primiparous females composed at least 40% of all females during 8 different calendar months (Fig. 5). In the Virginia population, no multiparous females occurred in the calendar months of January–April, and 96% of females sampled from January through March were nulliparous (only 2 of 56 were primiparous); multiparous females were observed primarily from May through October (Fig. 5).

*Mean cumulative reproductive output of females.*—Counts of placental scars in primiparous and multiparous females within the sample of pregnant females produced a surprising result, in that Virginia pregnant females had significantly more scars ( $\bar{X} = 3.07$ ,  $n = 82$ ) than Georgia pregnant females ( $\bar{X} = 1.47$ ,  $n = 109$ ;  $t = 3.10$ ,  $d.f. = 189$ ,  $P = 0.0023$ ); this was primarily due to the predominance of the scar counts of 10 and higher being found among the Virginia population (9.8% of its sample, compared to 2.7% of the Georgia sample; most of these doubtless represented 2 previous litters). However, apparently because there were significantly more parous

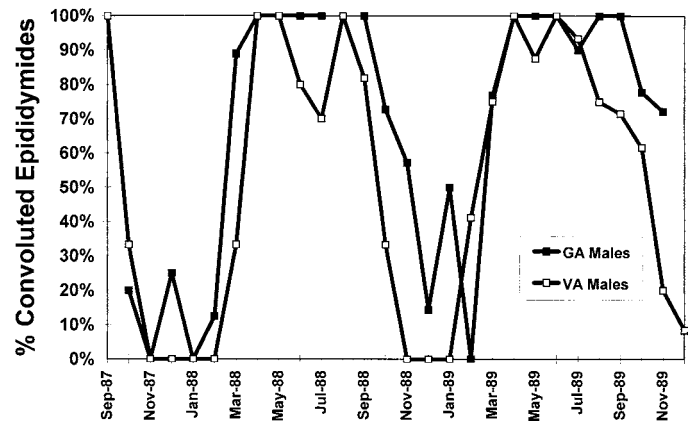


FIG. 4.—Percentage of adult male cotton rats per monthly sample from Georgia (GA) and Virginia (VA) whose proximate tubules of the cauda epididymides were classified as convoluted or highly convoluted (as opposed to looped), which is an indication of spermatogenic activity.

females among the sample of nonpregnant females (which predominantly occur in winter) in Georgia than in Virginia, all Georgia females showed a significantly higher mean number of placental scars ( $\bar{X} = 3.81$ ,  $n = 221$ ) than did all Virginia females ( $\bar{X} = 2.59$ ,  $n = 234$ ;  $t = 2.69$ ,  $d.f. = 453$ ,  $P = 0.0073$ ), and 15.8% of all Georgia females had 10 or more scars, compared to only 9.8% of Virginia females.

*Fat storage and weather.*—In the 1st year of the study, cotton rats of both sexes in both regions generally showed declining stores of subcutaneous fat over the winter and spring, from roughly November–December through May (possibly through July in the case of Georgia females; Fig. 6, top). However, in year 2, both males and females in Virginia showed a steady and sharp decline in fat stores from midwinter (December–February) through June, before rebuilding fat stores, whereas Georgia rats of both sexes maintained steady, intermediate levels of fat stores from March all the way through the breeding season (Fig. 6). Weather anomaly data indicated that January through September of this 2nd year (1989) had generally below-average temperatures in both regions, but especially so in southeastern Virginia (United States Department of Commerce, National Oceanic and Atmospheric Administration Weekly Weather and Crop Bulletins, 1989; Web data Graph 2). In winter and spring of 1988, temperature oscillations around long-term averages were highly concordant between the 2 regions.

## DISCUSSION

Litter sizes averaged almost 1 embryo larger in the Virginia populations of *S. hispidus* than in the Georgia populations; both averages fit the latitudinal trend for studies done over the range of the species (Cameron and McClure 1988). This agrees with Derting's (1997) field studies and was predicted on several principles, including both strategic (genotypic) and tactical (phenotypic or environmental) mechanisms. More northerly populations, as well as those nearer the edge of the species' range, would be expected to be more "r-selected" with

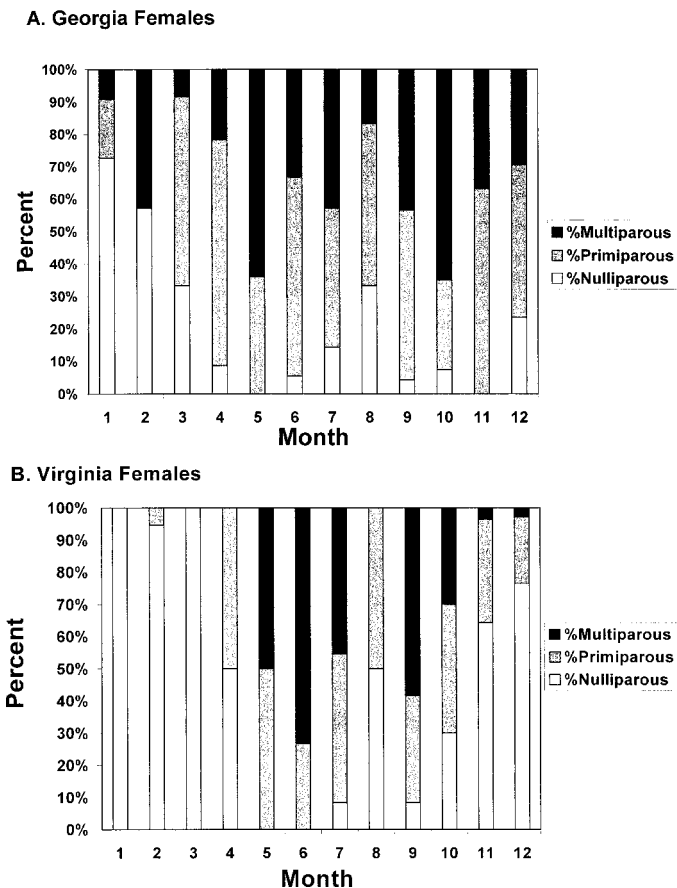


FIG. 5.—Proportion of calendar-month samples of adult female cotton rats from Georgia and Virginia that were nulliparous, primiparous, and multiparous at time of capture, as assessed by examination of the uterus and ovaries (see text for further explanation). Calendar months January (1) through December (12) combined for all years (see Appendix I for sample sizes).

a greater tendency toward semelparity, either to compensate for shorter growing seasons and harsher winters with their attendant higher mortality rates (Harvey and Read 1988), or as a part of a more “colonizer” suite of life-history parameters (Boyce 1979). Either way, greater fecundity would be the expected result for the Virginia population, because of selection pressures for productivity in harsher or more unpredictable environments (Millar 1977; Zeveloff and Boyce 1988) or less saturated habitats (Pianka 1970).

As other studies have found, this study’s significant interpopulational difference in reproductive output may be phenotypic rather than genotypic. Virginia females may realize higher natality (if not fecundity) due to the physiologically enhancing effects of higher forage quality in the more seasonal environment (Cameron and McClure 1988). Our ANCOVA results—that mass-specific litter sizes were larger in Virginia—support this scenario and the conclusion that Virginia females harness this environmental advantage to yield greater reproductive allocation compared to Georgia females. Other studies using this technique found that same-sized female cotton rats had larger litters when in higher-quality habitat

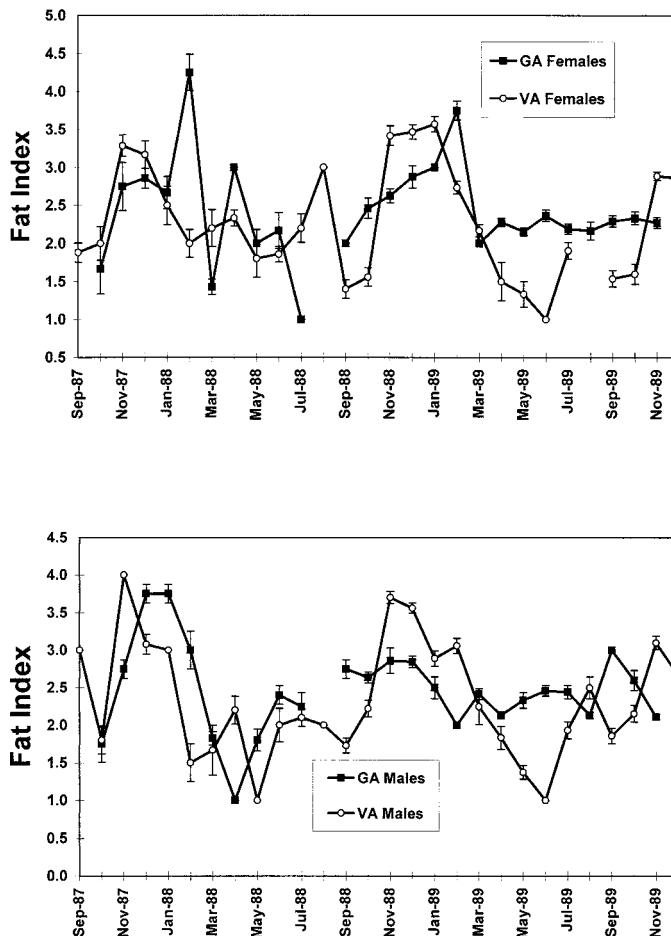


FIG. 6.—Mean fat index score for cotton rats from Georgia (GA) and Virginia (VA) per monthly sample. Index ranges from 0 to >4; females (above) and males (below). Bars indicate standard errors; lack of bar indicates sample size <4.

(Slade et al. 1996) and when given supplemental food (Campbell and Slade 1995). Cameron and Eschelmann (1996) found that diet-related differences in growth rates of cotton rats could account for substantial variation in age at 1st estrus.

The fact that the primary litter size (number of corpora lutea) was the same in the Virginia and Georgia populations yet the embryo count was significantly lower in the Georgia population implies that there is a higher prenatal mortality or embryo resorption rate in the Georgia population and further suggests that the litter-size difference between the populations is not genetically based but rather environmentally induced. This was Derting’s (1997) laboratory result when raising litters from different populations of *S. hispidus*, which showed significantly different litter sizes in field sampling. There was some indication (Fig. 2) that Virginia females maintained higher pregnancy rates in early summer of both years of the study than their Georgia counterparts; certainly, they achieved their highest pregnancy rates in May or May–June of both years. These would likely be times of maximum forage quality, and therefore females would best be able to allocate sufficient resources to carry all embryos to term. Because Georgia females are more

likely than Virginia females to be pregnant in October–March, when forage quality is lower and thermoregulatory demands are greater, this would explain their overall average higher rates of prenatal mortality. Apparently, the strategy for survival of late summer- or autumn-born Virginia rats is not to breed during the winter months, especially November through February, which would jeopardize somatic maintenance under cold stress and thus survival for the low likelihood of reproductive success. In the warmer environs of southern Georgia, rats can better afford some winter reproduction.

Georgia females would be expected to live somewhat longer than their more rapidly replaced Virginia counterparts, and with longer lifespan as well as a longer breeding season they may be somewhat more iteroparous and so amass a greater lifetime reproductive output, on average. But among pregnant females, the Virginia population had 3 times as many rats that had previously given birth to 10 or more offspring as the Georgia population, so it is likely that there is greater variance in lifetime reproductive output among Virginia females than among Georgia females. Relatively few Virginia females become “super-moms,” whereas relatively many die before reproducing or during or after production of their 1st litter.

Both males and females in Georgia populations of cotton rats were significantly larger and heavier than their Virginia counterparts. This is the reverse of the pattern predicted by Bergmann’s rule, and, more importantly, it would appear to contradict bioenergetic predictions that larger rats in more seasonal environments would be better able to ingest sufficient food resources to support larger litters (Mayr 1970; Porter and McClure 1984); although this argument may only apply to a summertime selection regime in northerly latitudes, whereas opposite constraints may apply in winter (Gadgil and Bossert 1970). Campbell and Slade (1993, 1995) found that the largest cotton rats in northeastern Kansas, where cold stress would be even more severe than in southeastern Virginia, had lower survival over the winter than medium-sized rats. But no consistent differences were found in body size between the study populations when considering only pregnant females and spermatogenically active males, except that pregnant females from Virginia, with their larger litters, were significantly longer (although not heavier) than their Georgia counterparts. This may be weak support for the prediction of Porter and McClure (1984) or for the Big Mother hypothesis (Ralls 1976), for which Campbell and Slade (1995) found evidence within the Kansas population.

More importantly, the substantially higher percentages of reproductive males and parous females in the Georgia population put the body-size differences (for all adults) into perspective and lead to the conclusion that the Virginia population has a younger age distribution, which is the combined result of higher natality and higher mortality. Growing populations tend to have greater proportions of younger age or size classes (Ricklefs and Miller 2000). Experimentally food-supplemented populations of *S. hispidus* were found to have proportionally more small adults and fewer reproductive females (Doonan and Slade 1995); this scenario again suggests that enhanced forage quality during the breeding

season in the more seasonal environment (i.e., Virginia) may be the proximate cause of that population’s greater fecundity.

The smaller proportion of reproductive animals may also be partially explained by the longer period of winter suspension of breeding in Virginia (i.e., October–December and March samples from the Virginia population have a conspicuously higher percentage of nonparous females and nonreproductive males than the Georgia population). The 1st primiparous females of the year appearing generally in April in Virginia (>95% of January–March samples nulliparous) and the 1st multiparous females appearing in May (plus, only 3% multiparous in November–December samples) indicate that females that have reproduced in summer and autumn do not survive the winter in Virginia. Apparently, any maternal investment toward the end of the breeding season in Virginia exhausts the mother’s residual reproductive value along with the resources she would need to be able to survive the winter (Trivers 1972). That means virtually the entire breeding population of females in the spring, when natality begins (not before April in Virginia), is composed of 1st-time mothers who, in all but exceptional years, were born no later than September or October. These females will have a chance for iteroparity only if they survive until midsummer.

There is an apparent increase in body length and mass of Virginia females from early winter through spring, reaching a peak approximately in June, which corresponds to the period of maximum pregnancy rate and peak seasonal litter sizes. Because these primiparous females in spring are older (7 or 8 months) than their Georgia counterparts, on average, they have grown to longer body length but are no heavier (Table 1), perhaps because these overwinter survivors in the more seasonal environment have been forced to allocate their more limited food resources and their body-fat resources more heavily to thermoregulation than to mass gain. In the colder of the 2 winters (1988–1989), Georgia rats of both sexes were able to maintain relatively high and stable fat stores, whereas fat stores of Virginia rats declined steadily, as both populations did in the average winter (1987–1988). This suggests that southern rats are better able to hedge against bioenergetic deficits during a cold winter than northern rats. Because female cotton rats are known to accumulate fat during pregnancy to prepare for the greater energetic demands of lactation (Randolph et al. 1977), after such periods of fat depletion, northern rats would especially need to increase energy intake during spring and summer to compensate. Both longer body length at 1st estrus and enhanced nutritional quality of their forage may enable northern females to do so. Surviving rats from the 1st birth pulse of April and May in Virginia grow and are recruited rapidly into a 2nd pulse of breeders, mostly in August and September, but some as early as June. The June through September breeding pulse includes substantial proportions of 2nd-time breeders, at 1st being composed entirely of April mothers that have had postpartum matings, but later necessarily including some of the April- or May-born young reproducing for a 2nd and last time, as survivors from the spring recruitment become rarer. There would also be some 2nd-generation progeny of spring-born rats appearing in autumn.



It is especially this young-of-the-year subset of the northern population that displays a “fast” life history (Randolph et al. 1977), taking advantage of high forage quality of summer; this is in contrast to autumn-born rats, which must suspend reproductive development in favor of somatic maintenance to enhance their overwinter survival. We see this as a more pronounced example of a pattern (i.e., a faster-growing summer cohort) that also occurs in more southerly populations (Layne 1974). Iteroparity in this population is mostly limited to the few autumn-born females that survive nearly a year or the spring-born females that can grow and mature rapidly enough to bear 1st litters in June–August and 2nd litters in August–October. Summer-born females would virtually all necessarily be semelparous. Virginia females may occasionally breed as late as November, as happened in 1 of 3 years for which we had data (1989), and when they do, they may have relatively large litters, which could correlate with more reproductive experience or a facultative “burst” of semelparity regardless of experience, which represents an optimal trade-off at a season when survival and residual reproductive value are rapidly waning (Charnov and Shaffer 1973; Sargent and Gross 1985). Thus, selection pressures for rapid maturation and high fecundity, on the one hand, and delayed maturation and survival, on the other hand, cycle seasonally and apply, respectively, to spring- and autumn-born Virginia rats. Such seasonal cycles of selection may actually select for plasticity rather than a fixed strategy (Abrams et al. 1996; Gotthard and Nylin 1995; Kemp and Jones 2001).

Results for Georgia females show that the spring breeding population likely is composed of a mixture of 1st-time and experienced mothers, with the former potentially born even later in the autumn than is the case for Virginia. In 2 of 3 years for which late autumn data were available, a substantial percentage of Georgia females was still pregnant in November and December, respectively, which was 1–2 months after reproduction ceased in Virginia females. Previous studies of the southeastern Virginia populations corroborate a November–February cessation of breeding in females (Rose 1986; although Rose and Mitchell [1990] reported 2 of 11 females pregnant in February 1984). In southern Georgia, a combination of milder winter conditions, allowing greater survival and higher growth rates of surviving younger rats and the survival of larger, experienced females, helps this population prepare for reproduction approximately a month sooner in spring than in the Virginia population. And yet, spring and early summer breeding activity and average litter sizes overall were higher in both years among Virginia females than Georgia females, so despite the late start the northern population more than catches up.

Although adult males in Virginia are likewise either forced to undergo testicular regression earlier or fail to survive as well in the autumn compared to Georgia males, there is less difference than for females between the populations in timing of the onset of spring reproduction in males. Males would have neither the additional bioenergetic constraints nor consequences of lactation in late autumn, so their overwinter survival and growth rates may be sufficiently greater than for parous females to give them the resources to match their southern counterparts in spring reproductive phenology. The significantly greater

relative mass of reproductive tissues in reproductively active Virginia males, compared to their Georgia counterparts, is further indication that their strategy is one of greater reproductive allocation, overall. The breeding season in Virginia being condensed into a somewhat shorter period than in Georgia would increase the level of sperm competition (Kenagy and Trombulak 1986; see also Ball and Parker [2000]), to which the response would be larger testes and seminal vesicles; as a result, fertilization rates could be greater, which potentially is a proximate cause of larger litters in Virginia.

The apparent midsummer lull in breeding activity for both sexes in both populations in this study has been reported previously for *S. hispidus* in Florida (Layne 1974), Kansas (McClenaghan and Gaines 1978), and South Carolina (O’Farrell et al. 1977) and is thought to be an artifact of the younger average age of the population in midsummer, compared to spring when the 1st pulse of recruitment from spring litters is observed. This seasonal bimodality also has been observed for other small mammals, such as *Microtus* (Rose and Gaines 1978) and *Peromyscus* (Bronson 1989; Terman and Terman 1999), in which the pattern is particularly pronounced for midlatitudinal populations (Bronson 1989), apparently because breeding is not noticeably pulsed in tropical populations and is reduced to a single annual pulse in high-latitude populations.

## CONCLUSIONS

Hispid cotton rats at the northern edge of their range in Virginia experience a shorter breeding season and higher mortality than populations in southern Georgia, where the climate is less seasonal and winters are substantially milder. Georgia cotton rats average larger, which may be either a cause (Stearns 1992) or a result of higher overwinter survivorship, than Virginia rats. Relative gonadal mass in reproductive males is significantly greater in Virginia. Litter sizes are significantly larger in Virginia. However, only in Georgia are cotton rats consistently reproductively active during November–February, when forage quality is lower and cold stress is greater; thus, embryo resorption and prenatal mortality are higher. Variance in lifetime reproductive output is likely greater among Virginia females than Georgia females, with some individuals being highly fecund (maximum litter size 13, compared to 9 in Georgia) and many not surviving to reproduce. The Virginia population has a younger age distribution, which explains why all adults average significantly smaller, and is further evidenced by the fact that 50% and 75% of adult females and males, respectively, were reproductively active in Georgia, whereas only 35% and 40% were reproductively active in Virginia. However, 1st-time breeding females in spring average older and longer (although not heavier) in Virginia than in Georgia, because they have had to survive a longer winter as nonparous females. In Virginia, females that reproduce in a given calendar year generally do not survive the winter to reproduce again the next spring, whereas substantial numbers of parous females overwinter to breed in spring in Georgia. In Virginia, the necessity for a dual strategy—autumn-born rats foregoing

reproduction over a 4- to 5-month winter in order to survive to spring recruitment, and spring-born rats growing rapidly and maturing early to breed in summer—would prevent significantly larger litters (compared to southern Georgia) from becoming a genetically fixed strategy, or at least such a seasonal cycle would confound the detection of a fixed strategy.

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APPENDIX I

Sample sizes of adult *Sigmodon hispidus* collected in south-central Georgia and southeastern Virginia, by month. Cumulative totals for each calendar month, all years combined, listed alongside last 12 months of the study.

Year	Month	Georgia females		Virginia females		Georgia males		Virginia males	
		Monthly	Cumulative	Monthly	Cumulative	Monthly	Cumulative	Monthly	Cumulative
1987	September			17				3	
	October	5		5		5		15	
	November	4		7		5		2	
	December	8		12		4		13	
1988	January	8		2		4		1	
	February	6		6		8		4	
	March	8		5		18		3	
	April	2		6		3		5	
	May	11		5		11		1	
	June	6		14		7		5	
	July	3		5		10		10	
	August	0		2		0		1	
	September	6		5		4		11	
	October	13		9		11		9	
	November	8		12		7		20	
	December	9		15		14		25	
1989	January	3	11	7	9	4	8	9	10
	February	4	10	30	36	1	9	17	21
	March	3	11	6	11	13	31	4	7
	April	21	23	2	8	17	20	6	11
	May	14	25	3	8	6	17	8	9
	June	12	18	1	15	13	20	1	6
	July	18	21	21	26	10	20	15	25
	August	12	12	0	2	16	16	4	5
	September	17	23	13	35	5	9	14	28
	October	9	27	10	24	10	26	13	37
	November	8	20	9	28	18	30	10	32
	December		17	7	34		18	12	50
Total		218		236		224		241	