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Reproduction in the Hispid Cotton Rat,  
*Sigmodon hispidus* Say and Ord (Rodentia: Muridae),  
in Southeastern Virginia

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*ABSTRACT.*— The hispid cotton rat, *Sigmodon hispidus* Say and Ord, a species of the southwestern United States that has been moving northward and eastward in this century, was first observed in Virginia in 1940. In this study of the cotton rat in southeastern Virginia, most males were reproductively competent from February through November, embryos were recorded from March through October, and litter sizes were comparable to those from other locations except Kansas. Also unlike the cotton rat in Kansas, animals grew at substantial rates during the winter in Virginia. The hispid cotton rat seems to have adjusted its breeding season in Virginia by the cessation of breeding early in autumn, which permits the last young of the season to attain nearly adult size before winter arrives. Both young and adults are able to maintain and even increase their autumnal body mass throughout the winter. Timing and length of the breeding season and the patterns of body growth suggest that the hispid cotton rat is well adapted to winter, and hence to persistence of the species, in southeastern Virginia.

The hispid cotton rat, *Sigmodon hispidus* Say and Ord, is a cricetine rodent that has dramatically expanded its distribution in the central and southeastern states in historic times (Genoways and Schlitter 1967). First recorded in Virginia from Mecklenberg Co. in 1940 (Patton 1941), it moved northward in the lower Piedmont into Amelia Co. (Lewis 1944) and then north of the James River in central Virginia (Pagels 1977). The current distribution is believed to extend from Virginia Beach westward to points north of Richmond and southwestward through Halifax Co., or approximately throughout the southeastern one-third of Virginia.

Because the hispid cotton rat has tropical affinities (Hall 1981, Zimmerman 1970), it is surprising that the species has been able to extend its range to the present northern limit of its distribution and to cope with winters in such states as Kansas, Tennessee, and Virginia. Furthermore, we expected to observe that this rodent has a shorter breeding season in those marginal populations than in Texas or Mexico, which are closer to the center of distribution for the species. In fact,



some features of the expected pattern have been reported in Kansas (McClenaghan and Gaines 1978), Oklahoma (Goertz 1965), and Tennessee (Dunaway and Kay 1964), although the details vary somewhat from location to location. Kilgore (1970) examined the possibility that northern populations might have larger litters than central populations as a way of compensating for increased winter mortality; he found significantly larger litter sizes in Kansas than in Texas.

The primary objective of our study was to examine details of reproduction and patterns of body growth in a population of cotton rats at the northern limit of the species distribution on the East Coast. Using monthly samples of live-caught cotton rats that were necropsied and examined for evidence of reproduction, we learned that cotton rats in Virginia suspended breeding from early November through late March, had litters no larger than those in central populations (Texas), and had a larger weight gain in males than in females during the winter.

#### MATERIALS AND METHODS

From October 1983 to November 1984, cotton rats were obtained using Fitch and Sherman live traps baited with chicken scratch feed (a mixture of wheat, millet, and cracked corn). Although not always attained, the goal was a sample of 30 animals per month. No animals were taken in January or August. The 250-ha study area, an old field in Portsmouth, Va., was dominated by grasses, *Panicum* spp. and *Andropogon* spp.; a spikerush, *Juncus effusus*; and, at the margins, young sweet gum trees, *Liquidambar styraciflua*. Other common species of plants found in the study area were trumpet creeper, *Campsis radicans*; cane, *Arundinaria gigantea*; saltbush, *Iva frutescens*; goldenrods, *Solidago* spp.; and giant ragweed, *Ambrosia artemisiifolia*. Less common were black oak, *Quercus nigra*; grape, *Vitis rotundifolia*; loblolly pine, *Pinus taeda*; smooth sumac, *Rhus copallina*; dogfennel, *Eupatorium capillifolium*; blackberries, *Rubus* spp.; briars, *Smilax* spp.; willows, *Salix* spp.; and cattails, *Typha angustifolia*. Traps were moved from place to place to prevent excessive depletion of the cotton rat at a local site.

All animals  $\geq 50$  g (lower limit of potential breeders) were killed with chloroform in the laboratory and frozen until necropsy, when the following information was recorded for each: (1) body mass (g), (2) overall body length (mm), and (3) length of tail (mm).

Additional data were recorded for females: (1) number of placental scars, (2) number of embryos, (3) uterine mass (uterus + embryos), (4) number of corpora lutea, and (5) parity class. The parity classes were defined as nulliparous females without embryos or placental scars (also



lacking well-developed mammary glands and nipples); primiparous females with one set of placental scars and corpora albicantia or with embryos and corpora lutea (but not placental scars or corpora albicantia); and multiparous females with more than one set of placental scars or with embryos, corpora albicantia, and placental scars. In the analysis of body mass, the mass of the uterus was subtracted so that pregnancy would not confound the results.

Additional data were recorded for males: (1) testes position (scrotal or abdominal), (2) paired testicular mass (mg), and (3) condition of epididymal tubules (looped or convoluted). Males were considered to be breeding if the epididymal tubules were convoluted (Jameson 1950). Data are presented as  $\bar{x} \pm SE$ .

## RESULTS

### FEMALES

The most reliable indicator of female reproductive state is pregnancy. Of 148 females, 48% were pregnant. However, no pregnant females were collected from November through February (Fig. 1). The level of breeding in females was high from March through October, when the average pregnancy rate was 68.7% (including October of both 1983 and 1984).

Using the Chi-square test, we found no differences ( $\chi^2 = 0.76$ , 2 df,  $P > 0.50$ ) in the proportions of females that were pregnant in the April-May, June-July, and September-October bimonthly periods (not sampled in August). Thus, as measured by pregnancy, females bred at a uniform rate during these months of peak activity.

Overall, litter size averaged  $5.00 \pm 0.284 SE$ . However, during the peak breeding months of April to October, females averaged  $5.18 \pm 0.274$  embryos per female. There was significant variation in litter size (= embryo counts) throughout the months of the breeding season (ANOVA:  $F = 30.46$ ,  $df = 4,62$ ,  $P < 0.005$ ) with largest litters ( $\bar{x} = 7.83 \pm 0.984$ ) in May. In contrast, females in April averaged only  $4.18 \pm 0.652$  embryos per female, and the two pregnant females in October 1983 had one and two embryos, unusually small litters for the cotton rat.

The pregnant females were divided into primiparous (those in their first reproductive experience) and multiparous (experienced breeders) groups to determine whether a difference in litter size was attributable to reproductive experience. Although there was a trend toward larger litters in multiparous females, there was no significant difference between the litter sizes of primiparous ( $\bar{x} = 4.76 \pm 0.378 SE$ ) and multiparous ( $\bar{x} = 5.72 \pm 0.371$ ) females during the "peak" breeding months ( $t_s = 1.74$ ,  $df = 65$ ,  $0.1 > P > 0.05$ ). Thus, season had greater influence on litter size than age of the female.



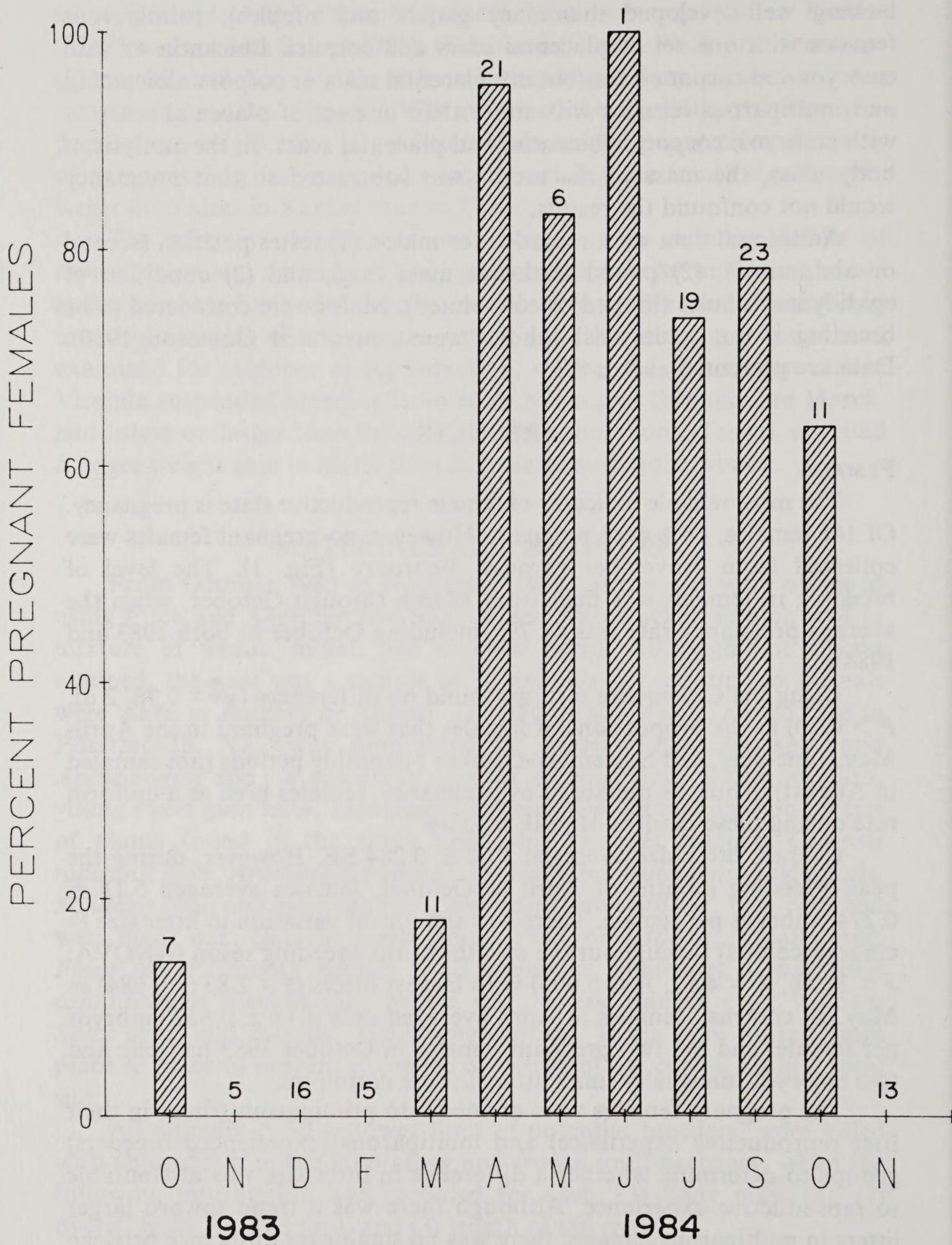


Fig. 1. Monthly percentages of females ( $\geq 50$  g) that were pregnant. Sample sizes are given above each bar.  $N = 148$ . (No collections in January and August.)



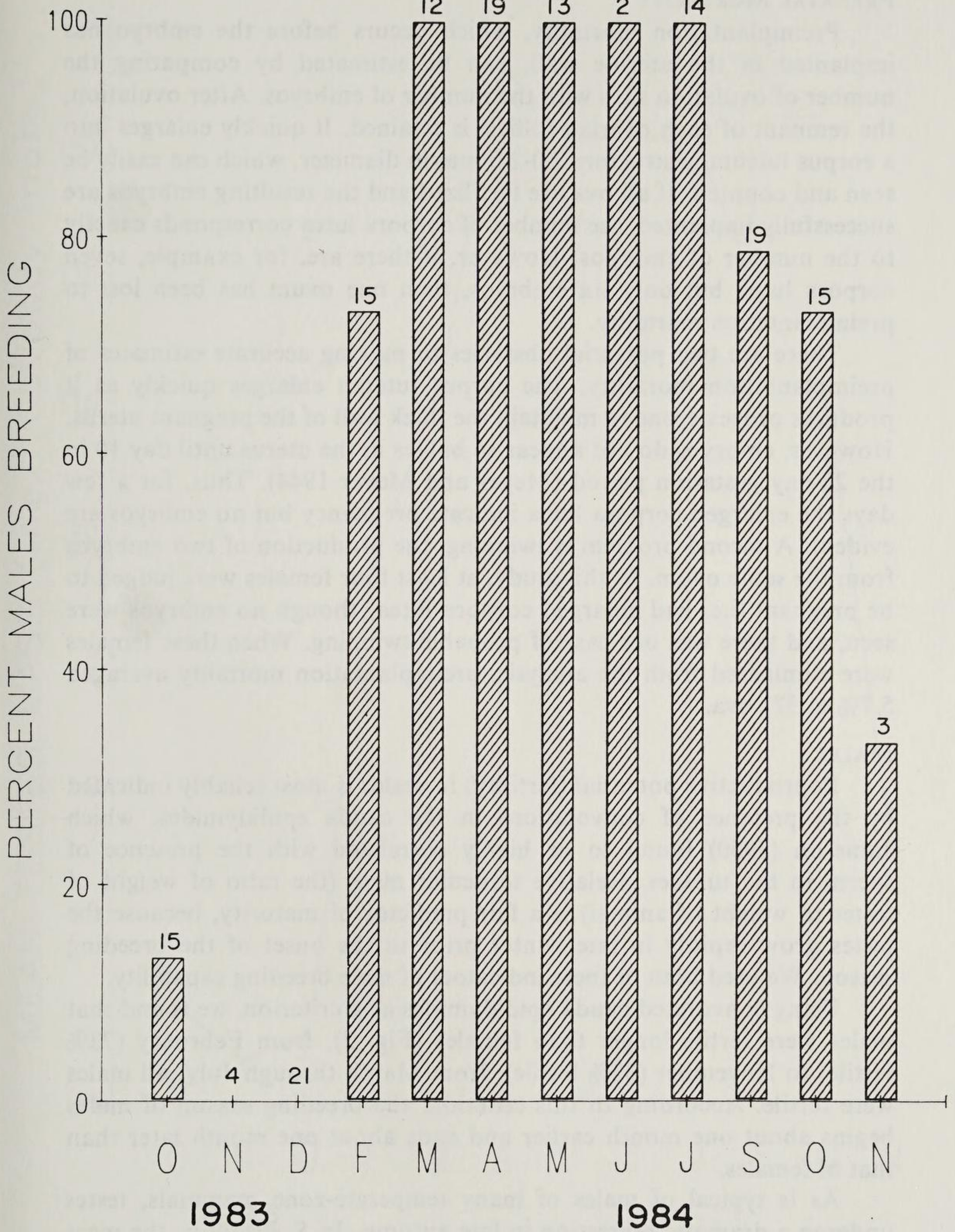


Fig. 2. Monthly percentages of males ( $\geq 50$  g) that were breeding based on the presence of convoluted cauda epididymides in the testes. Sample sizes are given above each bar. N = 152. (No collections in January and August.)



### PRENATAL MORTALITY

Preimplantation mortality, which occurs before the embryo has implanted in the uterine wall, can be estimated by comparing the number of ovulation sites with the number of embryos. After ovulation, the remnant of each ovarian follicle is retained. It quickly enlarges into a corpus luteum, a structure 2.0-2.5 mm in diameter, which can easily be seen and counted. If all ova are fertilized and the resulting embryos are successfully implanted, the number of corpora lutea corresponds exactly to the number of embryos. However, if there are, for example, seven corpora lutea but only six embryos, then one ovum has been lost to preimplantation mortality.

There are two potential obstacles to making accurate estimates of preimplantation mortality. The corpus luteum enlarges quickly as it produces progesterone to maintain the thick wall of the pregnant uterus. However, embryos do not appear as bulges in the uterus until day 10 in the 27-day gestation period (Meyer and Meyer 1944). Thus, for a few days the enlarged corpora lutea indicate pregnancy but no embryos are evident. A second problem is twinning, the production of two embryos from the same ovum. In this study, at least four females were judged to be pregnant (i.e. had enlarged corpora lutea) though no embryos were seen, and there was one case of probable twinning. When these females were eliminated from the analysis, preimplantation mortality averaged 5.7% of 371 ova.

### MALES

Reproductive potential (fertility) in males is most reliably indicated by the presence of convolutions in the cauda epididymides, which Jameson (1950) found to be highly correlated with the presence of sperm in the tubules. Relative testicular mass (the ratio of weight of testes to weight of animal) is a fair predictor of maturity, because the testes grow rapidly in late winter prior to the onset of the breeding season. We used both of these indicators of male breeding capability.

Using convoluted cauda epididymides as a criterion, we found that males were fertile longer than females (Fig. 2), from February (73% fertile) to November (33% fertile); from March through July, all males were fertile. According to this criterion, the breeding season of males begins about one month earlier and ends about one month later than that of females.

As is typical of males of many temperate-zone mammals, testes undergo a dramatic regression in late autumn. In *S. hispidus*, the mass of the paired testes of a 120-g male might be 2,000 mg at the height of the breeding season, compared with only 80 mg after testicular regression. With regression, the cauda epididymides lose their convolutions and become looped. Such males are no longer fertile.



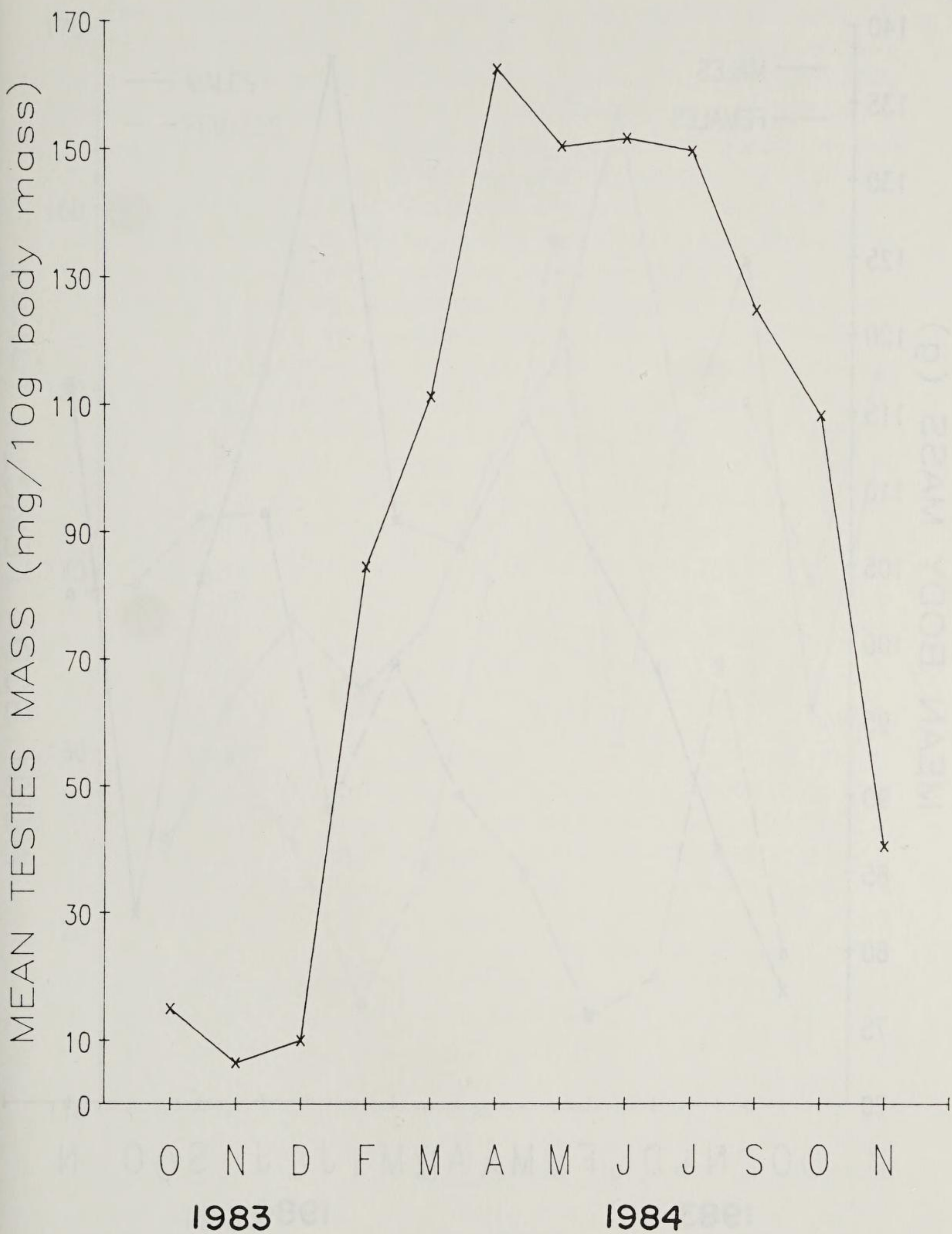


Fig. 3. Mean testicular mass per 10 g of body weight for each month of study. (Sample sizes as given in Fig. 2.)



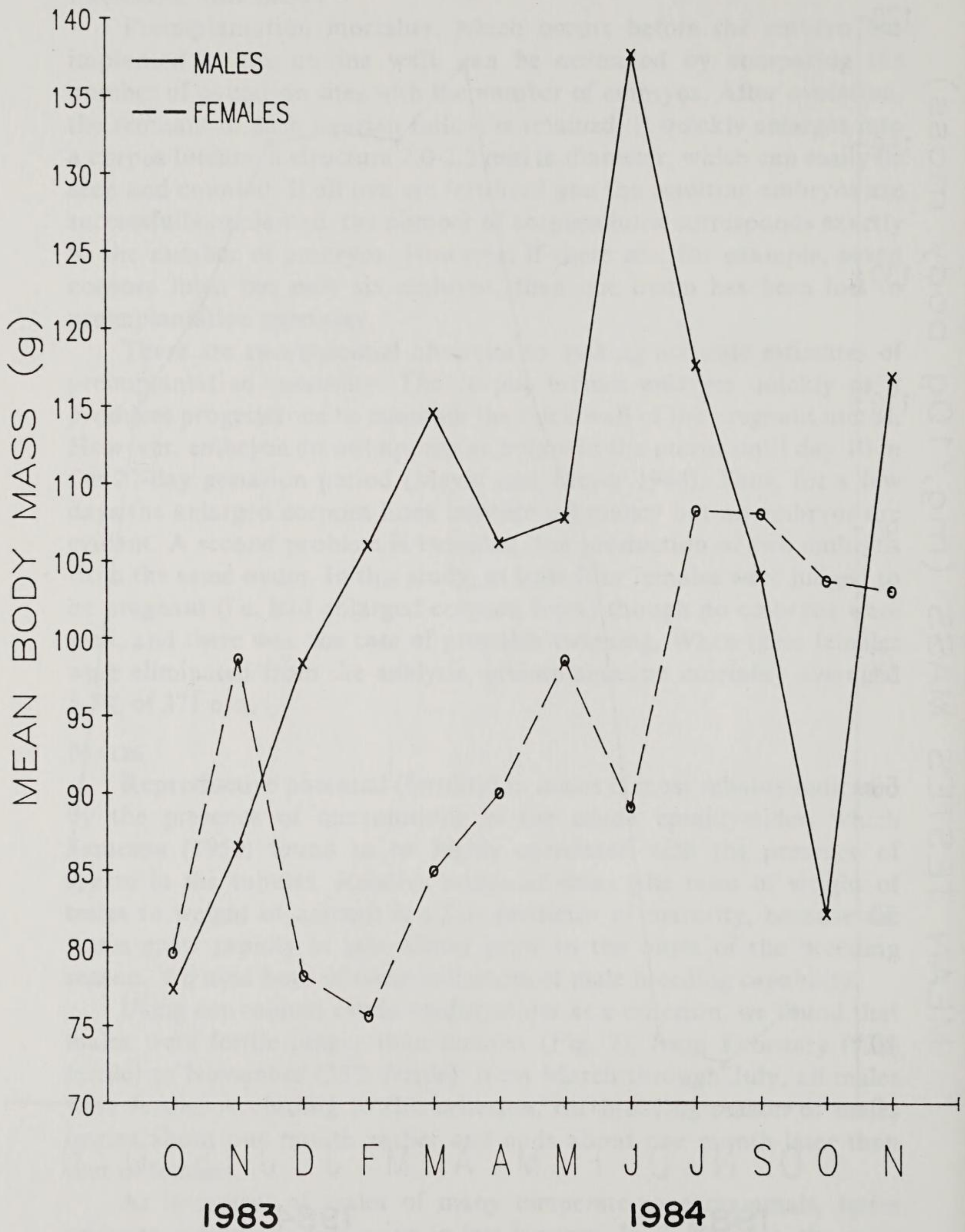


Fig. 4. Mean monthly body masses of male and female cotton rats. (Sample sizes as given in Fig. 1 and 2.)



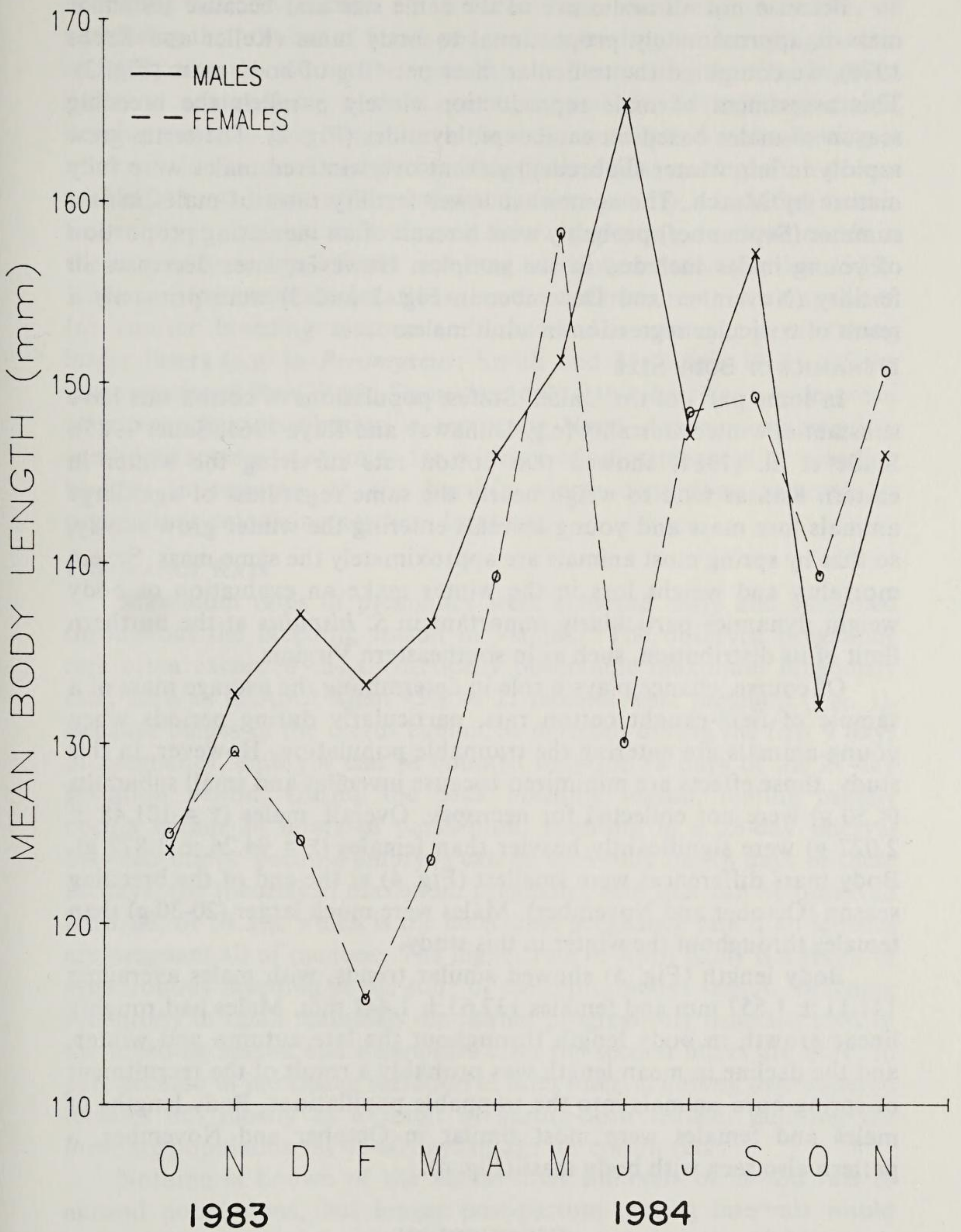


Fig. 5. Mean monthly body lengths (total length minus tail length) of male and female cotton rats. (Sample sizes as given in Fig. 1 and 2.)



Because not all males are of the same size and because testicular mass is approximately proportional to body mass (Keller and Krebs 1970), we computed the testicular mass per 10 g of body mass (Fig. 3). This assessment of male reproduction closely parallels the breeding season of males based on cauda epididymides (Fig. 2). The testes grew rapidly in late winter (February) so that overwintered males were fully mature by March. The somewhat lower fertility rates of males in late summer (September) probably were a result of an increasing proportion of young males included in the samples. However, later decreases in fertility (November and December in Fig. 2 and 3) were primarily a result of testicular regression in adult males.

#### DYNAMICS OF BODY SIZE

In some parts of the United States, populations of cotton rats have substantial winter mortality (e.g. Dunaway and Kaye 1964, Sauer 1985). Slade et al. (1984) showed that cotton rats surviving the winter in eastern Kansas tend to weigh nearly the same regardless of age; large animals lose mass and young animals entering the winter grow slowly, so that by spring most animals are approximately the same mass. Severe mortality and weight loss in the winter make an evaluation of body weight dynamics particularly important in *S. hispidus* at the northern limit of its distribution, such as in southeastern Virginia.

Of course, chance plays a role in determining the average mass of a sample of field-caught cotton rats, particularly during periods when young animals are entering the trappable population. However, in this study, those effects are minimized because juveniles and small subadults (<50 g) were not collected for necropsy. Overall, males ( $\bar{x} = 101.48 \pm 2.027$  g) were significantly heavier than females ( $\bar{x} = 94.26 \pm 1.872$  g). Body mass differences were smallest (Fig. 4) at the end of the breeding season (October and November). Males were much larger (20-30 g) than females throughout the winter in this study.

Body length (Fig. 5) showed similar trends, with males averaging  $141.11 \pm 1.557$  mm and females  $137.63 \pm 1.441$  mm. Males had roughly linear growth in body length throughout the late autumn and winter, and the decline in mean length was probably a result of the recruitment of spring-born animals into the trappable populations. Body lengths of males and females were most similar in October and November, a pattern also seen with body mass (Fig. 4).

#### DISCUSSION

Mammals seem to adjust the breeding rate to the mortality rate at a given location (Sadleir 1969). Mammals, particularly small mammals, can increase reproduction by one or more of the following means:



becoming sexually mature at an earlier age, increasing litter size, or increasing the number of litters per year (extending the breeding season or decreasing the interval between litters). Decreasing the time between litters is achieved by a short gestation period and rapid postnatal development, so that the interval between conception and weaning is minimal. In the most rapidly breeding individuals, mating often occurs within 24 to 48 hours after parturition; consequently, a lactating female frequently is pregnant with the next litter. In general, small mammals in the tropics have small litters and long breeding seasons (Sadleir 1969). However, in temperate locations, small mammals tend to compensate for shorter breeding seasons and increased mortality by producing larger litters (e.g. in *Peromyscus*; Smith and McGinnis 1968). Of the seven species of New World *Sigmodon*, only *S. hispidus* has a widespread and expanding distribution in temperate North America, making it a candidate species to examine for evidence of adjustments in its breeding biology in response to the harsher winter conditions endured by populations colonizing northern locations.

#### PREGNANCY RATE

Maximum rates of pregnancy were achieved early and sustained throughout the breeding season in Virginia. The observed pregnancy rate often exceeded the theoretically observable maximum pregnancy rate, such as in April when 95% of 21 females were pregnant (Fig. 1). Because bulges in the uterus cannot be detected during the first 9 days of pregnancy, embryos can be counted only for 18 days of the 27-day gestation period. During the peak breeding season, mating usually occurs within 24 hours of parturition, resulting in a 28-day interval between litters. Because embryos can be seen only for 18 days of these 28 days, the theoretical maximum pregnancy rate that can be observed is  $18/28$ , or 64.3%, which is the detectable pregnancy rate if all females are pregnant all of the time. The higher rate in April likely is a result of synchronous breeding at the start of the reproductive season. Breeding synchrony in small mammals diminishes progressively from the start of the breeding season and disappears after the second litters are born, in part because of increasing variation in litter interval among overwintered females but mostly as a result of spring-born females entering the breeding population (at 45-60 days of age for cotton rats).

Nothing is known of the actual litter intervals of cotton rats in natural populations, but longer post-partum mating intervals would lower the maximum observable pregnancy rate below the 64.3% value. The observed pregnancy rate during the breeding season (68.7%) slightly exceeded the theoretical value; that can be explained by sampling error or, more likely, by changes in the behavior of pregnant females.



Randolph et al. (1977) found that the fat accumulated during the last half of pregnancy was used during lactation, when energy demands outstripped the female's speed in processing food. It is plausible that females in the later stages of pregnancy would be increasingly attracted to the high-energy food source (mixed seeds) that was used as bait.

Although Dunaway and Kaye (1964) did not calculate monthly pregnancy rates, they did observe low levels and apparently sporadic breeding throughout what they judged to be a relatively mild Tennessee winter. In Oklahoma, Goertz (1965) found no pregnant females during a severe winter, but he did find pregnant females during November, December, and February of a milder winter. Goertz reported highest pregnancy rates during May to September. Haines (1961) recorded no embryos in Texas cotton rats from October to February, but he did record corpora lutea throughout the year. Haines observed the highest pregnancy rates between February and July, with low rates after September and the lowest rates in December. Thus, the breeding season seems to be somewhat earlier in Texas compared with Tennessee, Oklahoma, or Virginia.

In duration, methods, and analysis, our study most closely parallels that of McClenaghan and Gaines (1978), conducted near Lawrence, Kan. They found no breeding from November through March, which is similar to what we observed in the Virginia population. The pregnancy rate in Kansas was low (30%) in April, highest (over 80%) in May, and generally greater than 70% from June through October. Overall, the patterns of breeding in Virginia and Kansas were similar for both sexes.

#### LITTER SIZE

Within a species, litter size is affected by several interacting factors, including age, parity, body weight, and nutritional state (Sadleir 1969). In a recent exhaustive review, Cameron and McClure (1988) examined the patterns of breeding in female *Sigmodon hispidus* by evaluating published and unpublished laboratory and field data. Using a stepwise multiple regression analysis on data from 18 studies, Cameron and McClure (1988: table 2) examined the patterns of geographic variation in litter size and the effects of body size on litter size. By finding latitude, longitude, and body length to be significantly associated with mean litter size, their analysis "confirmed the existence of both north-south and east-west variation in litter size." Largest litters were reported for the large females of the north-central states.

A further analysis "indicated that latitudinal and longitudinal variation in litter size were due primarily to differences among subspecies" (Cameron and McClure 1988). Specifically, *S. hispidus texianus*, which had the largest litters at  $7.20 \pm 0.23$  SE, averaged  $8.35 \pm 0.35$  in Kansas



but only  $5.10 \pm 0.37$  in coastal Texas (Houston). Nutrition may also contribute to these differences within this subspecies (Cameron and McClure 1988; table 6). Although litters of *S. hispidus virginianus*, the subspecies in Virginia, were significantly larger than those of Mexican and Central American subspecies, they were significantly smaller than those of *S. h. texianus* (Cameron and McClure 1988).

The litter size of 5.00 for Virginia cotton rats lies in the range of values reported from other studies (Cameron and McClure 1988: table 2), although on the low side for "northern populations." Populations from Tennessee averaged 6.1 embryos per litter (Dunaway and Kaye 1961), from Oklahoma 6.0 (Goertz 1965), from western Kansas 6.7 (Fleharty and Choate 1973), and from eastern Kansas 9.0 (McClenaghan and Gaines 1978). Furthermore, laboratory animals derived from Houston, Kansas, and Tennessee populations and raised by McClure at Indiana University remained significantly different in average litter size even after 16-28 generations and 8-12 years in the laboratory (Cameron and McClure 1988: figure 2). Thus, the determination of litter size in *Sigmodon hispidus* is complex, involving both genetic and environmental factors.

Although Lawrence, Kan., and Portsmouth, Va., are both near 37° N latitude, the Kansas winters are longer and colder (average 2° C), in the absence of moderating oceanic effects. In coastal Virginia, snow falls only once or twice a year and periods of freezing weather rarely last more than a few days. Despite the more moderate conditions in Virginia (Cameron and McClure 1988: table 4), the Virginia cotton rats did not breed longer than the Kansas cotton rats, and Virginia litter sizes as well as body sizes were significantly smaller. However, female cotton rats in Virginia were pregnant at nearly maximum levels throughout the breeding season (Fig. 1), and there was a trend ( $0.1 > P > 0.05$ ) for multiparous females to have larger litters than primiparous females. Thus, differences in age of onset of breeding and in longevity (neither of which was measured in these studies) may be important in affecting geographic differences in the dynamics of these populations.

#### MALE BREEDING

The breeding season of males began in February and lasted to November (Fig. 2). Based on the breeding criterion of convolutions in the cauda epididymides, 73.3% of males were in breeding condition in February and 100% were fertile from March through June. McClenaghan and Gaines (1978), who also used epididymal convolutions to determine breeding condition in males, did not find 100% breeding in any month. Their highest monthly rates were just under 90% in June and August; and in all other months during the breeding season except May, fertility



rates were less than 60%. Haines (1961) measured spermatogenesis and found that the production of sperm remained high from February through October (which was the breeding season for males in our study). Dunaway and Kaye (1964), who assessed male reproduction based on live-caught animals, observed that just under 100% of males had descended testes (i.e. were mature) during the June-September period. They noted a decline in the percentages of mature males from October to December, but by January, the proportion of males with descended testes again began to increase.

Testicular mass is closely related to reproductive condition in males (Haines 1961). Our results agree with those of McClenaghan and Gaines (1978), who found testicular mass to be highest from June through September, also the peak breeding months for males as determined by convolutions of the cauda epididymides in the present study. In Kansas, smallest testicular masses were recorded for December, but we found the smallest testicular masses in the October to December period, with dramatic monthly increases from December through April. Testicular mass remained high from April through July and then declined sharply (Fig. 3), probably at first because of the recruitment of young males in the trappable population and later also because of testicular regression of adult males. Goertz (1965) reported large testicular masses from February through September and low values in the remaining months.

In Texas, Haines (1961) reported spermatogenesis in males with the largest testicular masses; he provided perhaps the best available information on the relationship between these two variables. He found the largest average testicular mass per 10 g of body mass during the period from February through August, after which testicular mass declined until November. McClenaghan and Gaines (1978) and Haines (1961) found that testicular regression resulted in a reduction to about 1/30th of the maximum testicular mass, compared with a value of about 1/26th in our study.

#### BREEDING SEASON

During the breeding season, 68.7% of females were pregnant, and in most of the same months all males were judged to be fertile. The breeding season in males started one month earlier and ended one month later than the breeding season in females. That pattern is common in mammals (Sadleir 1969), and it is interpreted as adaptive in that the energy costs for breeding in females are greater than those in males. As a result of the earlier onset of fertility in males, mature males are ready to copulate and produce fertile matings when females undergo the first estrous cycle of the spring.

The breeding season in Virginia closely paralleled that found by McClenaghan and Gaines (1978) in Kansas. Both locations are at or



near the northern limit of distribution for hispid cotton rats; therefore, it is not surprising to find some similarities. Differences also were noted. Although the breeding season in Virginia started a month earlier in both sexes, it lasted until October for females in both Kansas and Virginia. Another similarity in the breeding of *Sigmodon* in these two studies is the percentage of breeding females; the rate was relatively low during the first month in which pregnancies occurred and then rose sharply to near the maximal rate in the following month. In McClenaghan and Gaines (1978), this trend must be inferred because their study ended in April. However, if the high May level at the start of their study can be extrapolated to the preceding April, a large increase in breeding level occurred at the same time in Kansas and Virginia.

In Texas (Haines 1961), the breeding season began in the same month as in Virginia, but it ended one month sooner. This is an unexpected result if we assume that the breeding season has been shortened at more northerly locations because of the constraints of winter on the energy budgets of mammals. We would expect the breeding season to be longer at more southerly locations. Goertz (1965), who found pregnant females in some winter months, believed that breeding was possible in Oklahoma under the favorable conditions of mild winters.

#### EFFECTS OF BODY SIZE

Several factors affect patterns of body size in *Sigmodon hispidus*, including sex, latitude, subspecies, and nutrition. In some, but not all, populations males are larger than females, and northern populations tend to have larger skeletal sizes and, in some seasons, higher fat content. *Sigmodon h. texianus* is significantly larger than all other subspecies (Cameron and McClure 1988). McClenaghan (1977) found generally larger skull and skeletal variables for cotton rats from northern populations (Kansas and Virginia) than from southern localities (Mexico), but Kansas and Virginia populations differed in only one skeletal feature. However, the seasonal pattern of body growth of Virginia cotton rats differs from that of Kansas cotton rats, in which Slade et al. (1984) found that the large adult animals lost weight over the winter. By contrast, in Virginia, the males in particular gained body mass steadily throughout the winter months (Fig. 4). This pattern of winter increase is evident but less well defined for body length (Fig. 5), although males did increase in length nearly every month from October to May or June.

Mean body mass for females was low in October ( $79.7 \pm 6.77$  g) but it rose sharply to  $98.6 \pm 10.19$  g in November. The mean values for December and February were low, indicating that females were not gaining weight during this time. Because there was no breeding during these months, the lower mean mass in winter cannot be a result of the



recruitment of young, lightweight animals; therefore, we can assume that females either lose mass or fail to gain significant mass during the winter months. From February through July, the monthly mean mass of females rose steadily, indicating a real increase in body mass during this time. Then, when the young of the year finally entered the trappable population, the monthly mean mass of females (and males) declined.

Patterns of body length were similar to those of body mass. Although both length and mass are measures of body size, length may be a more reliable index of body growth in *S. hispidus* because (1) animals lose mass but not length during starvation or during winter, (2) both sexes divert resources away from growth and towards reproduction during the breeding season, and (3) females store up body fat during pregnancy in preparation for the greater energy demands during lactation (Randolph et al. 1977).

In conclusion, cotton rats in southeastern Virginia seem to be well adapted to the northern limit of their present distribution on the East Coast; their March-to-October breeding season and the sustained growth of overwintering individuals suggest high survival rates of both young and adults during the winter months. The modest litter size may indicate that, unlike Kansas populations, Virginia populations have not been selected for larger litter sizes to compensate for winter mortality.

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Reproduction in the Hispid Cotton Rat,  
*Sigmodon hispidus* Say and Ord (Rodentia: Muridae),  
in Southeastern Virginia

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ABSTRACT . — The hispid cotton rat, *Sigmodon hispidus* Say and Ord, a species of the southwestern United States that has been moving northward and eastward in this century, was first observed in Virginia in 1940. In this study of the cotton rat in southeastern Virginia, most males were reproductively competent from February through November, embryos were recorded from March through October, and litter sizes were comparable to those from other locations except Kansas. Also unlike the cotton rat in Kansas, animals grew at substantial rates during the winter in Virginia. The hispid cotton rat seems to have adjusted its breeding season in Virginia by the cessation of breeding early in autumn, which permits the last young of the season to attain nearly adult size before winter arrives. Both young and adults are able to maintain and even increase their autumnal body mass throughout the winter. Timing and length of the breeding season and the patterns of body growth suggest that the hispid cotton rat is well adapted to winter, and hence to persistence of the species, in southeastern Virginia. The hispid cotton rat, *Sigmodon hispidus* Say and Ord, is a cricetine rodent that has dramatically expanded its distribution in the central and southeastern states in historic times (Genoways and Schlitter 1967). First recorded in Virginia from Mecklenberg Co. in 1940 (Patton 1941), it moved northward in the lower Piedmont into Amelia Co. (Lewis 1944) and then north of the James River in central Virginia (Pagels 1977). The current distribution is believed to extend from Virginia Beach westward to points north of Richmond and southwestward through Halifax Co., or approximately throughout the southeastern one-third of Virginia.

Because the hispid cotton rat has tropical affinities (Hall 1981, Zimmerman 1970), it is surprising that the species has been able to extend its range to the present northern limit of its distribution and to cope with winters in such states as Kansas, Tennessee, and Virginia. Furthermore, we expected to observe that this rodent has a shorter breeding season in those marginal populations than in Texas or Mexico, which are closer to the center of distribution for the species. In fact, *Brimleyana* 16:43-59, July 1990

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some features of the expected pattern have been reported in Kansas (McClenaghan and Gaines 1978), Oklahoma (Goertz 1965), and Tennessee



(Dunaway and Kay 1964), although the details vary somewhat from location to location. Kilgore (1970) examined the possibility that northern populations might have larger litters than central populations as a way of compensating for increased winter mortality; he found significantly larger litter sizes in Kansas than in Texas.

The primary objective of our study was to examine details of reproduction and patterns of body growth in a population of cotton rats at the northern limit of the species distribution on the East Coast. Using monthly samples of live-caught cotton rats that were necropsied and examined for evidence of reproduction, we learned that cotton rats in Virginia suspended breeding from early November through late March, had litters no larger than those in central populations (Texas), and had a larger weight gain in males than in females during the winter.

#### MATERIALS AND METHODS

From October 1983 to November 1984, cotton rats were obtained using Fitch and Sherman live traps baited with chicken scratch feed (a mixture of wheat, millet, and cracked corn). Although not always attained, the goal was a sample of 30 animals per month. No animals were taken in January or August. The 250-ha study area, an old field in Portsmouth, Va., was dominated by grasses, *Panicum* spp. and *Andropogon* spp.; a spikerush, *Juncus effusus*; and, at the margins, young sweet gum trees, *Liquidambar styraciflua*. Other common species of plants found in the study area were trumpet creeper, *Campsis radicans*; cane, *Arundinaria gigantea*; saltbush, *Iva frutescens*; goldenrods, *Solidago* spp.; and giant ragweed, *Ambrosia artemisiifolia*. Less common were black oak, *Quercus nigra*; grape, *Vitis rotundifolia*; loblolly pine, *Pinus taeda*; smooth sumac, *Rhus copallina*; dogfennel, *Eupatorium capillifolium*; blackberries, *Rubus* spp.; briars, *Smilax* spp.; willows, *Salix* spp.; and cattails, *Typha angustifolia*. Traps were moved from place to place to prevent excessive depletion of the cotton rat at a local site.

All animals > 50 g (lower limit of potential breeders) were killed with chloroform in the laboratory and frozen until necropsy, when the following information was recorded for each: (1) body mass (g), (2) overall body length (mm), and (3) length of tail (mm).

Additional data were recorded for females: (1) number of placental scars, (2) number of embryos, (3) uterine mass (uterus + embryos), (4) number of corpora lutea, and (5) parity class. The parity classes were defined as nulliparous females without embryos or placental scars (also

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lacking well-developed mammary glands and nipples); primiparous females with one set of placental scars and corpora albicantia or with embryos and corpora lutea (but not placental scars or corpora albicantia); and multiparous females with more than one set of placental scars or with embryos, corpora albicantia, and placental scars. In the analysis of body mass, the mass of the uterus was subtracted so that pregnancy would not confound the results.

Additional data were recorded for males: (1) testes position (scrotal or abdominal), (2) paired testicular mass (mg), and (3) condition of epididymal tubules (looped or convoluted). Males were considered to be breeding if the epididymal tubules were convoluted (Jameson 1950).



Data are presented as  $\bar{x} \pm SE$ .

## RESULTS

### Females

The most reliable indicator of female reproductive state is pregnancy. Of 148 females, 48% were pregnant. However, no pregnant females were collected from November through February (Fig. 1). The level of breeding in females was high from March through October, when the average pregnancy rate was 68.7% (including October of both 1983 and 1984).

Using the Chi-square test, we found no differences ( $\chi^2 = 0.76$ , 2 df,  $P > 0.50$ ) in the proportions of females that were pregnant in the April-May, June-July, and September-October bimonthly periods (not sampled in August). Thus, as measured by pregnancy, females bred at a uniform rate during these months of peak activity.

Overall, litter size averaged  $5.00 \pm 0.284$  SE. However, during the peak breeding months of April to October, females averaged  $5.18 \pm 0.274$  embryos per female. There was significant variation in litter size (embryo counts) throughout the months of the breeding season (ANOVA:  $F = 30.46$ ,  $df = 4,62$ ,  $P < 0.005$ ) with largest litters ( $\bar{x} = 7.83 \pm 0.984$ ) in May. In contrast, females in April averaged only  $4.18 \pm 0.652$  embryos per female, and the two pregnant females in October 1983 had one and two embryos, unusually small litters for the cotton rat.

The pregnant females were divided into primiparous (those in their first reproductive experience) and multiparous (experienced breeders) groups to determine whether a difference in litter size was attributable to reproductive experience. Although there was a trend toward larger litters in multiparous females, there was no significant difference between the litter sizes of primiparous ( $\bar{x} = 4.76 \pm 0.378$  SE) and multiparous ( $\bar{x} = 5.72 \pm 0.371$ ) females during the "peak" breeding months ( $F = 1.74$ ,  $df = 65, 0.1 > P > 0.05$ ). Thus, season had greater influence on litter size than age of the female.

[Begin Page: Page 46, Fig. 1]

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ONDFMAMJ J SON

1983 1984

Fig. 1. Monthly percentages of females (>50 g) that were pregnant. Sample sizes are given above each bar.  $N = 148$ . (No collections in January and August.)

[Begin Page: Page 47, Fig. 2]

100

80

60

40

20

0

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ONDF

1983



A M  
J J  
1984  
S 0  
N

2. Monthly percentages of males (>50 g) that were breeding based on the presence of convoluted cauda epididymides in the testes. Sample sizes are given /e each bar. N = 152. (No collections in January and August.)

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Prenatal Mortality

Preimplantation mortality, which occurs before the embryo has implanted in the uterine wall, can be estimated by comparing the number of ovulation sites with the number of embryos. After ovulation, the remnant of each ovarian follicle is retained. It quickly enlarges into a corpus luteum, a structure 2.0-2.5 mm in diameter, which can easily be seen and counted. If all ova are fertilized and the resulting embryos are successfully implanted, the number of corpora lutea corresponds exactly to the number of embryos. However, if there are, for example, seven corpora lutea but only six embryos, then one ovum has been lost to preimplantation mortality.

There are two potential obstacles to making accurate estimates of preimplantation mortality. The corpus luteum enlarges quickly as it produces progesterone to maintain the thick wall of the pregnant uterus. However, embryos do not appear as bulges in the uterus until day 10 in the 27-day gestation period (Meyer and Meyer 1944). Thus, for a few days the enlarged corpora lutea indicate pregnancy but no embryos are evident. A second problem is twinning, the production of two embryos from the same ovum. In this study, at least four females were judged to be pregnant (i.e. had enlarged corpora lutea) though no embryos were seen, and there was one case of probable twinning. When these females were eliminated from the analysis, preimplantation mortality averaged 5.7% of 371 ova.

Males

Reproductive potential (fertility) in males is most reliably indicated by the presence of convolutions in the cauda epididymides, which Jameson (1950) found to be highly correlated with the presence of sperm in the tubules. Relative testicular mass (the ratio of weight of testes to weight of animal) is a fair predictor of maturity, because the testes grow rapidly in late winter prior to the onset of the breeding season. We used both of these indicators of male breeding capability. Using convoluted cauda epididymides as a criterion, we found that males were fertile longer than females (Fig. 2), from February (73% fertile) to November (33% fertile); from March through July, all males were fertile. According to this criterion, the breeding season of males begins about one month earlier and ends about one month later than that of females.

As is typical of males of many temperate-zone mammals, testes undergo a dramatic regression in late autumn. In *S. hispidus*, the mass of the paired testes of a 120-g male might be 2,000 mg at the height of the breeding season, compared with only 80 mg after testicular regression. With regression, the cauda epididymides lose their convolutions and become looped. Such males are no longer fertile.



**[Begin Page: Page 49, Fig. 3]**

170  
150  
130  
110  
90  
70  
50  
30  
10  
0  
Fig  
Hispid Cotton Rat  
49  
0 N D F  
A M J J S O N  
1983  
1984  
3 .  
Mean testicular mass per 10 g of body weight for each month of study,  
sizes as given in Fig. 2.)

**[Begin Page: Page 50, Fig. 4]**

50  
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1983 1984  
Fig. 4. Mean monthly body masses of male and female cotton rats. (Sample  
sizes as given in Fig. 1 and 2.)

**[Begin Page: Page 51, Fig. 5]**

Hispid Cotton Rat  
51  
1983  
1984  
Fig. 5. Mean monthly body lengths (total length minus tail length) of male and  
female cotton rats. (Sample sizes as given in Fig. 1 and 2.)

**[Begin Page: Page 52]**

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Because not all males are of the same size and because testicular  
mass is approximately proportional to body mass (Keller and Krebs  
1970), we computed the testicular mass per 10 g of body mass (Fig. 3).  
This assessment of male reproduction closely parallels the breeding



season of males based on cauda epididymides (Fig. 2). The testes grew rapidly in late winter (February) so that overwintered males were fully mature by March. The somewhat lower fertility rates of males in late summer (September) probably were a result of an increasing proportion of young males included in the samples. However, later decreases in fertility (November and December in Fig. 2 and 3) were primarily a result of testicular regression in adult males.

#### Dynamics of Body Size

In some parts of the United States, populations of cotton rats have substantial winter mortality (e.g. Dunaway and Kaye 1964, Sauer 1985). Slade et al. (1984) showed that cotton rats surviving the winter in eastern Kansas tend to weigh nearly the same regardless of age; large animals lose mass and young animals entering the winter grow slowly, so that by spring most animals are approximately the same mass. Severe mortality and weight loss in the winter make an evaluation of body weight dynamics particularly important in *S. hispidus* at the northern limit of its distribution, such as in southeastern Virginia.

Of course, chance plays a role in determining the average mass of a sample of field-caught cotton rats, particularly during periods when young animals are entering the trappable population. However, in this study, those effects are minimized because juveniles and small subadults (<50 g) were not collected for necropsy. Overall, males ( $\bar{x} = 101.48 \pm 2.027$  g) were significantly heavier than females ( $\bar{x} = 94.26 \pm 1.872$  g). Body mass differences were smallest (Fig. 4) at the end of the breeding season (October and November). Males were much larger (20-30 g) than females throughout the winter in this study.

Body length (Fig. 5) showed similar trends, with males averaging  $141.11 \pm 1.557$  mm and females  $137.63 \pm 1.441$  mm. Males had roughly linear growth in body length throughout the late autumn and winter, and the decline in mean length was probably a result of the recruitment of spring-born animals into the trappable populations. Body lengths of males and females were most similar in October and November, a pattern also seen with body mass (Fig. 4).

#### DISCUSSION

Mammals seem to adjust the breeding rate to the mortality rate at a given location (Sadleir 1969). Mammals, particularly small mammals, can increase reproduction by one or more of the following means:

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becoming sexually mature at an earlier age, increasing litter size, or increasing the number of litters per year (extending the breeding season or decreasing the interval between litters). Decreasing the time between litters is achieved by a short gestation period and rapid postnatal development, so that the interval between conception and weaning is minimal. In the most rapidly breeding individuals, mating often occurs within 24 to 48 hours after parturition; consequently, a lactating female frequently is pregnant with the next litter. In general, small mammals in the tropics have small litters and long breeding seasons (Sadleir 1969). However, in temperate locations, small mammals tend to compensate for shorter breeding seasons and increased mortality by producing larger litters (e.g. in *Peromyscus* Smith and McGinnis 1968). Of the seven species of New World *Sigmodon*, only *S. hispidus* has a widespread



and expanding distribution in temperate North America, making it a candidate species to examine for evidence of adjustments in its breeding biology in response to the harsher winter conditions endured by populations colonizing northern locations.

#### Pregnancy Rate

Maximum rates of pregnancy were achieved early and sustained throughout the breeding season in Virginia. The observed pregnancy rate often exceeded the theoretically observable maximum pregnancy rate, such as in April when 95% of 21 females were pregnant (Fig. 1). Because bulges in the uterus cannot be detected during the first 9 days of pregnancy, embryos can be counted only for 18 days of the 27-day gestation period. During the peak breeding season, mating usually occurs within 24 hours of parturition, resulting in a 28-day interval between litters. Because embryos can be seen only for 18 days of these 28 days, the theoretical maximum pregnancy rate that can be observed is 18/28, or 64.3%, which is the detectable pregnancy rate if all females are pregnant all of the time. The higher rate in April likely is a result of synchronous breeding at the start of the reproductive season. Breeding synchrony in small mammals diminishes progressively from the start of the breeding season and disappears after the second litters are born, in part because of increasing variation in litter interval among overwintered females but mostly as a result of spring-born females entering the breeding population (at 45-60 days of age for cotton rats). Nothing is known of the actual litter intervals of cotton rats in natural populations, but longer post-partum mating intervals would lower the maximum observable pregnancy rate below the 64.3% value. The observed pregnancy rate during the breeding season (68.7%) slightly exceeded the theoretical value; that can be explained by sampling error or, more likely, by changes in the behavior of pregnant females.

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Randolph et al. (1977) found that the fat accumulated during the last half of pregnancy was used during lactation, when energy demands outstripped the female's speed in processing food. It is plausible that females in the later stages of pregnancy would be increasingly attracted to the high-energy food source (mixed seeds) that was used as bait. Although Dunaway and Kaye (1964) did not calculate monthly pregnancy rates, they did observe low levels and apparently sporadic breeding throughout what they judged to be a relatively mild Tennessee winter. In Oklahoma, Goertz (1965) found no pregnant females during a severe winter, but he did find pregnant females during November, December, and February of a milder winter. Goertz reported highest pregnancy rates during May to September. Haines (1961) recorded no embryos in Texas cotton rats from October to February, but he did record corpora lutea throughout the year. Haines observed the highest pregnancy rates between February and July, with low rates after September and the lowest rates in December. Thus, the breeding season seems to be somewhat earlier in Texas compared with Tennessee, Oklahoma, or Virginia.

In duration, methods, and analysis, our study most closely parallels that of McClenaghan and Gaines (1978), conducted near Lawrence, Kan. They found no breeding from November through March, which is



similar to what we observed in the Virginia population. The pregnancy rate in Kansas was low (30%) in April, highest (over 80%) in May, and generally greater than 70% from June through October. Overall, the patterns of breeding in Virginia and Kansas were similar for both sexes.

#### Litter Size

Within a species, litter size is affected by several interacting factors, including age, parity, body weight, and nutritional state (Sadleir 1969). In a recent exhaustive review, Cameron and McClure (1988) examined the patterns of breeding in female *Sigmodon hispidus* by evaluating published and unpublished laboratory and field data. Using a stepwise multiple regression analysis on data from 18 studies, Cameron and McClure (1988: table 2) examined the patterns of geographic variation in litter size and the effects of body size on litter size. By finding latitude, longitude, and body length to be significantly associated with mean litter size, their analysis "confirmed the existence of both north-south and east-west variation in litter size." Largest litters were reported for the large females of the north-central states.

A further analysis "indicated that latitudinal and longitudinal variation in litter size were due primarily to differences among subspecies" (Cameron and McClure 1988). Specifically, *S. hispidus texianus*, which had the largest litters at  $7.20 \pm 0.23$  SE, averaged  $8.35 \pm 0.35$  in Kansas

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but only  $5.10 \pm 0.37$  in coastal Texas (Houston). Nutrition may also contribute to these differences within this subspecies (Cameron and McClure 1988; table 6). Although litters of *S. hispidus virginianus*, the subspecies in Virginia, were significantly larger than those of Mexican and Central American subspecies, they were significantly smaller than those of *S. h. texianus* (Cameron and McClure 1988).

The litter size of 5.00 for Virginia cotton rats lies in the range of values reported from other studies (Cameron and McClure 1988: table 2), although on the low side for "northern populations." Populations from Tennessee averaged 6.1 embryos per litter (Dunaway and Kaye 1961), from Oklahoma 6.0 (Goertz 1965), from western Kansas 6.7 (Fleharty and Choate 1973), and from eastern Kansas 9.0 (McClenaghan and Gaines 1978). Furthermore, laboratory animals derived from Houston, Kansas, and Tennessee populations and raised by McClure at Indiana University remained significantly different in average litter size even after 16-28 generations and 8-12 years in the laboratory (Cameron and McClure 1988: figure 2). Thus, the determination of litter size in *Sigmodon hispidus* is complex, involving both genetic and environmental factors.

Although Lawrence, Kan., and Portsmouth, Va., are both near 37° N latitude, the Kansas winters are longer and colder (average 2° C), in the absence of moderating oceanic effects. In coastal Virginia, snow falls only once or twice a year and periods of freezing weather rarely last more than a few days. Despite the more moderate conditions in Virginia (Cameron and McClure 1988: table 4), the Virginia cotton rats did not breed longer than the Kansas cotton rats, and Virginia litter sizes as well as body sizes were significantly smaller. However, female cotton rats in Virginia were pregnant at nearly maximum levels throughout the breeding season (Fig. 1), and there was a trend ( $0.1 > P > 0.05$ ) for multiparous



females to have larger litters than primiparous females. Thus, differences in age of onset of breeding and in longevity (neither of which was measured in these studies) may be important in affecting geographic differences in the dynamics of these populations.

#### Male Breeding

The breeding season of males began in February and lasted to November (Fig. 2). Based on the breeding criterion of convolutions in the cauda epididymides, 73.3% of males were in breeding condition in February and 100% were fertile from March through June. McClenaghan and Gaines (1978), who also used epididymal convolutions to determine breeding condition in males, did not find 100% breeding in any month. Their highest monthly rates were just under 90% in June and August; and in all other months during the breeding season except May, fertility

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rates were less than 60%. Haines (1961) measured spermatogenesis and found that the production of sperm remained high from February through October (which was the breeding season for males in our study). Dunaway and Kaye (1964), who assessed male reproduction based on live-caught animals, observed that just under 100% of males had descended testes (i.e. were mature) during the June-September period. They noted a decline in the percentages of mature males from October to December, but by January, the proportion of males with descended testes again began to increase.

Testicular mass is closely related to reproductive condition in males (Haines 1961). Our results agree with those of McClenaghan and Gaines (1978), who found testicular mass to be highest from June through September, also the peak breeding months for males as determined by convolutions of the cauda epididymides in the present study. In Kansas, smallest testicular masses were recorded for December, but we found the smallest testicular masses in the October to December period, with dramatic monthly increases from December through April. Testicular mass remained high from April through July and then declined sharply (Fig. 3), probably at first because of the recruitment of young males in the trappable population and later also because of testicular regression of adult males. Goertz (1965) reported large testicular masses from February through September and low values in the remaining months. In Texas, Haines (1961) reported spermatogenesis in males with the largest testicular masses; he provided perhaps the best available information on the relationship between these two variables. He found the largest average testicular mass per 10 g of body mass during the period from February through August, after which testicular mass declined until November. McClenaghan and Gaines (1978) and Haines (1961) found that testicular regression resulted in a reduction to about 1 / 30th of the maximum testicular mass, compared with a value of about 1 / 26th in our study.

#### Breeding Season

During the breeding season, 68.7% of females were pregnant, and in most of the same months all males were judged to be fertile. The breeding season in males started one month earlier and ended one month later than the breeding season in females. That pattern is common in mammals (Sadleir 1969), and it is interpreted as adaptive in



that the energy costs for breeding in females are greater than those in males. As a result of the earlier onset of fertility in males, mature males are ready to copulate and produce fertile matings when females undergo the first estrous cycle of the spring.

The breeding season in Virginia closely paralleled that found by McClenaghan and Gaines (1978) in Kansas. Both locations are at or

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near the northern limit of distribution for hispid cotton rats; therefore, it is not surprising to find some similarities. Differences also were noted. Although the breeding season in Virginia started a month earlier in both sexes, it lasted until October for females in both Kansas and Virginia. Another similarity in the breeding of *Sigmodon* in these two studies is the percentage of breeding females; the rate was relatively low during the first month in which pregnancies occurred and then rose sharply to near the maximal rate in the following month. In McClenaghan and Gaines (1978), this trend must be inferred because their study ended in April. However, if the high May level at the start of their study can be extrapolated to the preceding April, a large increase in breeding level occurred at the same time in Kansas and Virginia.

In Texas (Haines 1961), the breeding season began in the same month as in Virginia, but it ended one month sooner. This is an unexpected result if we assume that the breeding season has been shortened at more northerly locations because of the constraints of winter on the energy budgets of mammals. We would expect the breeding season to be longer at more southerly locations. Goertz (1965), who found pregnant females in some winter months, believed that breeding was possible in Oklahoma under the favorable conditions of mild winters.

#### Effects of Body Size

Several factors affect patterns of body size in *Sigmodon hispidus*, including sex, latitude, subspecies, and nutrition. In some, but not all, populations males are larger than females, and northern populations tend to have larger skeletal sizes and, in some seasons, higher fat content. *Sigmodon h. texianus* is significantly larger than all other subspecies (Cameron and McClure 1988). McClenaghan (1977) found generally larger skull and skeletal variables for cotton rats from northern populations (Kansas and Virginia) than from southern localities (Mexico), but Kansas and Virginia populations differed in only one skeletal feature. However, the seasonal pattern of body growth of Virginia cotton rats differs from that of Kansas cotton rats, in which Slade et al. (1984) found that the large adult animals lost weight over the winter. By contrast, in Virginia, the males in particular gained body mass steadily throughout the winter months (Fig. 4). This pattern of winter increase is evident but less well defined for body length (Fig. 5), although males did increase in length nearly every month from October to May or June. Mean body mass for females was low in October ( $79.7 \pm 6.77$  g) but it rose sharply to  $98.6 \pm 10.19$  g in November. The mean values for December and February were low, indicating that females were not gaining weight during this time. Because there was no breeding during these months, the lower mean mass in winter cannot be a result of the



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recruitment of young, lightweight animals; therefore, we can assume that females either lose mass or fail to gain significant mass during the winter months. From February through July, the monthly mean mass of females rose steadily, indicating a real increase in body mass during this time. Then, when the young of the year finally entered the trappable population, the monthly mean mass of females (and males) declined. Patterns of body length were similar to those of body mass.

Although both length and mass are measures of body size, length may be a more reliable index of body growth in *S. hispidus* because (1) animals lose mass but not length during starvation or during winter, (2) both sexes divert resources away from growth and towards reproduction during the breeding season, and (3) females store up body fat during pregnancy in preparation for the greater energy demands during lactation (Randolph et al. 1977).

In conclusion, cotton rats in southeastern Virginia seem to be well adapted to the northern limit of their present distribution on the East Coast; their March-to-October breeding season and the sustained growth of overwintering individuals suggest high survival rates of both young and adults during the winter months. The modest litter size may indicate that, unlike Kansas populations, Virginia populations have not been selected for larger litter sizes to compensate for winter mortality.

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