Research article

Developmental plasticity of postweanling cotton rats (*Sigmodon hispidus*) as an adaptation to nutritionally stochastic environments

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Abstract. Elucidating interrelationships between rate of growth and sexual maturation in unpredictable or stochastic environments could increase our understanding of life-history strategies of small mammals. It has been hypothesized that species living in environments where food availability is unpredictable might become sexually mature at smaller sizes and channel excess energy into reproduction rather than into compensatory growth. We explored this hypothesis in female cotton rats (*Sigmodon hispidus*) by feeding variable levels of dietary protein during early postweanling development (14–45 days of age) and monitoring compensatory growth and fitness after nutritional rehabilitation (45–100 days of age). Growth was optimum in females fed diets containing 16% protein, with minimal requirements estimated to be 12%. Females fed diets containing <12% protein exhibited suppressed development, including delayed puberty. However, these nulliparous females demonstrated compensatory growth during the early period of nutritional rehabilitation, regardless of the severity of previous restrictions in protein. No long-lasting fitness consequences from postweanling nutritional restrictions were apparent as we observed no difference in date of conception, body mass of dams at parturition, litter size, or rate of growth of neonates. We offer a possible adaptive explanation for this observed plasticity in growth and development.

Key words: compensatory growth, cotton rat, fitness, nutritional ecology, *Sigmodon hispidus*, stochastic environments

Introduction

Plasticity in growth and sexual development (morphological and physiological) is recognized as a life-history characteristic common to a number of different species (Stearns, 1982, 1992). Many have postulated that such plasticity can be

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adaptive, is at least partly under genetic control, and is most prevalent in stochastic environments (Berven, 1982; Caswell, 1983). However, few studies have explored this phenomenon in mammals and little is known about the sensitivity of developmental rates to stressors encountered during critical periods of ontogeny in wild species residing in stochastic environments. Such environments can have profound selective influences on the plasticity of developmental and reproductive traits of mammalian species, although most previous work has been confined to non-mammalian systems (Hickman, 1975; Hastings and Caswell, 1979). Clearly, many advantages to developmental plasticity can be envisioned, especially for short-lived species who must evaluate tradeoffs between current and future reproductive efforts in light of risks to their own short-term survival (Arendt, 1997).

Brody (1945) suggested that plasticity in development represents an adaptive response of organisms attempting to achieve or maintain homeostasis. Nutrient intake in a growing juvenile must be partitioned among competing demands for maintenance of existing tissue (highest priority) and accretion. As nutritional conditions in the environment become inadequate relative to demands for normal development, mammals adapt by reducing rate of growth. Ultimately, body size falls below that of adequately fed animals of the same chronological age. Just as remarkable is the period of replenishment or recovery when previously malnourished young encounter improvements in their nutritional environment. Although poorly studied in wild species, the ability of an organism to rapidly accelerate rate of body growth during nutritional rehabilitation (referred to as compensatory growth) has been widely documented in livestock and laboratory animals (Wilson and Osbourn, 1960; Kyriazakis and Emmans, 1992). Arendt (1997) hypothesized that periods of rapid compensatory, or catch-up, growth may have evolved to compensate for periods of environmentally-induced growth suppression, juvenile mortality risks, time constraints on development, or changes in nutrient availability. Although these possibilities have been explored in plants, a variety of poikilotherms, and a few bird species (reviewed by Arendt, 1997), they have not been adequately explored in mammalian systems.

Similar to rates of growth, the environment has a profound impact on shaping optimal reproductive strategies of organisms (Pianka, 1976). The literature is replete with examples of how reproductive effort of small mammals such as cotton rats differ across populations, habitats, climates, time, and other scales (Cameron and Spencer, 1981; Cameron and McClure, 1988; Langley and Shure, 1988; Slade et al., 1996). Although a tremendous amount of effort has been devoted to describing this great diversity in reproductive strategies in small-mammalian herbivores, only limited efforts have been devoted to examining and understanding the relationship between rates of growth and sexual maturation in nutritionally stressful or variable environments, relative

to life-history theory. Exceptions include a few tests of the Trivers–Willard hypothesis of maternal investment in reproduction (Trivers and Willard, 1973) in wood rats (*Neotoma floridana*; McClure, 1981; Sikes, 1995), grasshopper mice (*Onychomys leucogaster*; Sikes, 1996a, b), and golden hamsters (*Mesocricetus auratus*; Labov et al., 1986).

Tests of the Trivers–Willard hypothesis in small mammals have generally been confined to the period of prenatal or preweaning growth and have provided equivocal support for the assumptions of this hypothesis. They predict, among other things, that differences in body condition of young at weaning will be maintained into adulthood, ultimately influencing reproductive performance of offspring. Given that many females store and use body nutrient reserves to support their reproductive efforts, offspring are maternally buffered somewhat by environmental stressors prior to weaning (Pine et al., 1994). Once weaned however, herbivores such as the cotton rat are often faced with monumental nutritional challenges for postweaning growth, particularly with regards to protein, as demands for nutrients at this age are exceeded only by those of lactation (McClure and Randolph, 1980; Lochmiller et al., 1982). Predation pressures associated with postweaning dispersal and increased foraging (high nutritional demands) may increase foraging risks beyond its rewards during this period, further increasing potential for nutritional stress. Consequently, a more important question to understanding the life-history strategy of a small-mammalian herbivore may be one that addresses the long-term developmental and fitness consequences of nutritional stressors that are environmentally imposed at weaning and persist until adolescence. This question becomes especially intriguing for species like the cotton rat that inhabit environments that are nutritionally stochastic during the breeding season (Schetter et al., 1998). Sikes (1998) hypothesized that species that exist in environments where availability of food resources is unpredictable might become sexually mature at smaller sizes and channel excess energy into reproduction rather than into compensatory growth.

Like many mammalian species (Ims, 1997), the cotton rat shows considerable geographic diversity in several life-history traits, including those associated with reproduction and growth (Mattingly and McClure, 1985; Cameron and McClure, 1988). However, environmental factors responsible for this variation have been largely ignored experimentally. In this study we examined the phenomenon of developmental plasticity in the hispid cotton rat (*Sigmodon hispidus*), a medium sized herbivore inhabiting environments where unpredictable nutritional limitations often occur as a result of climatic or density-dependent changes (Goertz, 1964; Schetter et al., 1998). We focused our attention in this study on the question of how female cotton rats would respond to pre-adolescent nutritional constraints imposed at the time of weaning. We chose cotton rats as an experimental model because of their

exhibited plasticity when responding to changing environmental conditions (Slade *et al.*, 1996). We specifically evaluated fitness (reproductive performance) responses to differing levels of dietary protein, as earlier work has demonstrated the importance of protein in regulating reproduction, growth, and demographics of cotton rat populations (Randoph *et al.*, 1995; Hellgren and Lochmiller, 1997; Schetter *et al.*, 1998). We offer a possible adaptive explanation for observed plasticity in growth and reproductive development in the cotton rat inhabiting nutritionally stochastic environments.

Materials and methods

Experimental animals

Cotton rats used in these experiments were laboratory-bred females whose parents were from wild-caught stock maintained in our outbred-captive colony at Oklahoma State University. Animals were housed in an approved, windowless animal-care facility under a 16L:8D illumination cycle (0600–2200 CST light) provided by fluorescent lighting at 23–24 °C, 30–70% relative humidity, and 15 fresh-air changes/h. Animals had *ad libitum* access to a commercial laboratory rodent chow (Purina 5001, St. Louis, Missouri) and clean tap water at all times prior to the start of experimental trials. Adult cotton rats were housed as breeding pairs in polypropylene cages (48 × 27 × 20 cm) with stainless-steel lids. All experimental procedures were approved in advance by our local Animal Care and Use Committee, Oklahoma State University, Stillwater.

Nulliparous adult females were randomly bred to mature males under the above housing conditions and cages checked daily for newborn pups. Litters were weaned at 14 days of age; the minimum age of weaning in cotton rats is 12 days (McClure, 1987). Initial body mass was recorded to the nearest 0.1 g at weaning, and weaned females were randomly assigned to one of the experimental protein diets; no two weanling females from the same litter were assigned to the same experimental diet. Weanling females were housed singly in polypropylene cages (24 × 14 × 13 cm) with wire lids and hardwood-chips for bedding material; tap water and experimental diets were provided *ad libitum*. Females remained on their respective experimental diets until 45 days old. Female cotton rats typically reach sexual maturity (open vagina) around 40 days of age (Meyer and Meyer, 1944). Postweaning growth was monitored by recording age and body mass weekly. Because females were born at different time intervals and subsequently entered the experiment on different days, their age at the time we recorded weekly body mass was not consistent across all individuals, except for initial and day-45 body mass. Food intake, expressed as

g day-1, was measured at weekly intervals from weaning to 45 days of age by measuring the difference in the mass of food added to the ceramic-feed bowl and that remaining (includes the addition of spilt food). This measurement of food intake was regarded as an estimate, as it was often difficult to recover all spilt food from bedding material in the cage.

Experimental treatments consisted of seven formulated diets varying in their concentration of crude protein as casein (5, 8, 10, 12, 14, 16, and 20% casein, dry mass basis). All diets were formulated by PMI Feeds, Inc. (Richmond, IN) as isocaloric (ca. 4.29 kcal g^{-1}), complete rations with vitamin and mineral supplements according to the requirements for laboratory rodents. Diets were formulated by replacement of the casein source of protein in the 20% diet with an equal mass of sucrose to derive diets with a proximate analysis that was similar to the complete control diet, except casein. Each diet contained 10% cottonseed oil, 4% USP XIV Salt Mix (21415), and 2.1% USB Total Vitamin Supplement (23431) (United States Biochemical Co., Cleveland, OH). It has been estimated that adult cotton rats require a minimum of 12% crude protein in the diet to support reproduction (Hellgren and Lochmiller, 1997) and probably 8% protein for maintenance in a non-reproductive animal (National Research Council, 1995). Crude protein in diets of free-ranging cotton rats have been found to range from 15 to 27% in Oklahoma (Schetter, 1996). Diets were fed *ad libitum* in a milled state to minimize spillage and offered in ceramic crucibles. Sample sizes for each diet are presented in Table 1.

Compensatory development

The ability of chronically, protein-malnourished females to recuperate body mass through tissue accretion and become reproductively active was assessed over the period from 45 to 100 days of age. At 45 days of age, females were weighed, their vaginal opening inspected (open vs. closed) to assess who had reached puberty, and individuals transferred to a larger polypropylene cage (48 × 27 × 20 cm). At 45 days of age, females were paired with a randomly-selected, mature male from our captive colony; males were all maintained on commercial rodent chow prior to pairing. All females and their mates were provided *ad libitum* the Purina 5001 rodent chow from 45 to 100 days of age (period of nutritional rehabilitation). Body mass of females was recorded on a weekly basis as previously described; food intake was not measured because it was not possible to distinguish consumption between male and female pairs. We also inspected the vaginal opening and palpated for pregnancy when females were handled for weighing. We considered females to have reached puberty at the age when we first observed a perforate vagina, or if this age was greater than the age at conception, we assumed puberty was reached a day earlier than conception. When pregnancy was confirmed from either palpation

Table 1. Reproductive development and performance traits of female *Sigmodon hispidus* fed diets containing variable levels of dietary casein from age 14 to 45. Females were paired with a healthy mature male at day 45 and fed *ad libitum* a commercial rodent chow to 100 days of age

Characteristic	5% casein diet			8% casein diet			10% casein diet			12% casein diet			14% casein diet			16% casein diet			20% casein diet		
	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE
Age at puberty (days)	2	54.0	4.0	6	55.8	6.0	8	60.1	7.1	10	50.5	1.3	8	46.3	0.8	5	49.2	1.4	6	57.8	8.6
Age at conception (days)	2	80.0	20.0	6	56.8	6.0	8	64.0	7.9	9	54.2	1.1	7	68.0	8.9	5	50.8	1.0	5	81.2	11.5
Maternal performance																					
Body mass at parturition (g)	1	112.4	–	6	122.1	9.2	6	126.7	5.0	9	122.1	5.1	5	127.5	9.2	4	133.0	9.4	3	122.2	7.3
Body mass at day 14 of lactation (g)	1	92.8	–	5	122.3	8.8	6	121.4	6.6	9	116.4	5.6	4	116.5	6.6	4	126.0	9.2	3	116.5	6.8
Mass recovery (%)[a,b]	1	226.7[a,c]	–	5	106.2[b]	22.5	6	80.3[b,c]	4.8	9	72.5[c]	6.6	5	71.4[c]	9.7	4	61.1[c]	5.9	3	77.3[b,c]	5.8
Litter performance																					
Litter size	1	6.0	–	6	6.5	0.3	6	6.3	0.3	9	6.1	0.5	5	5.8	1.1	4	6.3	0.6	3	5.7	0.3
Day 7 mean pup mass (g)	1	6.3	–	6	6.3	0.7	6	6.9	0.2	9	6.7	0.2	5	7.2	0.2	4	7.3	0.3	3	6.7	0.1
Day 21 mean pup mass (g)	1	21.9	–	5	26.3	1.1	6	24.7	1.5	9	24.0	2.1	5	25.8	1.7	4	28.1	3.1	3	24.5	1.9

[a] Percent increase in body mass from day 45 (conclusion of feeding trial) to parturition (after birth).
[b] Animals fed diets containing ≤10% casein had greater ($p = 0.026$) recovery of mass than animals fed diets containing ≥12% casein based upon a *t*-test.
[c] Mean values in a row with different letters are statistically different ($p ≤ 0.05$). Variable means without letters did not exhibit dietary differences.

or a rapid gain in body mass, males were removed from the cage and females inspected twice daily for birth of the litter. Age at conception was calculated by subtracting 27 days from the age of females at parturition (Meyer and Meyer, 1944; Randolph et al., 1977). Offspring within each litter were enumerated (live and dead), and their sex and body mass at birth measured to the nearest 0.1 g within 12 h of birth; all offspring within a litter were toe-clipped for future identification. Total litter biomass at birth was the sum of all individual masses within the litter. Body mass of the dam was also recorded within 12 h of parturition (day 1 of lactation), and both offspring and dam body mass were recorded on days 7 and 14, when offspring were weaned. For each litter we recorded the percent of young weaned.

Statistical analyses

We used simple linear regression (PROC REG; SAS Institute, 1988) to determine rate of gain (slope) of females from 14 to 45 days of age for each experimental diet. Significant differences in rate of growth among diet groups were tested by comparing slopes of the resulting equations with indicator-variable regression (Neter et al., 1990: 351). Effect of dietary protein on body mass at 45 days of age and age at puberty were tested using a one-way analysis of variance (ANOVA). Differences in feed intake and efficiency of weight gain (g intake/g mass gained) among dietary groups was examined using two-way nested ANOVA with diet and age as main effects and animal nested in diet (PROC GLM; SAS Institute, 1988). Dietary effects on female body condition (e.g., body mass at parturition) after parturition were examined using analysis of covariance with litter size as a covariate (PROC GLM; SAS Institute, 1988). We tested for dietary effects on litter size, mean mass of pups at 7 days of age, and mean mass of pups at 21 days of age using a one-way ANOVA. We compared frequency of females among dietary groups that reached puberty by 45 days of age using Fisher's exact test (PROC FREQ; SAS Institute, 1988). Multiple comparisons between dietary groups were conducted when main effects were significant ($p < 0.05$) using Fisher's least squares differences (LSD) procedure (Hicks, 1993). We also observed that growth performance of females that were fed diets containing $\geq 12\%$ casein was similar, but was suppressed in those fed diets containing $\leq 10\%$ casein. Because of low statistical power (e.g. low sample sizes), we pooled data within these two groups to examine for differences in selected response variables for those females that were nutritionally restricted ($\leq 10\%$ casein) and those that were not ($\geq 12\%$ casein). Differences in the frequency of females that reached puberty by 45 days of age, that died prior to conception, and that conceived a litter within these two combined groups were tested using Fisher's exact test (PROC FREQ; SAS Institute, 1988). All mean values are presented with $\pm$ SE.

Results

Protein restriction

All postweanling cotton rats gained body mass during the period when experimental casein diets were fed (age 14–45 days), even the three individuals placed on a 5% protein diet (Fig. 1). Development of postweanling cotton rats was strongly influenced by the protein concentration of their diet. Growth during this period of intense development was linear for all diet groups, with age explaining 41 (5% protein diet group) to 94% (14% protein diet group) of the variation in body mass. Growth performance was so poor in those individuals receiving a 5% protein diet that we discontinued placing subjects in this treatment group after three animals. Comparisons of slopes (rate of gain) describing the regression relationship between age and body mass among diet groups indicated that 12% protein was close to the minimal amount of protein required to support optimum development (Fig. 1). Rate of gain was maximal for those fed the 16% protein diet with a slope of 1.67 g day^{-1}. Slopes describing growth rates for individuals on the 5, 8, and 10% protein groups were significantly less than those on the 14, 16, and 20% protein diets ($p < 0.05$ for all comparisons). A comparison of rates of gain between the 10 and 12% protein groups tended to differ as well ($t = 1.810$, df $= 118$, $p = 0.072$). Rate of gain in body mass was similar among those receiving 14, 16, and 20% protein in their diet ($p > 0.10$ for all comparisons), but progressively declined with decreasing levels of protein in the diet for the 10, 8, and 5% protein groups ($p < 0.001$ for all comparisons).

Final body mass of offspring at 45 days of age reflected nutritional history during the period of postweanling development (Fig. 2). Body mass at 45 days was maximal for those fed the 16% protein diet (77.5 ± 2.0 g), which was nearly twice that of offspring fed a 5% protein diet (39.1 ± 4.7 g). Mean intake (g day^{-1}) of food over the period 14–45 days of age differed among diet groups ($F_{6,51} = 3.73$, $p = 0.002$; Fig. 2). This difference was attributed to a lower rate of food consumption among individuals fed an 8% protein diet (6.47 ± 0.28 g day^{-1}) compared to other diet groups. Mean rate of food intake during the period of postweanling development was similar between the 5% protein group and those fed 10–20% protein in their diets (overall mean $= 8.75 \pm 0.29$ g day^{-1}; $p > 0.10$ for all comparisons). Comparing these rates of food intake with rates of gain in body mass (feed efficiency) revealed a significant diet effect ($F_{6,51} = 3.13$, $p = 0.011$; Fig. 2). Efficiency of gain in body mass was lowest for those fed a 5% protein diet during postweanling development, and was greater in the 16% protein group compared to those fed diets with 5–10% protein($p < 0.05$ for all comparisons). Efficiency of gain was nearly four times greater in those fed diets containing from 12 to 20% protein compared to the 5% protein group.
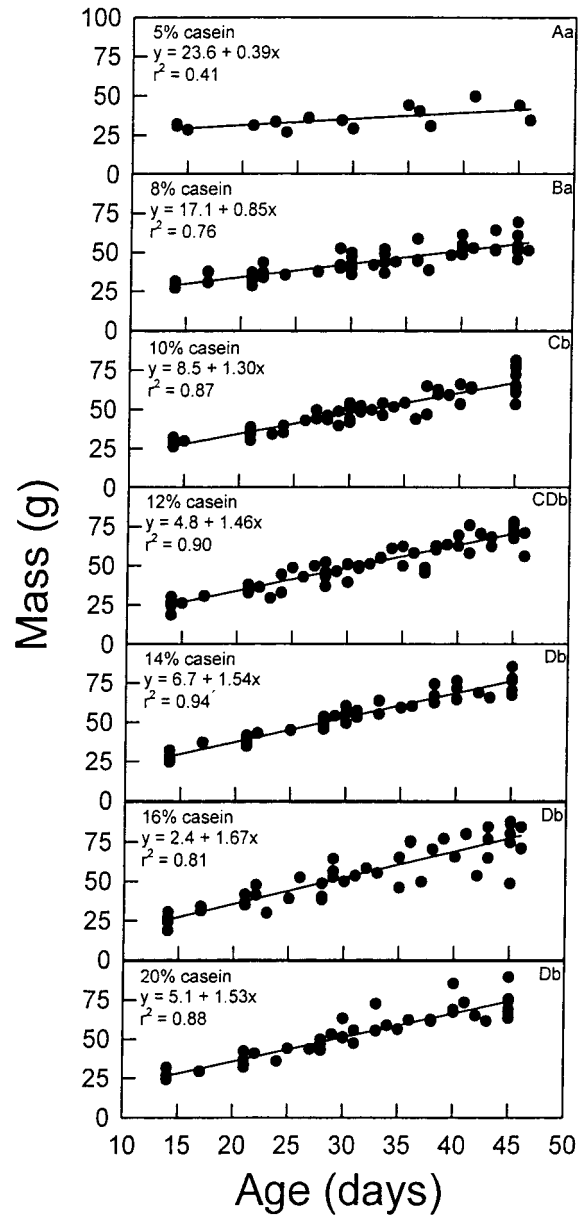
Figure 1. Growth curves of female cotton rats during the period of postweanling (14–45 days of age) development when fed 5–20% protein in isocaloric, balanced diets. Linear regression analysis was used to relate age (days) to body mass; all slopes were significantly different from zero ($p < 0.01$).
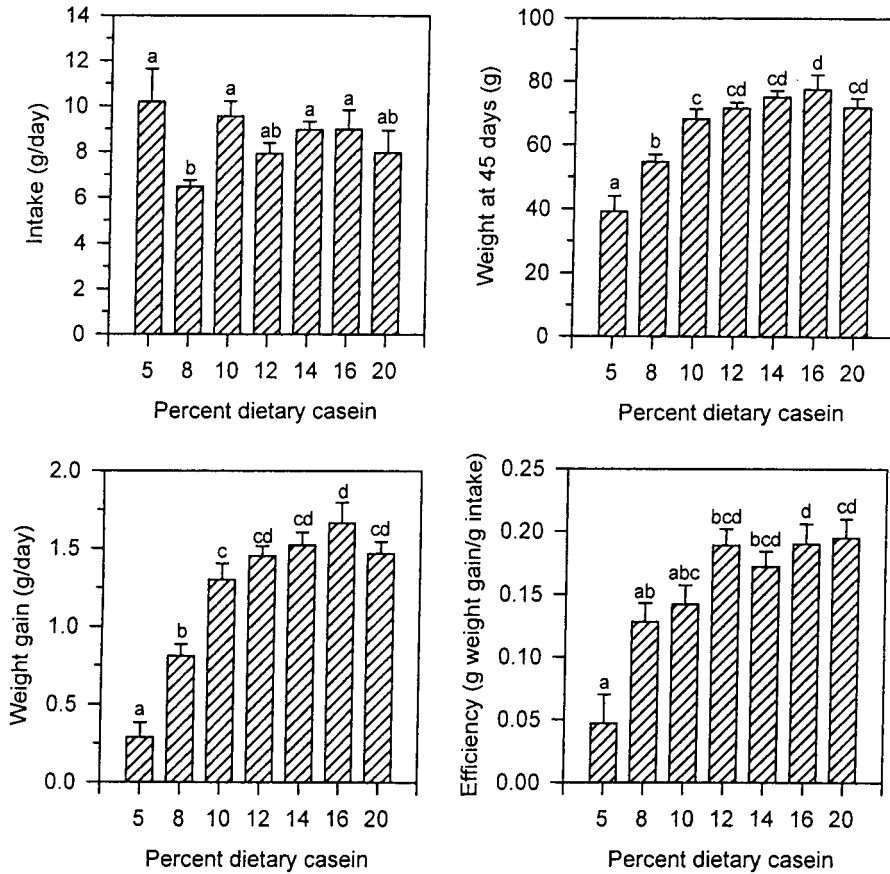
Figure 2. Mean (±SE) rate of food intake, body mass at 45 days of age, overall rate of gain in body mass, and efficiency of gain in body mass for female cotton rats fed varying levels of protein in isocaloric, balanced diets during the period of postweanling (14–45 days of age) development. Means with different letters above SE bars differed significantly at $p < 0.05$ using Fisher's least squares differences.

Compensatory development

Each female was paired with a healthy adult male at 45 days of age and placed on an *ad libitum* diet consisting of a commercial rodent chow as previously described in the methods. Fighting occurred between several mated pairs, which resulted in the death or injury of 16 females and so they were removed from any further analyses. We attempted to catch these fighting episodes early enough so that they could be separated before females were injured and males replaced with a different individual. There was no significant difference in the number of females that was lost to fighting among diet groups or between those previously fed ≥12% protein and those fed ≤10% protein in the diet ($p > 0.10$).

Females previously restricted in protein quickly gained body mass during the period of nutritional rehabilitation (45–100 days of age). However, statistical analyses of these response variables was not directly possible because of considerable variation in the date of conception among females that were mated and the consequences of additional mass from a gravid uterus (Table 1). Alternatively, comparisons were made among diet groups with respect to body mass at parturition (day 1 of lactation) and the percent increase in body mass from 45 days of age to the day of parturition (Table 1). Compensatory growth was evident by a greater percent increase in body mass (from 45 days of age to parturition) among those fed 5, 8, or 10% protein compared to those fed 12, 14, 16, or 20% protein in their diet ($p < 0.001$ for all comparisons). This compensatory growth resulted in no significant differences in body mass of females at parturition among any diet group comparisons ($p > 0.10$).

Reproductive performance of females was remarkably similar across treatment groups, indicating that any diet-induced suppression of reproductive development was temporary. Mean age at puberty was highly variable and showed no difference among individual diet groups ($p > 0.10$ for all comparisons). However, level of protein in the diet did appear to suppress reproductive development of females during the actual period of nutritional restriction. Examining the frequency distribution of females that had reached puberty by 45 days of age suggested a possible dietary effect when comparing the combined group of females fed a diet with ≤10% protein (12.5% reached puberty) to the group fed ≥12% protein (34.5% reached puberty; $p = 0.105$). Closer examination revealed the 12% diet group was intermediate relative to the frequency of females reaching puberty by 45 days of age. When we removed this group from the statistical analysis and compared the ≤10% protein group to the combined ≥14% protein (47.3% reached puberty) group, the percent sexually mature females was different ($p = 0.03$). However, this suppression in reproductive development was short-lived. Of those females that remained on experimental trial after pairing, only 3 of 16 females (18.7%) previously fed ≤10% protein and only 4 of 26 females (18.2%) previously fed ≥12% protein in the diet failed to conceive before 100 days of age; the difference between groups was not significant ($p > 0.10$).

Mean age of females at the time of conception was similar among individual diet groups ($F_{6,35} = 2.08, p = 0.082$; Table 1). There was no detectable decrease in the size of litters as a result of prior nutritional restrictions and associated suppression of maternal growth ($F_{6,27} = 0.19, p = 0.977$). Overall, litters averaged 6.14 ± 0.5 offspring. Likewise, development of offspring, as measured by mean body mass of pups within a litter, was similar across all possible diet-group comparisons ($F_{6,27} = 0.78, p = 0.594$ at 7 days old; $F_{6,26} = 0.48, p = 0.820$ at 21 days old; Table 1).

Discussion

Without question, dietary protein is a necessary ingredient for the maintenance of normal development of body mass and reproductive function in small mammals such as the cotton rat. Our results suggest that postweanling female cotton rats exhibit plastic growth in response to postweanling deficiencies in dietary protein. Although individuals fed diets containing ≤8% protein had reduced growth to 45 days of age, they exhibited compensatory growth and had reproductive parameters (mean age of females at the time of conception of their first litter, little size, and offspring development) similar to rats fed diets with ≥12% protein. These results are similar to those of Sikes (1995) who found that undernourished weanling eastern woodrats and grasshopper mice failed to maintain body condition differences into adulthood. Similarly, Sikes (1998) noted preweaning growth suppression in grasshopper mice due to large litters was temporary and had no lasting influence on reproduction in these individuals as adults. However, unlike these studies (Sikes, 1995, 1998), our cotton rats were exposed to nutritional restriction during the period of postweanling development. Because this is a period characterized by high rate of growth and reproductive maturation, the implications of nutritional restriction during this period on future reproduction could be serious.

Whether to breed or not is a fundamental decision that all females must make, and the outcome of this decision is greatly influenced by prevailing environmental conditions. A considerable volume of literature exists on this subject in birds, who frequently respond to varying environmental conditions by altering timing of breeding and clutch size (Martin, 1987). Intra-individual phenotypic plasticity with regards to clutch size and laying date appears to be a common adaptive strategy of many avian species residing in unpredictable environments where food supplies fluctuate from year to year (Hogstedt, 1980; Korpimaki, 1990). Plasticity in traits associated with reproductive performance and breeding behavior is probably an effective means of minimizing energetic and nutritional overloads of the female system, thus reducing risks to maternal survival. Such a strategy provides a potential avenue for birds to produce offspring during both stressful and high-quality years, thus improving overall fitness without necessarily jeopardizing their own well-being and life-time reproductive output (Korpimaki, 1990).

Trade-offs between competing demands for reproduction, growth, and maintenance is fundamental to evolution of life histories (Stearns, 1992). Theory predicts that individuals with a high probability of survival to the next breeding season should not take reproductive risks in the current season, thus optimizing lifetime fitness. However, when the probability of survival is low, the optimum strategy may be to invest at all costs, which Part *et al.* (1992) refer to as 'terminal reproductive investment' (Ots and Horak, 1996). We

propose that many small mammals such as the cotton rat have evolved life-history strategies similar to those described above for many avian species. One of the most critical determinants of life-time reproductive output and intrinsic rate of population increase in small mammals is age at sexual maturity (Tkadlec and Zejda, 1995). A reproductive trait of this importance would probably be under significant selection pressure for optimizing fitness, as discussed by Tkadlec and Zejda (1995) for microtine rodents. This is understandable given the realities of life expectancy in small mammals. With a life expectancy of less than 3 months (Cameron and Spencer, 1981), most female cotton rats born into the population can probably only expect to have one breeding opportunity prior to her death. How she decides to use this breeding opportunity reflects a culmination of life-history evolution, where in an unpredictable environment, a female must entertain a variety of fitness-dependent reproductive decisions or choices. One would logically conclude that myriad intrinsic and extrinsic environmental factors act in concert to influence the outcome of these reproductive decisions. Of these factors, current nutritional constraints and female condition are probably two of the most important to small-mammalian herbivores that are faced with the decision of whether or not to breed.

Current nutritional constraints are extrinsic and beyond the control of the species, but in an unpredictable environment, can change rapidly within a breeding season. In comparison, female condition is a dynamic, intrinsic attribute that is not only responsive to prevailing and historic nutritional constraints, but also to individual traits and hence could be subject to selection. The ability of a female to rapidly improve her body condition could have adaptive significance in such environments, especially with regards to early postnatal malnutrition. Without substantial developmental plasticity, females suppressed in size or biological maturity, either due to prenatal or postnatal malnutrition, could be at a severe disadvantage reproductively following rapid nutritional improvements in their environment. On the other hand, those females possessing a mechanism for rapid, compensatory development would possess a fitness advantage under such a scenario. Thus, plasticity in development may be an important trait of its own, under direct selection pressure as has been suggested by Caswell (1983) and others. Few studies have actually attempted to address the adaptive significance of plasticity in development within a species. In an artificial selection experiment with *Drosophila*, Hillesheim and Stearns (1991) demonstrated that phenotypic plasticity in body mass (reaction norms) could respond to selection pressures from food limiting environments. Although we are unaware of similar experimental studies with mammals, many have postulated on its occurrence.

Clearly, the environment is the ultimate regulator of phenotypic plasticity within a species, as demonstrated by our trials that varied the availability of

protein in the diet. The adaptiveness of developmental plasticity in the cotton rat, particularly with regards to compensatory growth and sexual maturation following periods of early postweanling nutritional stress, remains to be resolved. However, it may be useful to view this strategy as one analogous to environmental temperature and its almost universal impact on rates of growth and sexual maturation in amphibians (Smith-Gill and Breven, 1979). As we described above, one can easily imagine several fitness advantages for cotton rats possessing the ability to quickly replenish body mass and achieve sexual maturity in stochastic environments. Caswell (1983) hypothesized that plasticity in the rate of development is adaptive if reproductive value increases as a result. If this is universally true, then our experimental results would seem to suggest that the plasticity in development expressed by pre-adolescent cotton rats is indeed adaptive. Of course to truly be adaptive, we must also demonstrate that plasticity in these developmental traits has a clear genetic basis, which can not always be assumed (Smith-Gill, 1983). Although several approaches could be used to empirically address such a question, one could easily begin by implementing a series of artificial selection experiments in the laboratory (Hillesheim and Stearns, 1991).

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