

PATTERNS OF POSTNATAL GROWTH IN A LABORATORY COLONY OF *PEROMYSCUS LEUCOPUS*

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ABSTRACT.—Phenotypic variation in postnatal growth was examined in 52 litters of *Peromyscus leucopus*. Male and female growth trajectories were similar during the preweaning period, but diverged during the postweaning period, and partial compensatory growth was exhibited with smaller weanlings growing more rapidly during the postweaning period. Litter size was not related to growth form, but the sex ratio of a litter affected the growth trajectory, with increasing proportion of males in a litter associated with decreased male growth during the preweaning period and lower male mass at weaning. Maternal mass also was correlated with offspring growth; larger females had offspring that grew rapidly during the postweaning period and attained a higher breeding mass. In addition, loss of mass by mothers during the late preweaning period was correlated with heavier neonate and weaning mass, and faster offspring growth during the early preweaning period. Maternal mass also was associated with litter frequency; heavier females were more likely to become pregnant at postpartum estrus.

Although the growth of mammals can be portrayed by smooth sigmoidal curves (Zullinger et al., 1984), mass at any particular age actually is variable within a species, both among individuals and among litters (*Cynomys ludovicianus*, Anthony and Foreman, 1951; *Homo sapiens*, Brody, 1964; *Neotoma lepida*, Cameron, 1973; *Pseudomys gracilicaudatus*, Fox and Kemper, 1982; *Dicrostonyx groenlandicus*, Hansen, 1957; *Perognathus longimembris*, Hayden and Gambino, 1966; *Microtus ochrogaster*, Kruckenberg et al., 1973; *Peromyscus leucopus*, Lackey, 1978; Millar, 1975, 1978). Sources of this variation are not well known, nor is it well understood what effect this variation has on final size. This study examines variation in growth of *P. leucopus* to address these questions.

Variation in mass could profoundly influence fecundity and survival, particularly through its effects on fitness at two points in the growth trajectory, weaning and sexual maturity. These stages occur at approximately 21 and 42 days in the laboratory in *P. leucopus*. In this species, mass at weaning is correlated with survival time during a stress test (Fleming and Rauscher, 1978), and female mass is correlated with litter size (Lackey, 1978) and age at first breeding (Merson and Kirkpatrick, 1981).

Phenotypic variation in growth rate has been closely examined in laboratory rodents, and is caused by genetic, environmental, and maternal effects (Aberle and Doolittle, 1976; Calvert et al., 1985; Falconer, 1955; Moore et al., 1970; Nagai, 1977; Timon and Eisen, 1969). The relationship between phenotypic variation in growth during different phases of the growth trajectory has been examined extensively in *Mus musculus* (Monteiro and Falconer, 1966; Riska et al., 1984; Rutledge et al., 1972) and *Rattus rattus* (Atchley and Rutledge, 1980). These studies show that laboratory rodents exhibit compensatory growth (also called catch-up growth or targeted growth) in which phenotypic variation in mass decreases as animals approach adult mass (Eisen, 1976; Tanner, 1963). Despite the occurrence of compensatory growth, positive correlations between early and later masses have indicated that compensation is not complete (Riska et al., 1984; Williams and Hughes, 1975). Although compensatory growth has been examined only in *Rattus* and *Mus*, one study of *P. maniculatus* by Myers and Master (1983) found a strong positive correlation between mass at weaning and at breeding. This indicates that compensatory growth may not be strongly exhibited by *Peromyscus*.

If we examine mass at birth, weaning and sexual maturity, several patterns of growth might be predicted. Compensatory growth may be exhibited in growth trajectories if variation in mass

decreases as individuals reach adult mass, slow growth rate during part of the trajectory being compensated by more rapid growth during a later phase. Alternatively, similar adult masses also could be attained if slower-growing individuals grew for a longer period of time, without exhibiting increased compensatory growth. Variation in growth trajectories also may be related to sexual dimorphism in size. Variation in mass may increase throughout the growth trajectory, with some individuals always growing more slowly than others. This pattern may occur with individuals starting their growth trajectory at similar birth masses, or may begin with individuals starting at dimorphic birth masses. Alternatively, variation in mass may be low until some particular age at which time growth patterns diverge.

The purpose of this study was to examine the natural phenotypic variation in growth in *P. leucopus* in the laboratory, and determine the consequences of this variation on mass at age of sexual maturity. Three growth periods were examined: early preweaning growth, late preweaning growth, and postweaning growth. In addition, mass at birth and mass at weaning were determined to ascertain their effect on mass at sexual maturity. The effects of litter size, maternal mass, and sex of offspring on the overall growth trajectory also were tested.

METHODS

Peromyscus leucopus used in this study were field captured and first- or second-generation laboratory animals. The laboratory colony was established from mice captured at Devon, PA, 20 km W Philadelphia, PA. All female mice in the study previously had given birth to at least one litter. Females were housed in 27 by 17 by 13 cm clear plastic cages under 14L:10D photoperiod and given food (Purina Mouse Breeder Chow) and water ad lib. Males were placed with females on the day of birth, and removed when the litter was 3 days of age.

Only litters in which the female did not cannibalize the young were included in the analysis. Survivorship of these litters was high (97.4% to day 6, and 96.4% to weaning). Litter sizes used in the analyses were recorded on day 6.

Females and individual offspring were weighed at 3-day intervals from birth until day 18, then on alternate days until separation at 20–25 days of age. (Many mice were from an experiment on the effect of variable age of weaning on postnatal growth; mice included in this study were in treatments that produced no long-term effects on growth or mass.) Neonate mass was recorded at day 3, the first day at which individuals could be marked by ear clipping. Weaning mass was measured at day 20 or day 21. Breeding mass (also referred to as mass at sexual maturity) was measured at 42 days of age. Because all litters were not measured at the same age, residual values were used in the analyses. Residual values for a litter were the positive or negative deviations of the litter mean value from the predicted mean mass at that age calculated from the Gompertz equation (Zullinger et al., 1984) estimated from the growth trajectory of all individuals.

Several measures of growth were calculated from mean litter masses. Preweaning growth rate was the average gain in mass per day from day 0 to weaning (e.g., [mass day 20 – mass day 0]/20); postweaning growth rate was the average gain in mass per day from weaning to day 42. Early preweaning growth was the average growth rate during the first week of lactation, and late preweaning growth was the average rate from day 15 to day 20 or day 21 of lactation.

Fifty-two litters were included in the analysis; however, complete data were not available for all litters. Some litters lacked measurements at day 3 (to prevent further disturbing the female), and female masses were not recorded for all litters. Data are reported as $\bar{X} \pm SE$.

Multiple-regression analyses were employed to determine the relative independent contribution of each of the variables in explaining the variation in mass at weaning and mass at sexual maturity. Because the independent variables were highly correlated, their associated *F*-values calculated from type I sums of squares would reflect their order of entry into the model. Type III sums of squares, however, are order independent, and reflect the proportion of the variation that can be ascribed to the associated variable if all variables are included in the model (SAS Institute, Inc., 1982). The sum of all type III sums of squares does not equal the total sums of squares.

RESULTS

Variation in growth in Peromyscus leucopus.—Considerable variation in growth (approximately two-fold) existed among litters of *Peromyscus leucopus* reared in the laboratory under conditions of ad lib. food. By day 20, individuals ranged in mass from 6.2 to 13.1 g with a mean

TABLE 1.—Correlations among measures of offspring growth rate and mass in *Peromyscus leucopus*.

Measure	\bar{X} growth rate during:					
	Early preweaning (days 0-7)	Late preweaning (week before weaning)	Lactation	Postweaning (weaning to day 42)	Neonate mass	Weaning mass
Late preweaning growth	-0.09	1.00	—	—	—	—
Preweaning growth	0.75***	0.25	1.00	—	—	—
Postweaning growth	-0.34*	-0.08	-0.24	1.00	—	—
Neonate mass	0.47***	0.21	0.32*	-0.33*	1.00	—
Weaning mass	0.75***	0.32*	0.96***	-0.31*	0.60***	1.00
Breeding amss	0.18	0.17	0.47***	0.69***	0.07	0.45***

* = $P < 0.05$.*** = $P < 0.001$.

of 8.9 g (± 0.12 , $n = 102$), and on day 42, individuals ranged in mass from 10.8 to 19.7 g with a mean of 14.6 g (± 0.21 , $n = 98$). Fitting data from all individuals to the sigmoidal Gompertz function yielded estimated growth parameters of $K = 0.062$ (± 0.003), $I = 13.6$ (± 0.5), and $A = 17.6$ (± 0.2).

A nested analysis of variance of offspring growth of four females each producing three or four litters showed that variation in mass at weaning was related to differences between mothers ($F = 74.75$, $P < 0.0001$, $d.f. = 3$) and differences between litters within females ($F = 7.76$, $P < 0.0001$, $d.f. = 11$). Because this analysis indicates that the mass of individuals within a litter is similar, subsequent analyses used mean litter values for mass and growth to avoid biasing the results. In addition, no female contributed more than five litters to the study.

Correlations among growth and mass measurements.—Simple correlation analysis showed significant relationships among the growth and mass measures (Table 1). Growth during a

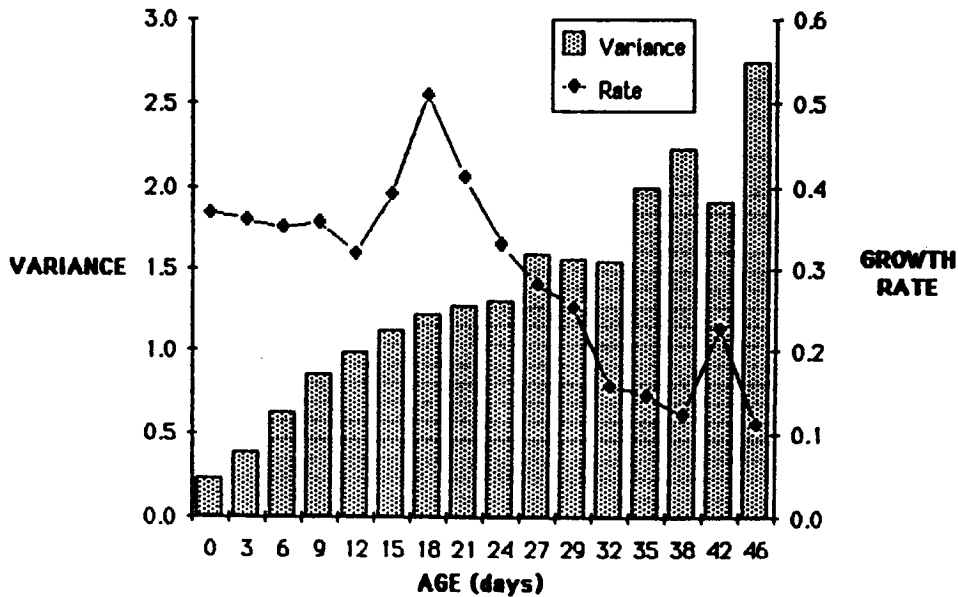


FIG. 1.—Growth rate (g/day) and variance of mass from birth to 46 days of age in *Peromyscus leucopus*. Growth rate is the average growth during the period encompassing the listed age and the next age; growth rate peaked between days 15 and 18. Variance was calculated from all individuals of age x ; it continued to increase throughout the period.

TABLE 2.—Multiple regression analyses of mass at day 42 and mass at day 20 in *Peromyscus leucopus*. Type III sums of squares are listed for each independent variable.

Source	d.f.	Sums of squares	F	P
Dependent variable: mass day 42				
Preweaning growth	1	0.15	1.01	0.32
Postweaning growth	1	127.02	874.70	0.0001
Weaning mass	1	9.28	63.92	0.0001
Error	45	6.53		
Total	52	172.10		
Dependent variable: mass day 20				
Neonate mass	1	5.17	187.9	0.0001
Early preweaning growth	1	0.00	0.00	0.95
Late preweaning growth	1	0.02	0.74	0.39
Preweaning growth	1	14.91	542.05	0.0001
Maternal mass	1	0.00	0.14	0.71
Error	39	1.07		
Total	44	68.64		

particular time interval appeared to be related negatively to growth during subsequent time intervals, although relationships were significant only for early preweaning growth and postweaning growth. Neonate mass was correlated positively with weaning mass, but not significantly correlated with breeding mass; weaning mass was correlated positively with breeding mass. Breeding mass was correlated positively with both preweaning growth and postweaning growth, although these two growth rates were related negatively.

Although growth in *P. leucopus* was compensatory in the sense that sequential growth rates were related inversely, there was no relationship between age and variance in mass (Fig. 1). Furthermore, peak growth rate was not associated with peak variance in mass.

Multiple regression analyses were performed to determine which variables best predicted mass at breeding (day 42) and mass at weaning (day 20; Table 2). When all variables that were significantly correlated were included in the models, mass at sexual maturity was significantly related to postweaning growth and weaning mass. Postweaning growth explained more than 70% of the variation in breeding mass when entered last into the model. Although 98% of the variation in weaning mass could be explained by the predictors, only neonate mass and preweaning growth rate were significant when entered last into the model, and neither explained more than 22% of the variation independent of the other variables. The analyses also were performed in both cases with all variables included in the models, and the results did not differ.

Litter size and offspring mass and growth.—Mean litter size was 3.6 (± 0.16 , $n = 52$, range 1–6). Litter size did not affect offspring mass at birth, weaning, or sexual maturity; neither did it affect growth rate during any stage.

Maternal mass and offspring mass and growth.—Maternal mass varied during the lactation period, with most females exhibiting a peak mass at day 12 or 15, followed by a decline in mass until weaning (Fig. 2). The mean peak mass for all females between days 12 and 15 was 23.3 g (± 0.35 , $n = 38$), whereas the mean mass at weaning was 22.0 g (± 0.34). The maximum loss in mass for any female during this period was 5.3 g. Change in maternal mass from days 12–15 to weaning was correlated positively with mass peak between days 12 and 15 ($r = 0.40$, $P < 0.01$), but not significantly related to maternal mass at weaning ($r = -0.30$, $P = 0.06$).

The pattern of mass loss during lactation was similar for dams that were concurrently pregnant and those that were not. However, females that were concurrently pregnant were significantly heavier than other lactating females, even on the first day of lactation preceding mating at the postpartum estrus (Fig. 2). Females concurrently pregnant and lactating averaged 1.8 g heavier on the day of birth of the first litter, and maintained this mass difference throughout the lactation period.

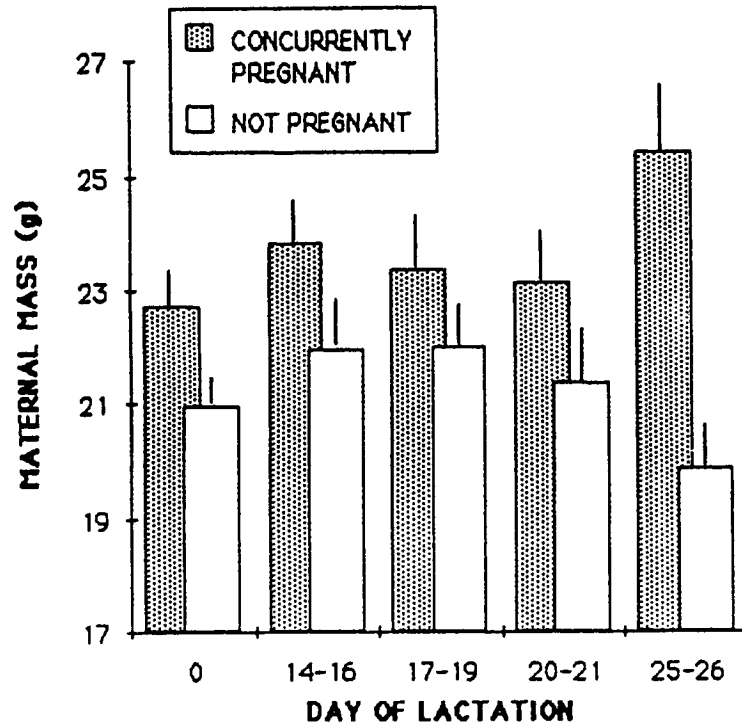


FIG. 2.—Mass (± 1 SE) during the lactation period of female *Peromyscus leucopus* that were subsequently found to be pregnant and those that were not. All females were paired with males from day 0 (birth of neonates) until day 3. Offspring were separated from females between day 21 and day 25.

When all dams were considered, change in maternal mass was correlated positively with birth and weaning mass of the current litter, and with preweaning and early preweaning growth (Table 3). Although change in maternal mass occurs during the period of late preweaning growth, it was not correlated significantly with this variable. Maternal mass at weaning was correlated positively with postweaning growth and with offspring breeding mass. In addition, maternal mass at weaning was correlated negatively with the same variables to which change in maternal mass was correlated positively, but correlations with maternal mass at weaning were weaker in all cases. Maternal mass for days 12–15 was not correlated significantly with growth or mass measures of offspring.

Sex, and offspring mass and growth.—Although adult male *P. leucopus* were significantly heavier than adult females in the field and in the laboratory, these differences were not expressed

TABLE 3.—Correlations between maternal mass and the growth and mass of offspring *Peromyscus leucopus*.

	Peak mass at days 12–15	Mass at weaning	Change in mass
Early preweaning growth	0.00	-0.32*	0.47**
Late preweaning growth	-0.04	0.11	-0.22
Preweaning growth	-0.01	-0.31	0.42**
Postweaning growth	0.28	0.49**	-0.28
Neonate mass	-0.04	-0.34*	0.46**
Weaning mass	-0.04	-0.38*	0.47**
Breeding mass	0.30	0.32*	-0.01

* = $P < 0.05$.

** = $P < 0.01$.

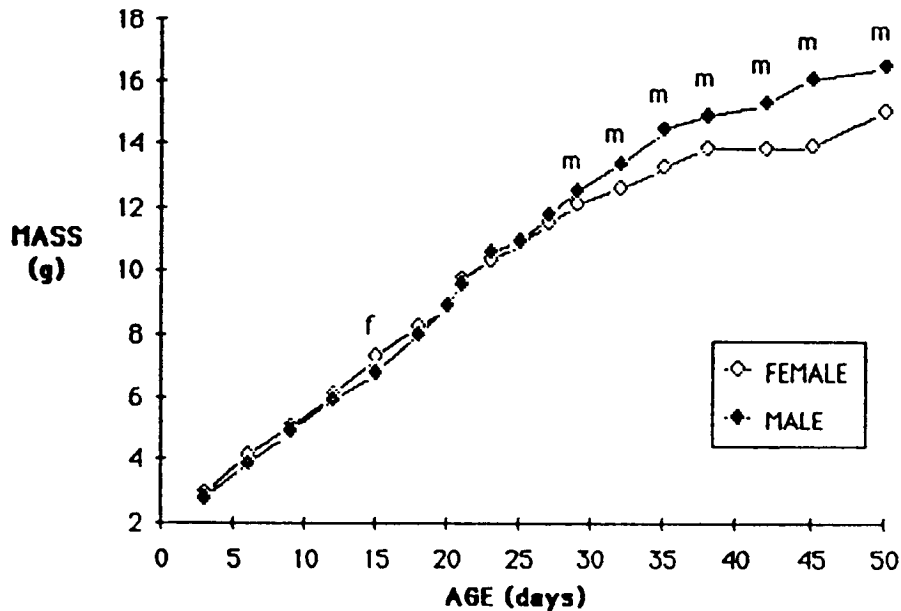


FIG. 3.—Growth of male and female *P. leucopus*; *t*-tests were used to compare male and female mass; *f* denotes females significantly heavier than males; *m* denotes males significantly heavier than females.

until the postweaning growth period (Fig. 3). In fact, females were heavier than males until day 18 of the preweaning period (differences were significant only on day 15). Estimates of the growth parameters from the Gompertz equation differed significantly between sexes for the asymptote (*A*) and the age at which the inflection point (*I*) occurs (males, $K = 0.059 (\pm 0.003)$, $A = 18.69 (\pm 0.28)$, $I = 14.5 (\pm 0.5)$; females, $K = 0.063 (\pm 0.004)$, $A = 16.84 (\pm 0.28)$, $I = 12.3 (\pm 0.7)$).

Correlations of growth and mass measures within each sex were similar to the relationships exhibited by litters. Early, late, and total preweaning growth rates did not differ significantly between male and female offspring. Males, however, grew significantly faster than females during the postweaning period (males, 0.274 g/day; females, 0.224 g/day, $t = 2.57$, $d.f. = 81$, $P < 0.01$).

The total number of male and female offspring did not deviate from a 1:1 ratio (sex ratio = 1.14, $X^2 = 0.71$, $P > 0.10$, $n = 171$), and the distribution of males to females within litters of size four was not different from expected ($X^2 = 1.96$, $P > 0.10$). However, the sex ratio of litters did affect growth rate (Fig. 4). Specifically, the proportion of males in a litter was related negatively to preweaning growth and weaning mass of male offspring (preweaning growth: $r = -0.29$, $P < 0.05$; weaning mass: $r = -0.32$, $P < 0.05$). The proportion of males in the litter had a similar effect on female offspring growth, but these correlations were not significant.

DISCUSSION

Effects of Sex on Growth

Male and female growth trajectories of *P. leucopus* were similar until an intermediate mass, then diverged. Males attained a greater adult mass by growing at a higher rate than females after weaning. Male mass first surpassed females at 23 days of age; this difference, however, was not significant until 32 days of age. A similar pattern in *Rattus rattus* was interpreted as a result of an earlier decrease of cell-division activity in females (Reuter, 1976).

In cricetid rodents, either growth trajectories of males are similar to females until the postweaning period, or males appear to be heavier than females from birth. Several dimorphic

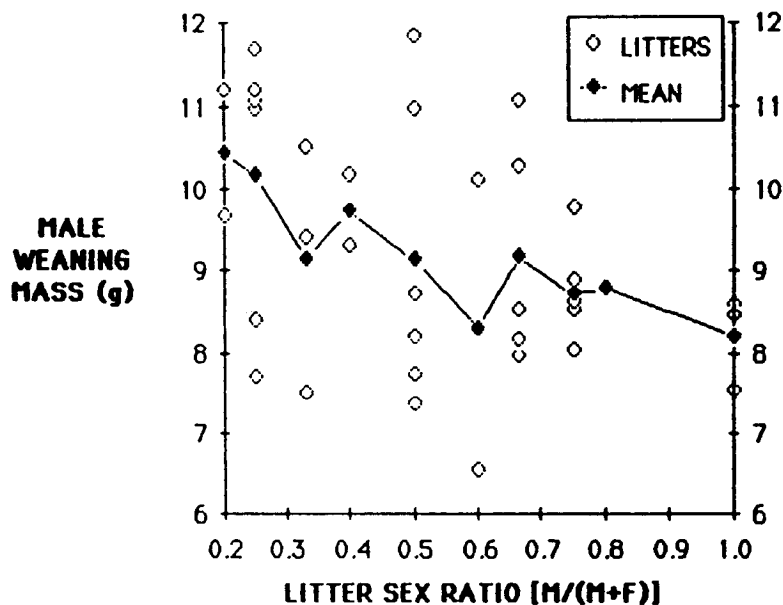


FIG. 4.—Male weaning mass as a function of litter sex ratio. The solid line connects the average male weaning mass calculated from each mean litter mass of male offspring at weaning.

cricetid rodents appear to show the pattern exhibited by *P. leucopus* with similar mass until weaning (*Zygodontomys microtinus*, Aguilera, 1985; *P. maniculatus labecula*, Drickamer and Bernstein, 1972; *Meriones unguiculatus*, Norris and Adams, 1972; *Onychomys leucogaster*, Pinter, 1970; *Neotoma stephensi*, Vaughan and Czaplewski, 1985), but several other cricetid rodents exhibit mass dimorphism from birth (*P. maniculatus nebrascensis*, Drickamer and Bernstein, 1972; *Neotoma floridana*, McClure and Randolph, 1980; *Akodon molinae*, Merani and Lizarralde, 1980). Relative growth trajectories of dimorphic species appear to be flexible in different subspecies (e.g., *P. maniculatus*). Relative trajectories also can be variable within one population under different environmental conditions (*Mesocricetus auratus*; Labov et al., 1986). Therefore, the adaptive significance of sexual dimorphism in growth trajectories is unclear.

Compensatory Growth in Peromyscus leucopus.

The negative relationship between preweaning and postweaning growth suggests that *P. leucopus* exhibits compensatory growth. Compensatory growth is exhibited by decreased variation in mass as size increases. Eisen (1976) suggested that decreasing variation should begin approximately after the stage of maximum growth rate (the inflection point for sigmoidal growth). Although growth in *P. leucopus* was compensatory in the sense that rates of adjacent intervals were related inversely, the expected relationship of peak variation in mass at an intermediate age was not seen. Furthermore, peak growth rate was not associated with peak variance in mass. Therefore, even under conditions of ad lib. food, mice that were small at weaning also were small at breeding. Millar (1983) made a similar conclusion about the growth of *P. maniculatus* based on correlation analysis. Weak evidence for compensatory growth in *Peromyscus* suggests that mechanisms for obtaining an optimal size have not been strongly selected. Perhaps the low expectation for future survival (Goundie and Vessey, 1986) of this small mammal has led to selection for a more opportunistic growth and breeding strategy (Bronson, 1985) and allocation of less energy to growth with age, regardless of the relative position of a mouse on the growth trajectory.

Maternal Effects on Growth

Selection on growth rate in a species can occur either directly on the pup through the rate of cell division, or indirectly through selection on maternal performance (Moore et al., 1970; Nagai, 1977). Maternal effects account for much variation in offspring growth (Bateman, 1954; Carmon and Golley, 1964). In fact, when decreased growth rate has been selected in the laboratory, decreased lactational performance has been the result (Falconer, 1955; Moore et al., 1970). Changes in maternal effects throughout the lifespan of a breeding female also may contribute to variation in offspring growth. Selection for increasing reproductive effort with age could result in such effects (Williams, 1966). This study indicates that maternal mass and changes in maternal mass during lactation strongly influenced offspring growth patterns, and potentially affected female fecundity.

Female mass and offspring growth.—Female mass and change in female mass (negatively but not significantly correlated) had different effects on growth of offspring. Larger females (that tended to lose less mass) produced offspring that grew more rapidly postweaning and that were larger at sexual maturity. Females that lost more mass produced heavier offspring at weaning, and also produced heavier neonates.

Millar (1975) found that lactating females showed a peak mass at approximately 12 days after parturition; however, change in mass during lactation was not significant. In addition, although Millar (1975) found that fat indices declined significantly during lactation, increased food consumption, not body reserves, provided the majority of energy required for nestling growth. Although Millar's study indicates that fat per se was not important for offspring growth, results of the present study indicate that mass loss (which may reflect fat loss) is related indirectly to offspring growth. Dams that lost mass during the last week of lactation had offspring that grew more rapidly during the early preweaning period and were significantly heavier at weaning. Because mass at weaning may be correlated with survival (Fleming and Rauscher, 1978), maternal mass loss may be an important factor in reproductive success.

Female mass and concurrent pregnancy and lactation.—Reproductive effort of small mammals can be increased by simultaneously investing in two litters, i.e., carrying one litter *in utero* while nursing another. Results of this study indicate that the frequency of concurrent pregnancy and lactation varies with female mass, and, therefore, may affect the relative fecundity of small and large females. Females that support a concurrent pregnancy during the lactation period will produce litters every 35 days (implantation is delayed 10 days in concurrently lactating females), instead of every 45 days (length of the lactation period of 21 days plus length of the gestation period of 24 days). Further study is needed to distinguish between alternative strategies that might link reproductive effort and simultaneously investing in two litters, such as female age and female condition.

Large and small female *Peromyscus* may have different reproductive tactics. In this study, smaller females invested greater effort into current litters (producing heavier neonates and weanlings, and losing more mass), whereas heavier females directed more energy into producing multiple litters (increasing the frequency of concurrent pregnancy and lactation) at a slight expense of mass of individual offspring. Further study of the effect of plasticity of reproductive tactics in *P. leucopus* will require measurement of food availability for lactating females and for postweaning juveniles, and changes in these resources throughout the breeding season.

Sex, Litter Size, and Growth

Theoretical consideration of sex ratios in mammals has demonstrated that females of varying quality may benefit from manipulating the sex of their offspring. When offspring reproductive success varies more in one sex and is influenced by parental investment, higher quality females invest more heavily in offspring of that sex (Clutton-Brock and Albon, 1982; Labov et al., 1986; McClure, 1981; Trivers and Willard, 1973). Although heavier *P. leucopus* females produce more male than female offspring (Goundie and Vessey, 1986), results presented herein suggest that this strategy may not result in greater reproductive success. In this study, natural variation in sex ratio resulted in decreased preweaning growth and weaning mass of male offspring in litters

that had higher numbers of males. Therefore, the simple predictions of greater resource allocation to males by high quality dams may not in fact be beneficial to *P. leucopus* if lighter males at weaning have lower survivorship or fecundity compared to heavier males.

Selection for Modification of Growth Trajectories

One question still emerges after examination of growth patterns within a species—why don't all offspring grow more rapidly? Examination of the phenotypic variation in growth indicated that adjacent portions of the growth trajectory were related negatively, and that mass at breeding was correlated most strongly with postweaning growth. A genetic analysis of covariation of growth would be worthwhile to determine if genetic correlations between periods of growth also are correlated negatively—suggesting that pleiotropic effects may prevent further increases in growth rate. In a review of growth-curve analyses, Fitzhugh (1976) noted that rate of maturation and final size are related inversely. In addition, an antagonistic balance between early and late growth has been suggested to occur in laboratory mice and rats, and negative genetic correlations exist between early and late growth in mice (Atchley, 1984; Riska et al., 1984). Although maximum mass at weaning and minimum age at breeding might both be selectively advantageous, negative pleiotropic effects for growth rate during the preweaning and postweaning periods may lead to selection for intermediate growth rates.

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