The effects of dietary protein content on growth and maturation in deer mice

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Abstract: Growth and female maturation appear to be limited by the availability of dietary protein in natural populations of deer mice (*Peromyscus maniculatus borealis*) in the Kananaskis Valley, Alberta. We examined the effects of dietary protein content on nestling growth rates and sexual maturation of female deer mice in two laboratory experiments. In the first, mice whose mothers were fed a low-protein mixture of sunflower seeds and oats (14% protein) exhibited slow growth prior to weaning and those fed high-protein cat food (30% protein) postweaning showed compensatory growth. Preweaning but not postweaning diet quality affected the proportion of females who were sexually mature at 42 days of age. Therefore, while deficient nestling growth can be compensated for, the effects of a low-quality maternal diet during lactation may have lasting effects on the maturation of female offspring. In the second experiment, mice raised on isocaloric diets of 14, 20, and 30% protein did not differ in growth as nestlings or juveniles. Differences among the three diets in the proportion of mature females at 42 days did not correspond to dietary protein levels as predicted. Dietary protein content from 14 to 30% appear to be sufficient for juvenile mice raised in captivity.

Résumé : La croissance et la maturation des femelles semblent tributaires de la disponibilité des protéines alimentaires chez les Souris sylvestres (*Peromyscus maniculatus borealis*) de la vallée de Kananaskis, en Alberta. Nous avons étudié les effets du contenu en protéines du régime alimentaire sur les taux de croissance des jeunes femelles au nid et sur leur maturation sexuelle au cours de deux expériences en laboratoire. Dans la première, les jeunes femelles nées de mères nourries d'un mélange de graines de tournesol et d'avoine, à faible contenu en protéines (14%), ont subi une croissance lente avant le sevrage et celles qui ont reçu un régime constitué de nourriture pour chats, riche en protéines (30%), après le sevrage ont subi une croissance compensatoire. La qualité du régime alimentaire avant le sevrage a influencé la proportion de femelles parvenues à maturité à l'âge de 42 jours, mais le régime alimentaire après le sevrage n'a pas eu d'influence sur la maturation. On peut donc dire que si une croissance déficiente au nid peut être compensée plus tard, la piètre qualité du lait maternel peut avoir des conséquences de longue durée sur la maturation sexuelle des rejetons femelles. Dans la seconde expérience, les souris nourries de régimes isocaloriques contenant 14, 20 et 30% de protéines ont toutes eu le même taux de croissance, au nid et après la sortie du nid. Les différences obtenues à 42 jours quant au nombre de femelles à maturité ne correspondaient pas au contenu en protéines du régime alimentaire, contrairement aux prédictions. Un contenu en protéines de 14 à 30% semble suffire aux Souris sylvestres gardées en captivité.

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Introduction

Female deer mice in the Kananaskis Valley, Alberta, rarely breed during the summer of their birth, despite having a breeding season that appears to be long enough to permit them to do so (Millar and Innes 1983, 1985; Teferi and Millar 1993; Millar 1994; McAdam and Millar, 1999*a*). In these populations most females do not mature until 1 year of age, despite a potential 50% increase in lifetime reproductive success in females who breed as young of the year (YY) (Teferi and Millar 1993).

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The results of a series of field supplementation experiments suggest that sexual maturation in these populations is not limited by the abundance of food per se (Teferi and Millar 1993; McAdam and Millar 1999*b*), but by the availability of dietary protein (McAdam and Millar 1999*b*). High preweaning growth rates have been consistently associated with early maturation (Lusk and Millar 1989; Teferi and Millar 1993; McAdam and Millar 1999*a*, 1999*b*), and most females who breed as YY conceive within days of leaving the natal nest (McAdam and Millar 1999*a*), which suggests that maternal diet during the period of offspring dependence may be of particular importance for maturation.

Deficiencies in dietary protein have been shown to both slow growth and delay maturation in some laboratory rodents (Goettsch 1960; Kirsch et al. 1968; Nakagawa and Mansana 1971; Nakagawa et al. 1974; Sasaki et al. 1982; Bronson 1985; Cameron and Eshelman 1996). In particular, deficiencies in specific amino acids such as arginine and valine have also been found to retard nestling growth and delay maturation (Glass et al. 1976; Pau and Milner 1982). The dietary protein requirements of deer mice, however, are

not known. Deer mice are omnivorous, much of their diet being composed of arthropods (Hamilton 1941; Jameson 1952; Williams 1959; Whitaker 1966; Martell and Macaulay 1981). For this reason, deer mice may require a higher dietary protein content than has been estimated for some herbivorous species (see Ditchkoff et al. 1998) whose digestive physiologies are more efficient at using low-protein diets (Robbins 1993). Wild-conceived deer mice from the Kananaskis Valley raised in the laboratory on standard rodent chow (~20% protein) have high growth rates (0.30–0.40 g/day; Millar 1982; Millar and Innes 1983; MacDonald 1997; Woolfenden and Millar 1997) and some females are sexually mature by 42 days of age (MacDonald 1997), but the effects of dietary protein on early growth and sexual development are not known.

The objective of this study was to examine growth and sexual maturation of female deer mice raised on diets with various protein contents in the laboratory; diet was controlled and growth was measured directly. We predicted that mice raised on high-protein food would have higher birth masses and growth rates and that a higher proportion of these females would mature than of those raised on low-protein food. These predictions were tested in two experiments. In the first experiment, we raised mice on one of two diets, which were previously added to wild populations of mice by McAdam and Millar (1999*b*), to examine the effects of both preweaning and postweaning diet quality on postnatal growth and female sexual maturation. These two diets differed not only in protein content but also in levels of several other nutrients. A second experiment was subsequently performed to specifically examine the effects of dietary protein content on growth and maturation, using isocaloric manufactured diets.

Methods

Adult female *P. m. borealis* were livetrapped at various locations throughout the Kananaskis Valley, Alberta (51°N, 115°W), and brought into the animal holding area at the Kananaskis Field Station (University of Calgary). Trapping occurred from 13 May to 21 June 1996 for the first experiment and 3 May to 17 June 1997 for the second experiment. These time periods coincided with gestation of the first litters of the season. Mice were housed in individual plastic cages lined with wood shavings or corn-cob bedding (Bed-O-Cobs, Andersons, Maumee, Ohio), provided with cotton nesting material and water ad libitum, and tested on one of five experimental diets. Bedding and food were replenished every 3 days. The daily photoperiod in the laboratory was adjusted to mimic increases in the number of daylight hours in the natural environment to a maximum light duration of 16 h, beyond which it was not changed.

Females were monitored daily for the presence of offspring and weighed every 3 days. Females who had not given birth 24 days after being brought into the laboratory were removed from the experiment. Neonates were uniquely toe-clipped to identify individuals. Females and their offspring (nestlings) were weighed on the day of parturition and every 3 days thereafter. Maternal body mass was measured (±0.5 g) using a Pesola spring balance, and offspring mass was measured (±0.001 g) using a Mettler PC 440 electronic balance. At 21 days of age, female nestlings were removed from their mother and housed individually. Mothers and their male offspring were removed from the experiment at this time.

Independent females (juveniles) were weighed every 3 days from 21 to 42 days of age. Individual growth rates of nestlings (0–21 days) and juveniles (21–42 days) were estimated as the slope of the linear regression of mass on age for each individual. Juvenile growth during these time periods is approximately linear (Millar 1982; Millar and Innes 1983; Millar and Millar 1989; Woolfenden and Millar 1997). At 42 days, juvenile females were killed by cervical dislocation and their ovaries were excised and stored in 5% neutrally buffered formalin. All ovaries were examined at the end of all experiments for the presence of antral follicles, indicating sexual maturation. Maturation was assessed at 42 days of age because this represents two equal time periods (21 days): from birth to weaning and from weaning to the end of the experiment. In addition, some females raised in captivity are mature at this age (MacDonald 1997), and most females who breed as YY in natural populations have conceived by 42 days of age (McAdam and Millar 1999*a*).

All trapping and holding protocols were approved by the local University Council on Animal Care (University of Western Ontario) and are in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Experiment 1

In the first experiment, adult females were randomly assigned a diet of either high-protein cat food (CO-OP No. 320C, Interprovincial Cooperative Ltd., Saskatoon, Saskatchewan) or a 3:1 mixture by volume of whole oats and unshelled sunflower seeds. These diets were used as separate food supplements in a concurrent field study (McAdam and Millar 1999*b*). The cat-food diet contained high levels of protein and most other nutrients (Table A1) and is henceforth referred to as the high-quality diet. The seed diet was low in protein and several other nutrients (Table A1) and is henceforth referred to as the low-quality diet. Female offspring raised on either the high- or low-quality diet prior to weaning were randomly assigned to either the high- or low-quality diet at the time of weaning. This resulted in four preweaning/postweaning diet treatments, high/high, high/low, low/high, and low/low, to which 10, 11, 11, and 10 females were assigned, respectively.

Experiment 2

In the second experiment, adult females were randomly assigned to one of three isocaloric diets containing 14, 20, or 30% protein (Purina Test Diets, Nos. 5773C-F, 5773C-G, and 5773C-H, respectively). In this experiment, female offspring received the same diet after weaning that their mother had received prior to weaning. Nutritional information on these diets is provided in Table A1.

Food consumption was measured every 3 days for mothers during pregnancy and lactation and for juvenile females after weaning. Bedding material was carefully checked for the presence of small food pieces at the time of weighing, but pieces smaller than 0.03 g were likely missed.

Statistics

All statistical analyses were performed using the STATISTICA (StatSoft Inc. 1994) software package. Litter size was included as a covariate in analyses of birth masses and nestling growth using analysis of covariance (ANCOVA). Litter sizes were log-transformed when necessary to maintain homogeneity of variance for ANCOVA (Zar 1996).

Food consumption was analysed as a repeated-measures ANCOVA (covariate = litter size) for mothers and a repeated-measures analysis of variance (ANOVA) for juveniles. The proportions of females who were mature at 42 days were compared among diet treatments as a three-dimensional contingency table for expt. 1 and a two-dimensional contingency table for expt. 2 (Zar 1996). All values are presented as the mean ± 1 SE.

Table 1. Birth masses and nestling growth rates of laboratory-born male and female *Peromyscus maniculatus borealis* raised on high-quality (cat food; 30% protein) and low-quality (seeds; 14% protein) food.

Diet quality	Sex	*n*	Birth mass (g)*	Nestling growth (g/day)†
High	Male	24	1.821±0.027*a*	0.392±0.010*a*
	Female	21	1.774±0.042*a*	0.365±0.010*a*
Low	Male	26‡	1.478±0.043*b*	0.196±0.011*b*
	Female	30	1.354±0.032*c*	0.168±0.011*b*

Note: Values are presented as the mean ± SE corrected for litter size. Values in each column followed by the same letter are not significantly different at $p < 0.05$ according to Tukey's test for unequal sample sizes.

*Litter size at birth was a significant covariate ($F_{[1,96]} = 19.8$, $p < 0.00003$).

†Calculated by linear regression of mass on age for each individual. Litter size at weaning was a significant covariate ($F_{[1,95]} = 23.2$, $p < 0.00001$).

‡Nestling growth could not be calculated for one male ($n = 25$).

Six of 234 offspring died within 9 days of birth and were included in the analysis of birth mass, litter size, and sex ratio but not nestling growth. Nine offspring died shortly after weaning and were only included in analyses of data obtained prior to weaning. In addition, 8 of the 328 slope estimates of postnatal growth did not adequately represent changes in individual mass over time (slope, $p > 0.05$) and were therefore not included in growth comparisons. When litter size was included in analyses as a covariate, litter size at birth was used for birth masses, whereas litter size at weaning was used for nestling growth. Nestling growth was highest for a litter size of four and decreased linearly with litter sizes greater than four. Nestlings from the two smallest litters (one of two offspring and one of three offspring) had low growth rates, similar to those of nestlings from litters of five. These small litters may have been insufficient to stimulate adequate maternal milk production, or may be indicative of poor maternal condition. These two litters were excluded from the analysis of nestling growth among the three isocaloric diets to maintain a linear relationship between the covariate (litter size) and the response variable (nestling growth rate).

Results

Experiment 1

Twelve of 23 and 9 of 18 females gave birth in the low- and high-quality diet groups, respectively. Females receiving the low- and high-quality diets did not differ in the date on which they were captured ($t_{[19]} = 0.540$, $p = 0.60$), the date on which they gave birth ($t_{[19]} = 0.05$, $p = 0.96$), the length of time they were in the laboratory prior to parturition ($t_{[19]} = 1.70$, $p = 0.11$), or litter size ($t_{[19]} = 0.27$, $p = 0.79$).

Females fed the high-quality diet had offspring with higher birth masses than females fed the low-quality diet, and within the low-quality diet treatment male offspring had higher birth masses than female offspring (Table 1). Nestling growth (0–21 days) was much higher for offspring of mothers fed high-quality food than those of mothers fed low-quality food (Table 1). In fact, 13 (21%) juveniles in litters produced by females fed the low-quality diet died prior to or at weaning, while no offspring ($n = 45$) of females fed high-quality diet died. The rate of juvenile growth (24–42 days), however, depended on both the preweaning and postweaning diets (preweaning diet by postweaning diet interaction: $F_{[1,36]} = 11.70$, $p = 0.002$). Juvenile females fed high-quality food after weaning had higher juvenile growth rates than those fed low-quality food. This difference was greatest for the juvenile females whose mothers were fed low-quality food prior to weaning (Table 2).

Table 2. Juvenile growth rates of laboratory-born female *P. m. borealis* and the proportion of those females who were mature at 42 days.

Peweaning diet quality	Postweaning diet quality	*n*	Juvenile growth rate (g/day)[a]	Proportion mature[b]
High	High	10	0.289±0.023	0.40
	Low	11	0.261±0.022	0.64
	Both			0.52
Low	High	11	0.423±0.024	0.09
	Low	9[c]	0.229±0.029	0.22
	Both			0.15

Note: Mice were raised on either a high-quality (cat food; 30% protein) or low-quality (seeds; 14% protein) diet prior to weaning and post weaning. Values are presented as the mean ± 1 SE.

[a]Interaction between preweaning and postweaning diets ($F_{[1,36]} = 11.7$, $p = 0.0016$).

[b]Postweaning diet ($\chi^2_{[3]} = 2.06$, $p > 0.50$), preweaning diet ($\chi^2_{[3]} = 6.38$, $p < 0.10$; Fisher's exact test, $p = 0.013$).

[c]Juvenile growth rate could not be calculated for one female ($n = 8$).

The proportions of females who were mature at 42 days of age did not differ between the two postweaning diet treatments ($\chi^2_{[3]} = 2.06$, $p > 0.50$). However, maturation was not independent of preweaning diet ($\chi^2_{[3]} = 6.38$, $p < 0.10$). When postweaning diet groups were combined for each preweaning treatment, a higher proportion of females raised on high-quality food prior to weaning was found to be mature than of those raised on the low-quality diet (Fisher's exact test, $p = 0.01$; Table 2).

Experiment 2

Twenty-six of the 35 females assigned to one of the three isocaloric diets gave birth in the laboratory (9/10 given 14% protein; 9/12 given 20% protein; 8/13 given 30% protein). The dams in the three treatment groups did not differ in the date on which they were brought into the laboratory (Kruskal–Wallis test, $H_{[2]} = 4.10$, $n = 26$, $p = 0.13$), the date on which they gave birth ($F_{[2,23]} = 2.00$, $p = 0.16$), or the length of time they were in the laboratory prior to parturition ($F_{[2,23]} = 0.56$, $p = 0.58$). Neither mean litter size ($F_{[2,23]} = 0.17$, $p = 0.85$) nor sex ratio differed among the three diet treatments ($\chi^2_{[2]} = 2.39$, $p > 0.25$), although litters raised on the 14% protein diet tended to be more female-biased (55% female) than litters raised on either the 20% (46% female) or 30% protein diet (37% female).

Male and female offspring raised on the isocaloric diets did not differ in birth mass (ANCOVA, factors: diet, sex; covariate: log litter size at birth; sex effect $F_{[1,112]} = 0.47$, $p = 0.49$) or nestling growth rate (two-factor ANCOVA as above, $F_{[1,118]} = 0.22$, $p = 0.64$), so the two sexes were examined together. Birth masses, corrected for litter size (covariate: log litter size at birth $F_{[1,117]} = 4.31$, $p = 0.04$), did not vary among the three diet treatments ($F_{[2,117]} = 1.37$, $p = 0.26$; Table 3). Nestling growth rates for litters of four or

Fig. 1. Consumption of isocaloric diets containing 14, 20, and 30% protein by adult female *Peromyscus maniculatus borealis* during late gestation and lactation. Data for the three diets are combined. Numbers at the top show the sample size for each time period.

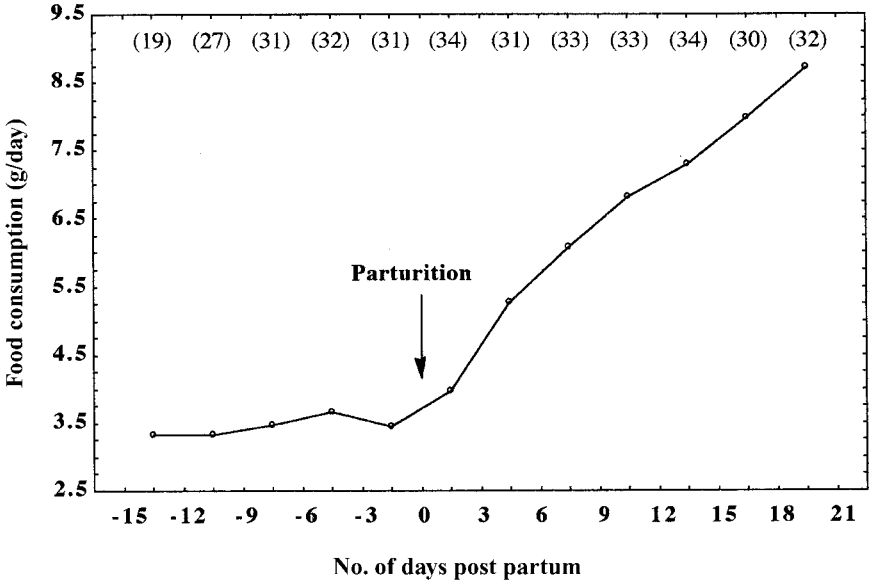


Table 3. Birth masses, nestling and juvenile growth rates, and maturation data for laboratory-born female *P. m. borealis* raised on an isocaloric diet of 14, 20, or 30% protein.

Protein content (%)	No. of dams	Birth mass (g)[a]	Nestling growth rate (g/day)[b]	Juvenile growth rate (g/day)[c]	Proportion mature[d]
14	9	1.736±0.038 (43)	0.403±0.006 (40)	0.230±0.017 (22)	0.70 (23)
20	10	1.778±0.030 (49)	0.369±0.007 (45)	0.222±0.024 (22)	0.32 (22)
30	8	1.724±0.035 (29)	0.393±0.008 (35)	0.272±0.031 (12)	0.54 (13)
All	27	1.750±0.020 (121)	0.387±0.004 (120)	0.236±0.013 (56)	0.52 (58)

Note: Values are presented as the mean ± 1 SE. Numbers in parentheses are sample sizes.
[a]ANCOVA, $F_{[2,117]} = 1.37$, $p = 0.26$ (covariate: log litter size at birth, $F_{[1,117]} = 4.31$, $p = 0.04$).
[b]Calculated by linear regression of mass on age (0–21 days) for each individual (ANCOVA, $F_{[2,116]} = 0.85$, $p = 0.43$; covariate: litter size at weaning, $F_{[1,116]} = 101.02$, $p < 0.000001$).
[c]Calculated by linear regression of mass on age (23–42 days) for each individual (ANOVA, $F_{[2,53]} = 1.1$, $p = 0.35$).
[d]Mature at 42 days of age ($\chi^2_{[2]} = 6.45$, $p < 0.05$).

more offspring did not differ among the three diets when corrected for litter size (covariate: litter size at weaning, $F_{[1,116]} = 101.02$, $p < 0.00001$; main effect, $F_{[2,116]} = 0.85$, $p = 0.43$). Juvenile growth rates also did not differ among the three diets ($F_{[2,53]} = 1.06$, $p = 0.35$; Table 3).

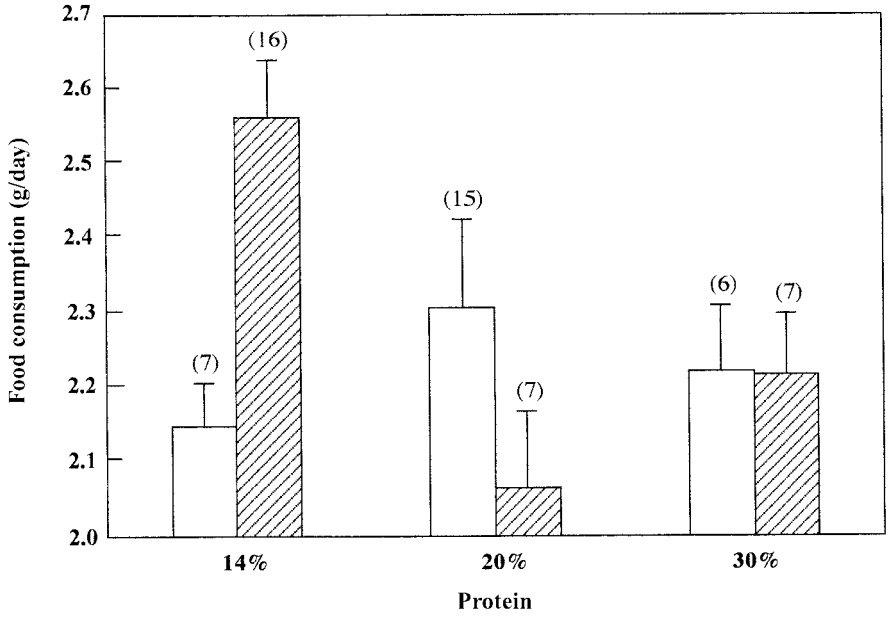
More than half of all females were mature at 42 days of age, and the proportion of mature females differed among the three diets ($\chi^2_{[2]} = 6.45$, $p < 0.05$) but did not follow any consistent pattern across diets. The 14% protein treatment yielded the highest proportion of mature females, while the 20% protein treatment had the lowest (Table 3).

Females consumed approximately 3.5 g of food per day throughout gestation. Maternal food consumption during lactation, corrected for litter size, did not differ among the three isocaloric diets (repeated-measures ANCOVA, diet main effect: $F_{[2,19]} = 1.13$, $p = 0.34$), but increased throughout lactation (time main effect: $F_{[6,120]} = 150.39$, $p < 0.0001$) to a maximum of approximately 8.7 g/day at 21 days after parturition (Fig. 1). Food consumption by juveniles increased from 1.9 g/day at weaning to 2.6 g/day at 42 days of age (repeated-measures ANOVA, age effect: $F_{[6,282]} = 26.43$, $p < 0.0001$). Juvenile food consumption depended on both the diet received and whether the females were found to be mature at 42 days (repeated-measures ANOVA, diet by maturation interaction: $F_{[2,47]} = 3.51$, $p = 0.038$). When juvenile consumption was averaged across the seven time intervals, juvenile females fed the 20 and 30% protein diets and females fed the 14% protein diet who were not yet mature at 42 days ate approximately 2.2 g/day. However, juvenile females in the 14% protein treatment who were found to be mature at 42 days ate an additional 0.4 g/day (2.6 g/day; Fig. 2).

Discussion

Diet composition clearly influences both nestling growth rates and maturation of females in deer mice. Nestling mice whose mothers were fed the low-quality diet grew, prior to weaning, at about half the rate of those whose mothers were fed cat food. Nestlings whose mothers were fed the high-quality diet grew at a rate similar to those reported previously for nestling deer mice in captivity (Millar 1982; Millar

Fig. 2. Average consumption (mean + SE) of isocaloric diets containing 14, 20, and 30% protein from 21 to 42 days of age by juvenile female *P. m. borealis* found to be mature at 42 days of age (hatched bars) and by females who were not yet mature at 42 days of age (open bars) (two-factor ANOVA, diet by maturation interaction: $F_{[2,52]} = 5.12$, $p = 0.01$). The number above the bars show the number of females in each category (n). Food consumption for each individual was averaged across seven 3-day intervals.



and Innes 1983; MacDonald 1997; Woolfenden and Millar 1997), indicating that nestlings raised on sunflower seeds and oats were deficient in their growth. In fact, growth indices (mass at 21 days/21; Teferi and Millar 1993) of mice raised on seeds were even lower than growth indices of YY mice in wild populations during "poor" years for YY growth (McAdam and Millar 1999*a*). Although some degree of compensatory growth occurred in those females fed high-quality food after weaning, some variation in weaning mass remained at 42 days of age. Variation in size at weaning has also been found to persist into adulthood in wild populations (Millar 1983; Myers and Masters 1983).

Dietary deficiencies prior to weaning resulted in a significant decrease in the proportion of females who were mature at 42 days of age, regardless of postweaning diet. Although juvenile mice can partially compensate for deficient growth as nestlings, the effects of a poor-quality maternal diet on maturation appear to be long-lasting (to at least 42 days of age). These results are consistent with observations of natural populations of mice and voles (McAdam and Millar 1999*a*; Andreassen and Ims 1990).

Absolute levels of dietary protein (14, 20, and 30%), however, did not affect birth mass, growth, or sexual maturation as we had predicted. Mice from all three diets had high birth masses, and postnatal growth rates that were similar to previously reported values for mice raised on standard laboratory-rodent diets (Millar 1982; Millar and Innes 1983; MacDonald 1997; Woolfenden and Millar 1997). The one difference among the three isocaloric diet treatment groups was the proportion of female mice who were mature at 42 days of age, but patterns of maturation among diets did not reflect protein content. In general, growth rates and the proportion of females who were mature at 42 days indicate that mice were able to acquire all the necessary nutrients for growth and maturation from all three isocaloric diets.

Maternal body size is not a good predictor of breeding success in deer mice (Millar et al. 1992), which meet the increased energetic demands of reproduction through increases in food consumption rather than through fat deposition prior to reproduction (Millar 1989). In this study, dams did not compensate for differences in protein content among the three diets through differential consumption. It is unknown whether females buffer dietary protein deficiencies during reproduction through the catabolism of endogenous protein. Juvenile females, unable to rely on previously consumed protein, showed some differences in food consumption in the 14% protein treatment, depending on whether or not they were mature at 42 days of age. Within the 14% protein treatment, females who were mature at 42 days of age ate approximately 0.5 g/day more food than females in the 14% protein treatment who were not yet mature at 42 days of age. Given the importance of preweaning diet and not postweaning diet on maturation (expt. 1), it is likely that maturation led to the increase in consumption rather than an increase in food consumption leading to maturation.

It is unclear why mice on the seed diet grew so poorly. The protein content of the seed diet was estimated on the basis of a 3:1 mixture by mass of sunflower seeds and oats, as presented. Disproportional consumption of seeds may have altered the amount of protein consumed, because sunflower and oat seeds have different protein contents (22% in sunflower seeds and 12% in oats; Scherz and Senser 1994), but even consumption of oats alone would reduce the dietary protein content to only 12%. We propose two explanations for the deficient growth of nestlings raised on seeds. First, the protein provided in the isocaloric and high-quality diets was from animal sources (casein and chicken, respectively), whereas the low-quality diet consisted only of plant protein (seeds). Whereas animals require specific amino acids and not proteins per se, animal proteins are thought to be more

useful to consumers than plant proteins, which are usually less available to digestion and provide a less appropriate combination of amino acids (Robbins 1993). The seed diet had the lowest levels of 4 of the 10 essential amino acids (histidine, leucine, lysine, and methionine; Table A1). Dietary deficiencies in essential amino acids generally reduce growth and reproduction (Robbins 1993), but the relative importance of the 10 essential amino acids is not known.

Second, other minerals and vitamins unrelated to protein were low in the sunflower and oat seed diet (Table A1). Female deer mice from the same area raised on a low-sodium diet (0.01% NaCl) had lower nestling growth rates than females raised on a control diet (Woolfenden and Millar 1997). However, the growth rates of these sodium-deficient mice (0.30 g/day; Woolfenden and Millar 1997) were well above those of the females raised on the low-quality diet (0.07% Na) in this study (0.17 g/day). It is unlikely, therefore, that a low-sodium diet was the sole reason for the deficient growth. The effects of deficiencies of other nutrients (e.g., calcium) on the growth and maturation of deer mice are not known.

This study emphasises the importance of diet for growth and maturation of deer mice. The quality of the mother's diet affects the growth of her offspring. While juvenile mice can compensate for deficient growth before weaning, the effects of maternal diet quality on the sexual maturation of female offspring persist to at least 42 days of age. Manufactured diets with 14–30% protein are adequate for growth and maturation of mice in captivity; however, two a posteriori hypotheses are proposed to account for the large differences in growth and maturation between mice raised on seeds and those fed a manufactured diet of similar protein content.

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Appendix.

Table A1. Nutritional composition of the five diets used in the study.

Nutrient	Units	Low quality[a]	High quality	14% protein	20% protein	30% protein
Energy	kcal/g	4.07	*3.70*	**4.11**	**4.11**	**4.11**
Fat	%	**17.57**	*9.00*	10.00	10.00	10.00
Protein	%	14.39	**30.00**	*14.03*	20.01	**30.00**
Arginine	%	1.19	**1.63**	*0.53*	0.76	1.14
Histidine	%	*0.36*	0.71	0.39	0.56	**0.84**
Isoleucine	%	0.76	1.09	*0.73*	1.04	**1.56**
Leucine	%	*1.19*	2.67	1.32	1.88	**2.82**
Lysine	%	*0.64*	1.37	1.11	1.58	**2.37**
Methionine	%	*0.30*	0.58	0.49	0.76	**1.14**
Phenylalanine	%	0.84	1.32	*0.73*	1.04	**1.56**
Threonine	%	0.60	0.97	*0.59*	0.84	**1.26**
Tryptophan	%	0.22	0.28	*0.17*	0.24	**0.36**
Valine	%	0.91	1.33	*0.87*	1.24	**1.86**
Calcium	g/kg	*0.8*	**10.0**	6.0	6.0	6.0
Sodium	g/kg	*0.07*	**3.2**	2.0	2.0	2.0
Iodine	mg/kg	*0.045*	**1.93**	0.6	0.6	0.6
Selenium	mg/kg	*0.053*	**0.44**	0.2	0.2	0.2
Vitamin A	mg/kg	*0*	3.6	0.66	0.66	0.66
Vitamin D	mg/kg	*0*	0.042	**0.055**	**0.055**	**0.055**
Vitamin E	mg/kg	*1.4*	15.1	**34.4**	34.4	**34.4**
Vitamin K	mg/kg	0.04	0.25	*0*	0	*0*
Thiamin	mg/kg	*0*	9.2	**20.0**	**20.0**	**20.0**
Riboflavin	mg/kg	*0*	9.4	**20.0**	**20.0**	**20.0**
Pantothenate	mg/kg	*5.3*	34.4	**60**	60	60
Folic Acid	mg/kg	*0.25*	**4.1**	4.0	4.0	4.0
Biotin	mg/kg	*0.10*	0.12	**0.4**	0.4	**0.4**
Vitamin B_{12}	mg/kg	*0*	0.053	**20.0**	20.0	**20.0**
Choline	mg/kg	*0*	**2100.0**	2000.0	2000.0	2000.0

Note: The maximum value in each row is shown in boldface type, while the minimum is shown in italics.

[a]Estimated nutrient composition from Scherz and Senser (1994), based on a 3:1 mixture by mass of whole oats and sunflower seeds.