EFFECT OF WEATHER ON INDIVIDUAL GROWTH RATES IN COTTON RATS, SIGMODON HISPIDUS

MARIA A. EIFLER AND NORMAN A. SLADE

Natural History Museum and Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, KS 66045-2454
Present address of MAE: Department of Biology, University of Wisconsin—Stevens Point, Stevens Point, WI 54481-3897

Weather can influence many aspects of mammalian life histories through its impact on growth rates. We examined the seasonal effect of rain, mean temperature, snowfall, and snow cover on changes in body mass among individual young (<60 g) and adult (>60 g) cotton rats (Sigmodon hispidus) in northeastern Kansas from March 1978 to December 1993. Weather significantly affected growth rates among all sex-season-size groupings except for young cotton rats in summer. In seasons other than summer, weather accounted for 53-68% of the variation in growth rates of young rats. Weather generally accounted for less of the variation in growth rates of adult cotton rats. When significant, snow cover was associated negatively and rainfall was associated positively with growth rates of all cotton rats. High temperatures in summer adversely affected growth rates of adult cotton rats but were associated with higher growth rates among all size-sex combinations in autumn. Growth rates of adult females in spring and adult males in autumn were highest at intermediate temperatures and lower at extremes. In autumn, response of growth rates of adult males to mean temperature varied with body mass. Intrapopulational variation in responses to weather may reflect different environmental and reproductive constraints at various points in the life cycle.

Key words: Sigmodon hispidus, cotton rats, body mass dynamics, growth, weather

Weather influences many aspects of small-mammal ecology, including length of the breeding season (Mills et al., 1992), reproductive effort (Mills et al., 1992), microhabitat use (Baar et al., 1975; Dawson and Lang, 1973; Sealandier, 1952; West, 1977), social interactions (Turner et al., 1975; West and Dublin, 1984), and activity patterns (Doucet and Bider, 1974; Eifler and Slade, 1998; Gentry and Odum, 1957; Getz, 1961, 1968; Marten, 1973; Martin, 1983; Sidorowicz, 1960; Vickery and Bider, 1981). Seasonal weather patterns also can result in changes in morphology, such as the amount of insulation (Bolshakov, 1984; Hart, 1956; Hart and Heroux, 1953; Kostelecka-Myrcha et al., 1970), fat deposition (Fleharty et al., 1973; Hayward, 1965), or in changes in physiology (Hart and Heroux, 1953; Sealandier, 1952). Some investigators have speculated that weather accounts for seasonal differences in growth rates of individual small mammals (Mills et al., 1992; Porter and McClure, 1984; Slade et al., 1984), though none have attempted to correlate specific weather variables with growth data. When examined within a population, the long-term relationship between growth rates and weather provides a means of beginning to explore energetic tradeoffs between growth, reproduction, and maintenance.

The cotton rat (Sigmodon hispidus) is a good subject for investigations on the interplay between weather, growth rates, and energetics. Intrapopulational variation in body mass can be prominent. Some breeding individuals are <60 g, but others are >250 g (McClanaghan and Gaines, 1978; Slade et al., 1984). Intrapopulational differ-
ences in body mass also have been associated with variation in life-history traits such as litter size (Goertz, 1965; Kilgore, 1970; McClenaghan and Gaines, 1978), survivorship (Campbell and Slade, 1993), and seasonal growth rates (Slade et al., 1984). Severe weather has been used to explain interand intrapopulational differences in reproductive patterns, overwinter survivorship, and body mass among cotton rats (Campbell and Slade, 1993; Dunaway and Kaye, 1961; Goertz, 1964, 1965; Langley and Shure, 1988; Sauer, 1985; Slade et al., 1984).

Cotton rats are of subtropical origin (Hooper, 1949) but have expanded their range northward, reaching into northern Kansas and southern Nebraska during the last 50 years (Cockrum, 1948; Farney, 1975; Jones, 1960; Rinker, 1942). Highly seasonal environments in northern regions of their range can adversely affect cotton rats by reducing available food and cover at certain times of year (Langley and Shure, 1988). Some animals die (Dunaway and Kaye, 1961; Goertz, 1964, 1965; Langley and Shure, 1988; Sauer, 1985; Slade et al., 1984).

To determine how environmental variables interact with body mass, we examined the relationship between weather variables and seasonal changes in body mass of individual cotton rats in northeastern Kansas near the northern limit of their range. We investigated the extent to which seasonal differences in growth rates (Slade et al., 1984) were attributable to weather by examining the correlation between growth rates and weather and comparing the strength of the relationship seasonally. We expected the correlation between weather variables and growth rates to be weakest in summer when resources were abundant, but of increasing importance in other seasons. We predicted that growth rates would be most influenced by weather in winter because small mammals may require several times more food to maintain body temperatures during sub-freezing weather (Haines, 1971). Low ambient temperatures and insufficient food to maintain body temperature may combine to result in “cold-weather starvation” among small mammals (Howard, 1951:300). We also expected adverse weather in winter to be more strongly correlated with growth rates of smaller, rather than larger, cotton rats. Small cotton rats have proportionately smaller fat reserves than larger individuals (Fleharty et al., 1973), are more likely to lose heat to the environment because of their higher surface-to-volume ratio (Calder, 1984; Louw, 1993), and are likely to have higher metabolic rates (Schmidt-Nielsen, 1984). In combination, differences in fat reserves, heat loss, and metabolism could serve to increase energetic stress of small animals proportionately more than larger animals at a time when food is scarce. Smaller body size also results in lower maintenance costs, but smaller cotton rats that survive the winter continue to grow whereas larger cotton rats lose mass (Slade et al., 1984). To accomplish growth, smaller animals need resources in addition to those required for maintenance. Finally, we predicted that the importance of specific weather variables to
growth rates would vary with size, sex, and season as individual cotton rats shift their energetic balance among growth, maintenance, and reproduction.

MATERIALS AND METHODS

We analyzed trapping records collected in an old field from March 1978 to December 1993 at the Nelson Environmental Studies Area of the University of Kansas’ Ecological Reserves, 14 km NE of Lawrence, Jefferson Co., Kansas (39°05’N, 95°15’W). Typically, the climate in northeastern Kansas is highly variable both within and between seasons and is characterized by hot humid summers, cold dry winters, and mild transitional seasons (Dickey et al., 1977). July and August are usually the hottest months (mean maximum ca. 32°C; mean minimum 20.4°C for July and 19.5°C for August), and January is coldest (mean maximum 4.4°C; mean minimum −6.3°C). Average precipitation amounts to < 1,000 mm/year (914-965 mm) falling on ca. 95 days. About 5% of the annual precipitation occurs as snow (<500 mm/year, or ca. 50 mm precipitation). Most of the annual precipitation occurs from April through September; February is the month of maximum snowfall (Dickey et al., 1977).

We trapped at monthly intervals, although occasionally sessions were omitted or rescheduled during winter when weather conditions were severe enough that trap deaths could be high. The trapping grid had 99 stations, each with two Sherman live-traps (30.5 by 7.6 by 8.9 cm). Fewer stations (76) were used from March 1978 to April 1979, but trapping protocol remained constant. Traps were locked open on the grid most of the time; they were set in the afternoon prior to a trapping session and baited with scratch grain (cracked corn, *Zea mays*; wheat, *Triticum aestivum*; grain sorghum, *Sorghum vulgare*). During cold months, polyester fiberfill was provided in each trap. Boards were placed over the top of traps to provide protection from rain, snow, and sun. Traps were checked five times over the 3 consecutive days of a trapping session: morning and afternoon on the first 2 days and morning of the 3rd day. Captured animals were ear-tagged and weighed, and their sex, reproductive condition, and location on the grid recorded.

To determine growth rate, we calculated change in body mass of an individual from its first capture in one trapping session to its first capture in the next session and divided that change by the number of intervening days. Thus, more than one growth rate could be calculated for an individual if it was captured in more than two trapping sessions. We excluded obviously pregnant females because of large weight gains and losses associated with pregnancy. We judged a female to be pregnant when her abdomen was distended or her pubic symphysis open. We excluded the record for the trapping session when she was judged near parturition and for prior and subsequent sessions. We report growth rates in grams per week for comparison to previously published growth rates for cotton rats (Cameron and Spencer, 1983; Slade et al., 1984), but used grams per day in analyses comparing growth rates with weather variables. Captures were partitioned by season (winter, December–February; spring, March–May; summer, June–August; autumn, September–November) and by body mass at first capture in each interval. Cotton rats have short life spans; populations turnover in as little as 5 months (Goertz, 1964) to as long as 10 months (Cameron, 1977). They can grow to sexual maturity by 2 months of age (Meyer and Meyer, 1944) and have seasonally variable mass-specific growth rates (Slade et al., 1984). To maximize our ability to attribute changes in mass to concomitant changes in weather, we excluded calculations of growth rates that spanned intervals of more than three trapping sessions or 100 days.

Weather data for the period spanning our trapping records were obtained from the Hilltop Weather Station in Lawrence, Kansas (Stokes, 1994). We summarized weather variables for the time period between pairs of trapping sessions used to calculate a growth rate (= trapping interval); hence, each growth rate and its associated weather variables were calculated over the same interval. We examined effects of mean temperature, rainfall (total cm), snowfall (total cm), and proportion of days in a trapping interval with ≥2.5 cm of snow on the ground (= snow cover) on growth rates. Except where noted in the text, we determined effect of weather on growth rates using multiple linear regression. We included body mass as a predictor in each model because growth rates among cotton rats vary significantly with body mass (Slade et al., 1984); inclusion of body mass as a predictor per-
mitted us to determine mass-specific variation in growth rates attributable to weather. When fitting models, we first considered all predictor variables, removed the least significant predictor of growth rate, and reran the analysis. With each model, we ran a lack-of-fit test and included variables to account for interactions and curvilinearity (by squaring variables) with each iteration. Correlation between mean temperature and mean temperature squared was so high that collinearity precluded calculations. To remove the high correlation, we adjusted mean temperature by first calculating the mean of all individual mean temperatures associated with each growth rate (= grand mean) and subtracted that grand mean from each individual mean. We used resulting values (deviation of individual mean from grand mean) and their squares in the analyses. Missing data, particularly for snowfall, were obtained from National Weather Service records for Lawrence and Topeka. We used Minitab (version 10 for Windows; State College, PA) for data analyses.

**RESULTS**

**Preliminary partitioning of data.**—We used 779 growth rates from females and 890 from males in our analyses. Initial plots of growth rates as a function of mass indicated that smaller animals grew at a higher rate than larger animals. In particular, growth rates appeared to change at ca. 60 g, around the point at which *Sigmodon hispidus* reaches sexual maturity (McClenaghan and Gaines, 1978; Meyer and Meyer, 1944; Odum, 1955). Using approximate mass at sexual maturity as a cutoff, we found that separate linear regressions of growth rate on animals ≤60 g and >60 g yielded significantly different slopes (*F* = 36.7; *d.f.* = 2, 1,665; *P* < 0.0001). Consequently, we partitioned our data into two groups: young animals (≤60 g; *n* = 600) and adults (>60 g; *n* = 1,069). We also analyzed each season separately because growth rates of cotton rats varied significantly with season (General Linear Model [GLM]; young, *F* = 188.11; *d.f.* = 3, 592; *P* < 0.0001; adult, *F* = 111.61; *d.f.* = 3, 1,061; *P* < 0.0001; Table 1). Finally, the interaction between sex and season also

**Table 1.** Mean growth rates in g/week ± SE (n) by sex and season obtained from general-linear-model analysis. Young cotton rats are ≤60 g and adult cotton rats are >60 g in body mass. An asterisk next to the value for females indicates that sex is a significant predictor of growth rates within a size class and season (*P* ≤ 0.05; regression analysis).

<table>
<thead>
<tr>
<th>Season</th>
<th>Males</th>
<th>Females</th>
<th>Both sexes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>14.65 ± 1.50 (53)</td>
<td>14.86 ± 1.18 (79)</td>
<td>14.70 ± 1.07 (110)</td>
</tr>
<tr>
<td>Summer</td>
<td>12.67 ± 0.71 (159)</td>
<td>13.77 ± 0.60 (278)*</td>
<td>14.07 ± 0.47 (49)</td>
</tr>
<tr>
<td>Autumn</td>
<td>7.77 ± 0.21 (215)</td>
<td>6.15 ± 0.18 (340)</td>
<td>6.90 ± 0.13 (345)</td>
</tr>
<tr>
<td>Winter</td>
<td>1.10 ± 0.54 (33)</td>
<td>0.97 ± 0.46 (46)</td>
<td>1.03 ± 0.36 (79)</td>
</tr>
</tbody>
</table>

...
TABLE 2.—Seasonal means ± SD and range for weather variables used in analyses; n refers to the number of growth rates that were calculated during each season.

<table>
<thead>
<tr>
<th>Season</th>
<th>n</th>
<th>Rain (cm)</th>
<th>Snow (cm)</th>
<th>Mean temperature (°C)</th>
<th>Snow cover (proportion days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring</td>
<td>97</td>
<td>8.31 ± 5.57</td>
<td>5.02 ± 10.71</td>
<td>11.09 ± 5.26</td>
<td>0.002 ± 0.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.17-23.62</td>
<td>0-34.06</td>
<td>1-19.5</td>
<td>0-0.104</td>
</tr>
<tr>
<td>Summer</td>
<td>160</td>
<td>13.97 ± 15.20</td>
<td>0</td>
<td>25.09 ± 2.67</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.33-53.19</td>
<td>18-29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn</td>
<td>1,026</td>
<td>7.82 ± 6.30</td>
<td>0.74 ± 1.62</td>
<td>14.89 ± 5.35</td>
<td>0.037 ± 0.080</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0-31.88</td>
<td>3.5-27</td>
<td></td>
<td>0-1</td>
</tr>
<tr>
<td>Winter</td>
<td>386</td>
<td>3.83 ± 3.38</td>
<td>7.35 ± 9.49</td>
<td>2.21 ± 2.79</td>
<td>0.164 ± 0.170</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0-16.59</td>
<td>-6-8</td>
<td></td>
<td>0-0.622</td>
</tr>
</tbody>
</table>

was significant for young animals (GLM, \( F = 9.66; d.f. = 3, 592; P < 0.0001; \) Table 1) and approached significance for adults (GLM, \( F = 2.41; d.f. = 3, 1,061; P = 0.066; \) Table 1); hence, we looked for the effect of sex within each season. When sex significantly affected growth rates, we further partitioned the data by sex.

Overall trends.—Mean growth rates were highest in spring for both adult and young cotton rats (Table 1); mean growth rates in summer approached rates in spring for young animals but decreased by ca. 20% among adult cotton rats (Table 1). In autumn, mean growth rates fell by ca. 50% compared with spring for young cotton rats and by 60% for adults (Table 1). Seasonal mean growth rates were lowest in winter. Among young animals, growth rates averaged <10% of the rate of animals in spring, and those of adult cotton rats were slightly negative in winter (Table 1). Extremes in growth were both attained by females; young females in summer grew faster and adult females in winter grew slower (a negative value) than any other sex-season combination (Table 1).

Effects of weather.—Weather during the 15.5 years of our study was consistent with typical weather patterns for the region (Dickey et al., 1977). Rainfall and mean temperature were highest during summer and lowest during winter (Table 2). Mean temperatures were slightly higher in autumn than spring, but rainfall was similar. Snowfall was highest in winter but also was quite high in spring. Occasional heavy snowfalls occurred in autumn (Table 2). In general, seasonal weather variables we measured were not substantially intercorrelated (\(-0.236 \leq r \leq 0.244; -1.65 \leq t \leq 1.69; P > 0.05\), except for mean temperature and snowfall in winter and spring (\( r = -0.65 \) and \( -0.75, t = -4.7 \) and \( -7.27, P < 0.0001 \), respectively). In addition, we found significant but lower correlations between mean temperature and both snow cover (\( r = -0.47, t = -3.52, P = 0.001 \) and snowfall in autumn (\( r = -0.35, t = -2.5, P = 0.02 \)).

Weather significantly affected growth rates of young cotton rats in all seasons except summer, accounting for 53–67.9% of the variation in growth rates (Table 3). During spring, only snowfall was significantly related to growth rates. In autumn, young male cotton rats grew significantly faster than females (Table 1). However, the sexes were affected differently by weather (Table 3). Rain was related positively to growth rates of males, but growth rates of females in autumn were related negatively to snow cover and significantly related to the interaction between mass and rainfall (Table 3). In winter, growth rates of young cotton rats were related positively to rainfall, related negatively to mean temperature, and related curvilinearly to snowfall (Table 3).

Growth rates for adult male cotton rats were significantly higher than those of females in all seasons except summer (Table 1). Weather significantly influenced growth
### Table 3.
Regression analyses of growth rates and weather variables. The response variable used in all analyses was change in mass (g/day). Significant predictor variables are marked with asterisks; the overall significance level of the model is in the "Model P" column. When sex was a significant predictor of growth rate, we analyzed males and females separately. Mass = mass of the animal at the start of the growth interval; Rain = average cm of rain that fell during the growth interval; Snow = average cm of snow that fell during the growth interval; Meant = mean temperature calculated over the growth interval for each animal; Snowcov = the proportion of days during the growth interval with an inch or more of snow on the ground; Other = variables created to account for significant lack of fit in models due to curvilinearity (squared terms) or interactions: A = \((\text{adjusted mean temperature})^2\); B = mass \(\times\) adjusted mean temperature; C = mass \(\times\) rain; D = (snow cover)^2.

<table>
<thead>
<tr>
<th>Coefficients for predictor variables</th>
<th>Young cotton rats</th>
<th>Adult cotton rats</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mass</td>
<td>Rain</td>
</tr>
<tr>
<td>-------------------------------------</td>
<td>------</td>
<td>------</td>
</tr>
<tr>
<td>Spring Young</td>
<td>0.010</td>
<td>-0.114*</td>
</tr>
<tr>
<td>Summer (males)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer (females)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn (males)</td>
<td>-0.008***</td>
<td>0.039***</td>
</tr>
<tr>
<td>Autumn (females)</td>
<td>-0.015***</td>
<td>-0.003</td>
</tr>
<tr>
<td>Winter</td>
<td>-0.011***</td>
<td>0.119***</td>
</tr>
<tr>
<td>Autumn (males)</td>
<td>-0.008***</td>
<td>0.058***</td>
</tr>
<tr>
<td>Autumn (females)</td>
<td>-0.006***</td>
<td>0.025***</td>
</tr>
<tr>
<td>Winter (males)</td>
<td>-0.004***</td>
<td>-0.051***</td>
</tr>
<tr>
<td>Winter (females)</td>
<td>-0.006***</td>
<td>-0.026***</td>
</tr>
</tbody>
</table>

* 0.01 < \(P\) ≤ 0.05; ** 0.001 < \(P\) ≤ 0.01; *** \(P\) ≤ 0.001.
rates in all seasons, except for males in spring \( (P > 0.05; \text{Table 3}) \). Growth rates of females in spring were affected positively by rainfall. Growth rates of females also were related curvilinearly to mean temperature (Table 3). Growth rates were highest at intermediate mean temperatures (ca. 7–11°C) and lowest at extremes. Growth rates at high mean temperatures (ca. 14–19.5°C) were very low. Growth rates at low mean temperatures (1–2°C) were greater than those at high mean temperatures but less than those at intermediate temperatures.

Growth rates of adults in summer were related negatively to mean temperature; other weather variables did not influence growth rates of adults (Table 3). In autumn, growth of both sexes was related negatively to snow cover and related positively to mean temperature. Growth of males, however, also showed a positive relationship to rainfall and to the product of mass and adjusted mean temperature. Growth of adult males was related curvilinearly to adjusted mean temperature in autumn (Table 3), with growth rates increasing as mean temperature increased until 17°C; growth rates above 17°C declined. The regression model for adult males accounted for twice the variation in growth rates as the model for adult females (Table 3). During winter, weather influenced growth of adult males and females similarly; growth rates were related negatively to mean temperature and snow cover (Table 3).

**DISCUSSION**

Weather can have a substantial influence on growth rates of cotton rats, particularly and most consistently among young animals (note high \( R^2 \) values in Table 3). Our predictions were generally supported by our results for young animals, but support was less straightforward among adult cotton rats. Growth rates of young cotton rats were least affected by weather in summer, and the relationship between weather and growth was intermediate in autumn relative to the other three seasons. However, the highest proportion of variation in growth rates of young cotton rats was explained by weather in spring, not in winter (Table 3). Furthermore, importance of specific variables changed seasonally (Table 3), but the effect of specific weather variables on growth patterns was not consistent across size and sex groupings, perhaps because the annual cycle of resource availability and climatic stress at northern latitudes interact to shift energetic balance among growth, reproduction, and maintenance during different times of the life cycle of cotton rats.

**Spring.**—Spring is a crucial season for young cotton rats because individuals are growing rapidly (Table 1) and coming into breeding condition for the first time while food plants are just beginning to grow (Weaver and Fitzpatrick, 1934). Rapid body growth accelerates attainment of sexual maturity and may promote reproductive success. In early spring, sexual maturity occurs at a lower body mass than later in the breeding season (McClenaghan and Gaines, 1978). Furthermore, females of larger body mass have more young (Campbell and Slade, 1995; Kilgore, 1970; McClenaghan and Gaines, 1978), heavier young (Campbell and Slade, 1995), and higher recruitment of juveniles (Campbell and Slade, 1995). Among males, larger body size may increase success at gaining mating opportunities (Andersson, 1994).

Snowfall significantly affected growth rates of young animals in spring (Table 3). Snowfall can inhibit foraging if plants are covered and therefore less accessible to cotton rats. Snowfall in spring is also highly correlated with low mean temperatures \( (r = -0.75) \). Because of their relatively small body size, young cotton rats have proportionately high surface-to-volume ratios (Schmidt-Nielsen, 1984), which increases their heat loss to the environment via conductance. Consequently, young animals need to produce more heat per gram of body tissue than adults (Louw, 1993) and may use available energy for thermoregulation rather than growth under the cold conditions.
damp conditions occurring with snowfall. Severe weather can delay growth of food plants (Weaver and Fitzpatrick, 1934), but young overwintering cotton rats become more active as temperatures decline and are quite active during daylight hours (Eifler and Slade, 1998), probably because they lack stored food or fat reserves. Hence, growth rates of young cotton rats are particularly sensitive to weather during spring.

Among adults, growth rates of males were independent of weather in spring. But, as with young cotton rats, growth rates of adult females showed a stronger relationship to weather in spring than in other seasons when body mass imposed an important reproductive constraint (Campbell and Slade, 1995; McClenaghan and Gaines, 1978). In contrast to young cotton rats, growth rates of adult females were linked positively to rainfall, not negatively linked to snowfall (Table 3). Activity of adults does not increase in response to colder temperatures (Eifler and Slade, 1998). Rather, response of the growth rates of adult females to rainfall is likely to be related to the increase in resource availability associated with spring rain (Weaver and Fitzpatrick, 1934). Growth rates of adult females in spring changed more per millimeter of rain than did growth rates of any other size-sex combination in any season (coefficient of 0.214 versus 0.003–0.119; Table 3), underscoring the importance of resource availability to adult females during spring when they are replenishing fat reserves depleted during winter (Fleharty et al., 1973). Growth rates of adult females may be particularly responsive to rain (and resource availability) during spring because pregnancy, which can occur in early spring (McClenaghan and Gaines, 1978), is very energetically costly for cotton rats (Randolph et al., 1977). In addition, growth rates of adult females were related curvilinearly to temperature in spring and were particularly low during warm springs (14–19.5°C; Table 3), which suggested that heat can constrain diurnal activity of larger individuals, an observation borne out by the negative relationship between mean temperature and growth rates of adults in summer.

**Summer**.—Growth rates of young cotton rats were independent of weather in summer, but growth rates of adults were constrained as temperatures increased (Table 3). Cotton rats in eastern Kansas are inactive during the middle of the day in summer (Prochaska and Slade, 1981). Although the effect of temperature on summer activity in *S. hispidus* has not been described, research on other small mammals indicates that temperature can be an important factor influencing diel activity cycles (Getz, 1961; Marten, 1973; Martin, 1983; Sidorowicz, 1960; Vickery and Bider, 1981). Adult cotton rats may be less active when temperatures are high and more likely to forage when summer temperatures are more moderate, either because larger animals have greater difficulty unloading excessive heat than small animals (Louw, 1993), or because larger animals may be able to go for longer periods of time without eating and rely on fat reserves, limiting their excursions to periods of more favorable weather. In either case, high temperatures would be associated with slower growth.

**Autumn**.—Weather had a pronounced relationship with growth rates among all cotton rats in autumn, but the relationship differed with each size-sex grouping. Growth rates of all cotton rats responded to a combination of weather conditions that influence continued resource availability, with slight variations among groups (Table 3). Snow cover, which increases the difficulty of finding food, was negatively associated with growth rates of most cotton rats in autumn (young males excluded; Table 3). Although the seasonal mean for snow cover was highest in winter, the highest proportion of days with ≥2.5 cm of snow on the ground occurred in autumn (Table 2). Snow in autumn may be aberrant or may shorten the growing season (Weaver and Fitzpatrick, 1934) and may introduce added phys-
iological stress at a time when food supplies are beginning to diminish. Likewise, the large range of mean temperatures in autumn, which can be nearly as hot as summer or as cold as winter (Table 2), may be difficult to accommodate physiologically. In particular, cold temperatures, which were associated with lower growth rates, may be particularly stressful as cotton rats balance the need to find food with heat loss associated with foraging in cold temperatures (Howard, 1951). The higher growth rates that were associated with higher temperatures suggest that cotton rats restrict foraging to times when temperatures are more moderate, or at least devote less energetic expenditure to heat production than at lower temperatures.

Winter.—During winter, extended periods of snow cover were related to low growth rates among all cotton rats (Table 3). Snow cover in winter makes foraging more difficult because green plants, if present at this time of year, grow very low to the ground (Weaver and Fitzpatrick, 1934) and are less accessible when covered with snow.

All cotton rats also showed an inverse relationship between growth rates and mean temperature (Table 3). The seemingly paradoxical relationship between growth and temperature during winter could reflect changes in activity patterns in response to winter temperatures. If cotton rats move about very little during cold winter temperatures, perhaps only for brief forays to obtain food, energetic costs could be only slightly above maintenance. However, if cotton rats become more active during warmer winter conditions, perhaps taking longer to forage or exploring more, their energetic costs could be higher, particularly since “warm” winter temperatures are still quite cold (ca. 2–5°C). Higher energetic costs could result in lower growth rates during periods of warmer winter weather. Activity patterns of cotton rats can vary with winter temperatures (Eifler and Slade, 1998), but more detailed studies examining the relationship between metabolic rates, activity patterns, and weather (temperature and snowfall) during winter are needed to understand this result.

Growth rates of young cotton rats in winter also were associated positively with rainfall; increasing rainfall was always associated with higher growth rates (Table 3). Rainfall in spring, autumn, and winter is associated with warmer temperatures than snowfall. Growth rates may be enhanced with rain because moderate temperatures are less energetically stressful (Louw, 1993). Alternately, moist mild conditions enhance vegetative growth and either delay vegetative dormancy (autumn and winter) or prompt vegetative regrowth (Weaver and Fitzpatrick, 1934).

Although growth rates of cotton rats did not vary seasonally in coastal Texas where mild weather predominates and resources are continuously available (males, $\bar{x} = 4.15$ g/week; females, 4.67 g/week—Cameron and Spencer, 1983), seasonal differences in growth rates of cotton rats do occur in the highly variable climate of northeastern Kansas. Mean growth rates in summer reported in our study (4.37–15.77 g/week) were not as variable as those reported previously (–6.7–20.1 g/week—Slade et al., 1984), but the extremes reported by Slade et al. (1984) can be attributed to reproductive females. Excluding these females, our rates are similar. When compared with growth rates in the less seasonal environment of coastal Texas (0.6–6.33 g/week—Cameron and Spencer, 1983), cotton rats near the northern limit of their range grow more rapidly and with more annual variability (–0.44–15.77 g/week)—differences that can now be linked to weather.

ACKNOWLEDGMENTS

We thank H. Shirer for collecting and M. Stokes for compiling weather data. We are indebted to several generations of students who contributed to trapping efforts over the 15 years of our study. Our work was supported by the E. Raymond Hall Fund of the University of Kansas.
Natural History Museum and University of Kansas General Research Fund Grants 3022-0038 and 3191-0038 (NAS). H. Alexander, W. Busby, D. Eifler, R. Timm, and two anonymous reviewers provided helpful comments on the manuscript. This research was done in partial fulfillment of a Ph.D. degree in the Department of Systematics and Ecology at the University of Kansas (M. A. Eifler).

LITERATURE CITED


Associate Editor was Edward J. Heske.