

California State University, Northridge

METABOLISM OF THREE SPECIES OF YOUNG AND ADULT PEROMYSCUS

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requirements for the degree of Master of Science in

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by

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ABSTRACT

METABOLISM OF THREE SPECIES OF YOUNG AND ADULT PEROMYSCUS

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The purpose of this investigation was to study the metabolism of three species of young and adult Peromyscus by means of oxygen consumption. Young Peromyscus were used to determine the timing of the onset of homeothermy and to ascertain whether age or weight triggered that onset. The zone of thermal neutrality for P. maniculatus was 22.5°C - 25°C and for P. californicus was 20°C - 25°C. In P. boylii only one point was determined, 25°C, for the temperature intervals used in this study. The mean basal metabolism of adult P. maniculatus is 3.8 cc of oxygen per gm hr⁻¹ at 25°C, of P. boylii 2.3 cc of oxygen per gm hr⁻¹ at 25°C, and of P. californicus 1.9 cc of oxygen per gm hr⁻¹ at 25°C.

In developing young there is a linear relationship between weight and metabolism. The onset of homeothermy in three species of Peromyscus is a function of weight, and homeothermy is fully developed in the three species of Peromyscus prior to weaning.

INTRODUCTION

Studies of metabolic rates through measurement of oxygen consumption have been frequently conducted for small mammals. These rates of metabolism have been suggested as providing a useful character in the study of speciation (Morrison, 1948), and have been studied for their intrinsic value as well. More recently, evidence has been presented which suggests that metabolic rates in some cases can be used to measure adaptation to local environments, thus suggesting that metabolism might be an "ecotypic phenomenon" (Bowers, 1971). Therefore, studies of metabolic rates of adult mammals take on an additional significance in attempts to define the parameters by which populations have become adapted to the environmental conditions under which they can live.

The high metabolic rates attained by birds and mammals are instrumental in supporting perhaps the single most advantageous physiological characteristic in birds and mammals, namely, homeothermy. At hatching or birth, however, not all birds (Breitenbach and Baskett, 1967; Wekstein and Zolman, 1971) or mammals (Conklin and Heggeness, 1971; Chew and Spencer, 1967; Mount and Stephens, 1970; Taylor, 1960; Hill, 1947; Gulick, 1937 and others) possess well developed thermo-regulatory abilities. The smallest homeotherm which can maintain its body temperature over a 24 hour period (versus an animal that may utilize daily torpor to conserve energy) theoretically weighs 2.4 to 2.5 grams (Pearson, 1948; Lasiewski, 1963). Therefore, any animal that does not exceed this critical weight

at birth should not be expected to be a stable homeotherm at this time. Furthermore, some mammals, whose birth weight does exceed the critical weight, still do not have the facility to maintain a constant body temperature (Bowers, 1971; Chew and Spencer, 1967; Mount and Stephens, 1970).

Chew and Spencer (1967) have stated that two factors influence the development of homeothermy: weight and age. From their observations, they suggested that the preeminence of one factor is significant for homeometabolism. Weight was considered of greater importance for Peromyscus maniculatus, although these authors stated that the critical factor must certainly differ among species.

The availability of several species of Peromyscus in Southern California affords an opportunity for comparative metabolic studies among species of a single genus. Using oxygen consumption as a means of measuring metabolic rates, three species, P. maniculatus, P. boylii and P. californicus, were studied in order to 1) ascertain basal metabolic rates and thermal neutral zones of adults and 2) to determine the onset of homeothermy in young mice and to determine which parameter (age or weight) was a more critical factor.

MATERIALS AND METHODS

All metabolic studies were performed in a Beckman G-2 paramagnetic oxygen analyzer. This reversed range instrument had two sensitivity ranges, 16-21% and 20-21%, and all recordings were performed at the higher range (20-21%). In order to maintain a constant temperature, the metabolic chamber was placed in a Temperature Control Box from Precision Scientific which had a range of 5-50°C and was accurate to $\pm 0.5^\circ\text{C}$. The results were recorded on an Electronic 15 Honeywell recorder connected to the G-2.

Circuit: The block diagram (fig. 1) illustrates the design used for the metabolic studies. A detailed description of the apparatus follows and all numbers refer to figure 1. Number 1 was a Neptune positive or negative Dyna-pump. The pressure side of the pump was connected to an aquarium 3 gang valve (number 2). This valve served to regulate the flow of air to the system; since the air flow must be regulated, the extra valve openings were used as vents, as the pump could not be regulated. Numbers 3 through 7 were "U" tubes inside the temperature control box. Numbers 3 and 4 were filled with activated charcoal, which removes smog, dust, and other gasses from the air. The contents of these tubes were changed every six months. Number 5 was filled with soda lime for the removal of CO_2 from the ambient air, while 6 and 7 were filled with fresh Drierite (anhydrous CaSO_4) for water removal from the air. Number 8 was the animal chamber, which was a wide mouth 1 gallon jar, fitted with a screw top through which two holes were drilled. One piece of 1/4 inch copper tubing was soldered in each hole and together they served

as inlet and outlet ports. Inside the jar, the animal was housed in a cylindrical cage (3¼ inch high and 3½ inch in diameter) constructed of 1/4 inch hardware cloth. This cage was elevated from the floor of the jar by a one inch ring made of 1/4 inch hardware cloth. The bottom of the jar was filled with Drierite. A rubber tube connected to the outlet port extended to about the middle of the cage when the jar top was in place. This addition to the outlet port served to extend the orifice, resulting in a more efficient mixing of air. The jar was sealed during the experiment by screwing the top on securely and by placing vinyl electrical tape around the top and the adjacent portion of the jar. Number 9 was filled with soda lime, and numbers 10 and 11 were filled with Drierite. These tubes were very important since the oxygen analyzer would have responded to oxygen in compound form, such as the carbon dioxide and water produced by the animal through respiration and excretion during the experimental period. These products must be removed from the air before it enters the analyzer. Number 12 was a Manostat Flowmeter (36-541-09) for monitoring the air flow, which must remain constant, during a given experiment. The flow rates used, which were controlled by opening and closing the gang valve vents (number 2), were 400 ml per minute for adults and 340 ml per minute for the young. Number 13 was the oxygen analyzer.

Calibration: The oxygen analyzer was calibrated by running two gasses at specific flow rates through the analyzer. These gasses contained oxygen at the minimum and maximum of the range to be used. All the metabolism studies were performed at the 20-21% range; there-

fore, the upper range gas used was ambient air (oxygen concentration of 20.94%), and the lower range gas was a certified gas (19.95% oxygen and 80.05% nitrogen) from Matheson Chemical Co.

Ambient air was pumped through the analyzer and the recorder was positioned by the zero potentiometer at the upper range (line "A" in fig. 2) and allowed to stabilize for five minutes. After stabilization the certified gas was passed through the analyzer and three to five minutes was allowed for the recorder to span the graph and stabilize (line "B" in fig. 2). Positioning of the lower range gas was controlled by the span adjust potentiometer. The distance transversed by the recorder represents a decrease in oxygen concentration of 0.99% (20.94% - 19.95%).

Conditions: Adults of P. boylii and P. maniculatus were trapped during June through December, 1970, at an altitude of 1500 feet in Tic Canyon of the San Gabriel Mountains, 10 miles north of the city of San Fernando, Los Angeles County, California. Peromyscus californicus were borrowed from a breeding colony maintained at California State University, Northridge and originally trapped on the western slope of the San Gabriel Mountains in Riverside County, California. Mice used in the thermal neutral zone (TNZ) studies (P. maniculatus, P. boylii) were given a minimum of two months to accommodate to laboratory conditions.

When placed in the metabolism cage, adults had been in a post-absorptive state for 24 hours. Adults were given 30 minutes to adjust to the conditions within the temperature control box. A 30 minute metabolism run followed and the last five minute period of this

run was used in metabolic determination. Metabolic runs were all made between 0800 and 1600 hours when these mice are normally inactive. These same adults for each species were repeatedly used in these studies. The metabolic rate for each individual was measured three times at each temperature interval during three successive weeks. The temperature intervals used were 2.5°C and 5°C. Two females and three males (P. boylii, two males and two females) were randomly selected for these studies. Each mouse was housed separately when not in the metabolic chamber. Young mice used were born in captivity and study began two days after birth. When placed in the temperature control box, each individual was given 20 minutes to adjust to the conditions. A metabolic run of 20 minutes followed immediately. Young on many occasions were suckling and had to be forcefully removed from the nipple of the female. This was most effectively accomplished by holding the mother by the tail and lightly pinching off the nostrils of the young. Young were selected at random from any of eight mated pairs of P. boylii, ten mated pairs of P. californicus or one mated pair of P. maniculatus. In all metabolism studies both young and adult individuals were weighed before and after the experiment, and the mean weight of these measurements was used in all calculations.

Calculations: Oxygen consumption was calculated for an open-circuit system from the formula of Depocas and Hart (1957). The formula is $V_{O_2} = VI \frac{PI_{O_2} - PE_{O_2}}{PB}$ where V_{O_2} is the volume of oxygen consumed by the animal per minute, VI the volume of air flowing into the chamber per minute, PE_{O_2} the partial pressure of oxygen flowing

out of the metabolic chamber, PI_{O_2} the partial pressure of oxygen on the inflowing air, and PB the barometric pressure. The symbols used were from the Committee on Standardizations of Definitions and Symbols in Respiratory Physiology (1950). The calibration (fig. 2) of the known oxygen content of gasses (air and certified gas) resulted in a deflection of 263 mm, the distance from "A" to "B", for a 0.99% difference. Ambient air was the baseline gas "A"; and if the line was extended (dotted line) and measured from the baseline to the level created by respiration of the animal, line "C", that distance "A" to "C" was 43 mm. The fraction 43/263 times (0.99%) was the percentage decrease in oxygen from the ambient air. The result of multiplying 43/263 times (0.99%) equal 0.16%; and this was subtracted from 20.94% equaling 20.78% oxygen exiting from the metabolism chamber. PI_{O_2} , the partial pressure of ambient oxygen, was 159 mmHg. The partial pressure of oxygen exiting from the metabolic chamber was calculated by $PE_{O_2} \times PB$ (20.78% x 760) which equaled 157.9 mmHg. The barometric pressure (PB) was 760 mmHg and VI was 370 ml of air per minute. Now substituting in the formula-- $V_{O_2} = \frac{370 (159 - 157.9)}{760}$ -- the calculated value is 0.538 cc of oxygen per minute. This value is the total amount of oxygen consumed by the animal per minute. All TNZ values are reported per gram weight per hour at 25°C.

RESULTS

Thermal neutral zone of adults.—The amount of oxygen consumed per gram body weight per hour is plotted on the ordinate with the environmental temperature plotted on the abscissa of figure 3. Paired "t" tests were applied to all data. The statistical tests for P. maniculatus (fig. 3A) showed that at 22.5°C and 25°C the means were not significantly different ($p < 0.60$). All other means were significantly different ($p < 0.05$). For P. boylii (fig. 3B) all means were significantly different ($p < 0.05$). For P. californicus (fig. 3C) the means at 20°C, 22.5°C, and 25°C, T_A were not significantly different: respectively, they were $p < 0.90$ and $p < 0.75$. Therefore, from this data, the range of thermoneutrality for P. maniculatus is 22.5°C through 25°C, T_A . A thermal neutral range for the temperature intervals used in this study was not discernible for P. boylii, but a thermal neutral "point" occurred at about 25°C, T_A . The minimal mean metabolic rate for P. maniculatus was 3.67 cc of oxygen per gm hr⁻¹, for P. boylii, 2.33 cc of oxygen per gm hr⁻¹, and for P. californicus 2.0 cc of oxygen per gm hr⁻¹.

Metabolic patterns of young Peromyscus.—A typical metabolic pattern for a P. maniculatus litter of four is shown in fig. 4A. At four days of age, the average oxygen consumption of the litter shows that the animals are hypometabolic and are unable to respond metabolically to ambient temperature. On day eight (fig. 4A), their metabolic response for the first time was within the range of an adult P. maniculatus, demonstrating a response to the environmental

temperature and showing an ability to maintain a constant body temperature. From days 18 to 60, a typical metabolic pattern that falls within the range of an adult P. maniculatus (compare with fig. 3A) is evident.

In fig. 4B and 4C, P. boylii and P. californicus showed a similar metabolic response. On day 4, P. boylii and P. californicus were hypometabolic to the environmental temperature. On day 6, both P. boylii and P. californicus demonstrated for the first time oxygen consumption values that fall within the range of adults (compare with fig. 3B and 3C). By extrapolation, the metabolic response of the young shows that when born they do not have the ability to maintain their own body temperature. However, several days after birth these animals show the onset of homeothermy.

Homeothermy as a function of weight or age.—Table 1 contains the mean weight of three litters of P. maniculatus and four litters of P. californicus, and the mean metabolic activity at a specific age for each species. As the mean weight increases, there is an increase in mean metabolic activity. For P. boylii a more pronounced weight difference in a single animal as compared to the normal population is shown in fig. 5. The abnormally slow weight gain caused a long delay in the first metabolic response of the animal to the environmental temperature (see fig. 4B). A comparison of metabolic records of the normal and abnormal P. boylii (4B) shows a long delay before the time of first metabolic response. On day 24, a second litter (three young) were born to the mother of the abnormal individual of P. boylii and possibly the competition for food (since

the abnormal P. boylii was still nursing) was the reason for the delay in weight gain from day 24 to day 30 (fig. 5).

Data presented earlier (fig. 4) showed that the first increase in metabolic activity had occurred in P. maniculatus (4A) by the eighth day and in P. boylii (4B) and P. californicus (4C) by the sixth day. The mean weight of individuals of P. maniculatus was 4.7 gms (fig. 5) by the eighth day, P. boylii was 4.0 gms (fig. 5) by the sixth day, and P. californicus was 6.4 gms (fig. 5) by the sixth day.

Figure 6 compares the weight of the newborn with metabolic responses. There is a highly significant correlation between weight and metabolic activity in the initial growth stages of the three species of Peromyscus. Thus, the highly significant relationship demonstrated (fig. 6) strongly suggests that the onset of homeothermy is a function of weight.

Figure 7 is a comparison of weight with the frequency of the first metabolic activity within the ranges of the adults of each species. To clarify what is meant by frequency, an example (using P. maniculatus) shows that its oxygen consumption range is 2.0 to 5.7 cc of oxygen per gm hr⁻¹ (fig. 3A). Each young which showed for the first time a metabolic rate that was 2 or more cc of oxygen per gm hr⁻¹ was considered to have a frequency of 1. The number of individuals reaching this point was then plotted against weight. The same criteria were repeated for each species. Seventy-nine percent of the P. maniculatus individuals showed a metabolic rate in the adult range somewhere between 4 to 5 grams of weight (fig. 7A).

Fig. 5 suggests that at 4 to 5 grams, the animal is from 5 to 8 days of age. Fig. 7B shows that in P. boylii all of the individuals fall between 4.2 and 5 grams. Fig. 5 shows that in that weight range the animal is between 6 and 8 days of age. Fig. 7C shows that in P. californicus 70% of the individuals fall between 6.2 and 7.1 grams. Fig. 5 shows that at that weight range the animal is between 6 and 9 days of age. Fig. 8 is a comparison between age and metabolic activity. The equations of the regression lines and their corresponding correlation coefficients are for P. maniculatus (8A) $y = (-0.02 x) + 2.9$, $r = -0.04$; for P. boylii (8B) $y = 0x + 3.0$, $r = 0$; and for P. californicus (8C) $y = (-0.01x) + 3.4$, $r = -0.03$. These data show that for these three species of Peromyscus no correlation exists between oxygen consumption and the first 18 days of life.

DISCUSSION AND CONCLUSIONS

Thermal neutral zone.—The TNZ for P. maniculatus was 22.5°C to 25°C and for P. californicus 20°C to 25°C; however, P. boylii did not exhibit a zone but rather a single point 25°C for the temperature intervals used in these studies. These ranges are lower than those obtained by Chew and Spencer (1967) and Murie (1961) for P. maniculatus, and McNab and Morrison (1963) for P. maniculatus and californicus. There are at least two major possible explanations for the differences. First, perhaps the apparatus had a systematic error resulting in data of lower values. However, in comparison with data from Pearson (1960), whose apparatus differed from that of the present study, one individual of Reithrodontomys megalotis tested here was extremely close (4.86 cc gm hr⁻¹ at 25.5°C {Pearson} and 4.61 cc gm hr⁻¹ at 25.5°C), even though the animals used were from different areas. This does not exclude the possibility of a systematic error; however, it does decrease its probability. A second, and more likely explanation, is that the difference is real. Conspecific individuals taken from different geographic areas should show differing metabolic values. Populational differences in metabolic rates within the same species are highly variable and adaptive throughout the species range (Bowers, 1971). Chew and Spencer (1967) used animals born in captivity from original stock trapped at Berkeley, California. McNab and Morrison (1963) used adults from Berkeley, California and Las Vegas, Nevada in their study. Murie (1961) used individuals taken at Berkeley and Death Valley, California in his study. Perhaps the differences in TNZ are due to a

population difference as suggested by Morrison (1948). The data from Murie (1961) show some difference in oxygen consumption for conspecific individuals from two populations. McNab and Morrison (1963) summarize the data supporting the concept that metabolism is an adaptive physiological phenomenon and their paper supports such an adaptation. Brown (1968) and Packard (1968) also lend support to a concept of adaptive metabolic differences among populations.

In looking at metabolic data one finds a great deal of variation. This as of yet unexplained variation can be looked at and considered as natural variation related to either different populations or wild versus laboratory reared strains. The evidence for this was apparent from work by Bowers (1971). In his study of the cotton rat (Sigmodon h. hispidus) he found that basal metabolism varied greatly with that population which had the wider geographic range. In contrast, that population which was highly restricted geographically had a narrow range of basal metabolism. Even more striking was the fact that the laboratory populations were very distinct from the wild populations. Bowers (1971: 136) concluded from his studies that genetic differences between the populations could cause metabolic differences and "...that metabolism can be used as an index in some cases to measure adaptation to local environmental conditions, suggesting metabolism might be an ecotypic phenomenon." One can conclude that the differences that are noted in TNZ of the three species of Peromyscus in this study, when compared to the work of others, are probably due to population and/or ecological variations. Perhaps this accounts for the differences in

oxygen consumption between the P. californicus of this study and the data on P. californicus of McNab and Morrison (1963) which had been captured recently.

The variability of TNZ of the same species of animal from differing geographic areas suggests its potential adaptiveness to environmental variations. If this assumption is true, it is possible that the genetics of metabolism are plastic to the habitat, or that the genotype is more rigid and the animal is forced to seek a habitat that is best suited to his metabolism.

Ontogeny of homeothermy.—The smallest theoretical homeotherm weighs approximately 2.4 grams. Therefore, it is not incongruous that mammals born weighing less than this critical weight may not have yet developed stable homeothermy. Brody (1945) and Pearson (1948) determined that the energy used by a homeotherm increased geometrically, as the surface area to volume ratio increases. In young altricial mammals, before insulative capabilities fully develop, the surface area to volume ratio is greater than in the adult; therefore, the group would expend much energy in maintaining body temperature, leaving less energy for growth (Larimer, 1968). By being hypothermic, more energy is available for growth and development, and it would seem logical that neonates that are hypothermic at birth must develop stable homeothermy prior to weaning and that this process must be a gradual one.

Meriones unguiculatus (McManus, 1971), laboratory white rats (Hill, 1947; Conklin and Heggeness, 1971), domestic pigs (Mount and Stephens, 1970), doves (Breitenbach and Baskett, 1967), domestic

chickens (Wekstein and Zolman, 1971) are some mammals and birds that develop homeothermy post-natally. Studies of the laboratory rat show that the development of homeothermy possibly begins on the first day of birth and it increases significantly on the ninth day, but it is not fully developed even after 21 days (Conklin and Heggeness, 1971; Hill, 1947; Gulick, 1926; Brody, 1943; Taylor, 1960). Possibly this long delay in the development of homeothermy is the response of this animal to the constant conditions of the laboratory. Gerbils develop homeothermy during days 10-18 of life (McManus, 1971). In this study of Peromyscus, no relationship between age and the onset of homeothermy was demonstrable.

In the present study the three species of Peromyscus at birth showed no metabolic response at a temperature of 25°T_A . However, before weaning, all demonstrated a fully developed metabolic response. In ascertaining what factor caused the onset of homeothermy, only a comparison between weight and oxygen consumption showed a linear relationship (Figs. 6 and 8). Newborn pigs also demonstrate a linear relationship between weight and metabolic activity (Mount and Stephens, 1970). Chew and Spencer (1967) determined that the onset of homeothermy of P. maniculatus was due to weight increase. In their paper the critical weight was 4.8 to 5.4 gms. In this study the critical weight was between 4 and 5 grams. It therefore seems likely that for certain species age may be the critical factor, whereas for others weight may be of greater importance.

The three species of Peromyscus used in this study were hypothermic at birth and at a critical weight began to develop a

homeothermic response. All three species showed a fully developed ability to maintain a constant body temperature at least five days before weaning.

Table 1. Oxygen consumption values for comparable ages in the young of P. maniculatus and P. californicus. See text for explanation.

Table 1. Oxygen Consumption Values for Comparable Ages but Differing Weights in the Young of Two Species of Peromyscus

Species	Age In Days	Mean Weight	Mean Oxygen Consumption Per gm hr ⁻¹	N (individuals)
Maniculatus	8	4.7	2.3	4
Maniculatus	8	5.4	3.0	4
Maniculatus	8	6.1	3.2	3
Californicus	6	4.5	3.3	2
Californicus	6	5.0	3.7	2
Californicus	6	7.2	4.0	2
Californicus	6	7.6	4.1	3

Figure 1. Schematic drawing of metabolism apparatus (see text for explanation).

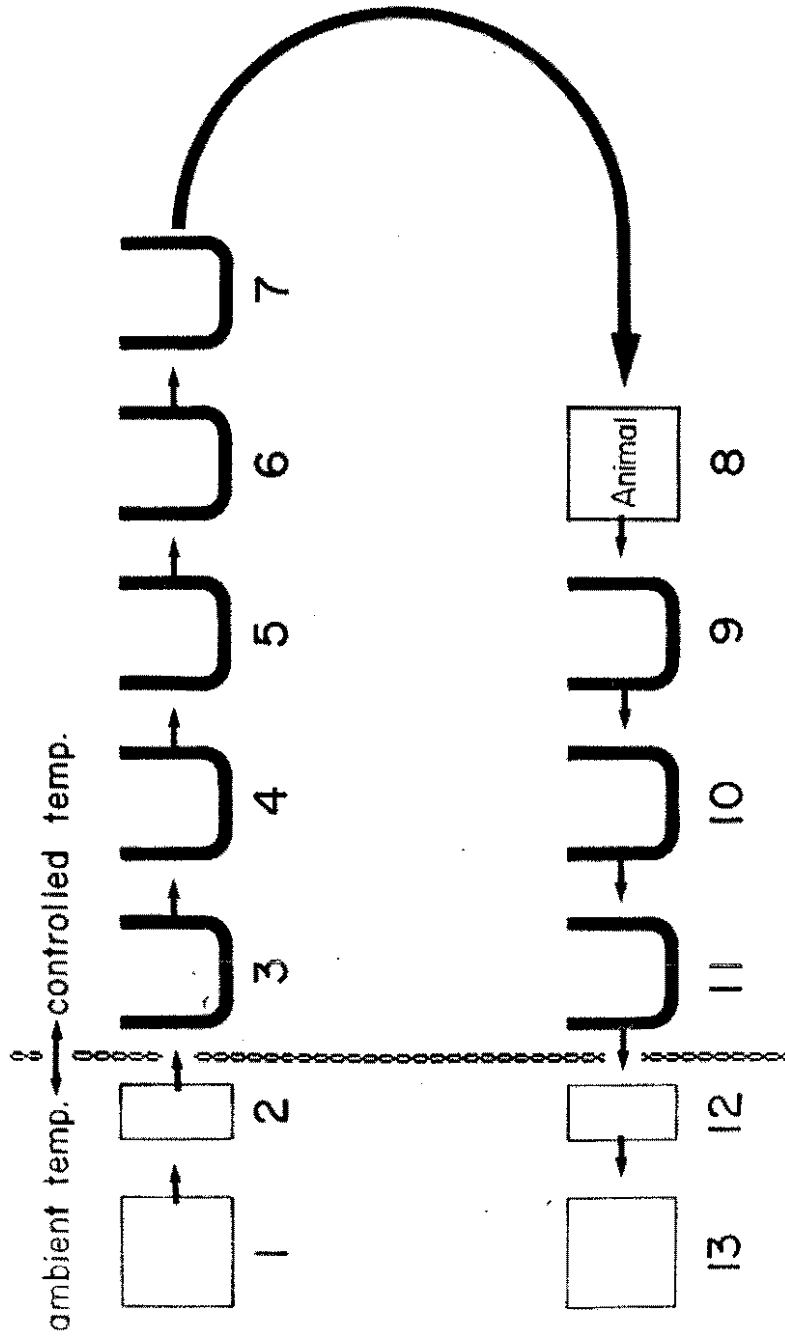


Figure 2. A record of calibration and of a metabolic study. "A" is ambient air baseline, "B" is the certified span gas displacement line and "C" the deflection of oxygen consumed by an animal in 30 minutes.

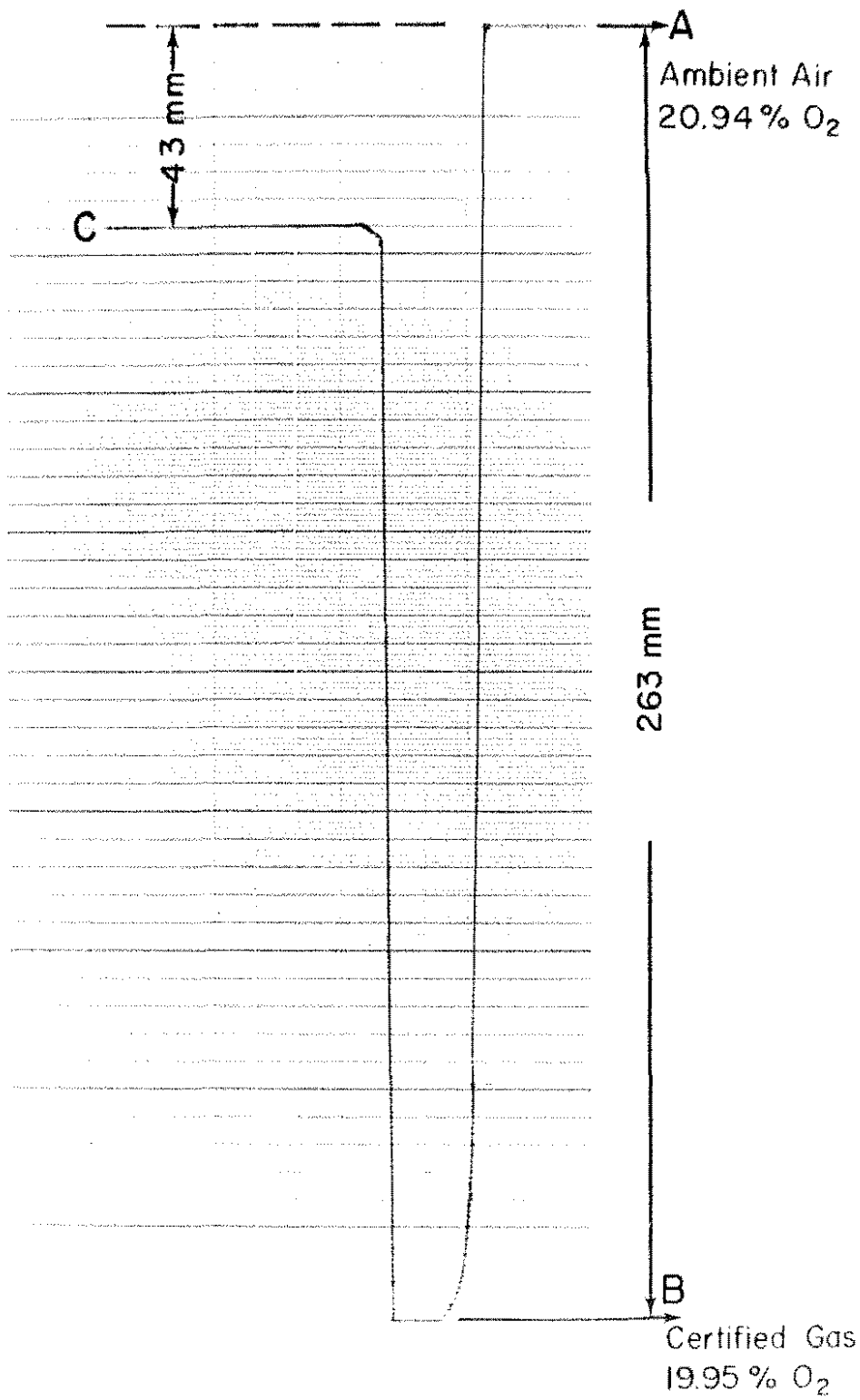


Figure 3. Thermal neutral zone as determined by oxygen consumption for A) P. maniculatus (n = 15), B) P. boylii (n = 12) and C) P. californicus (n = 15); solid dots are individual measurements; horizontal bars = mean; * = standard error of mean (SEM).

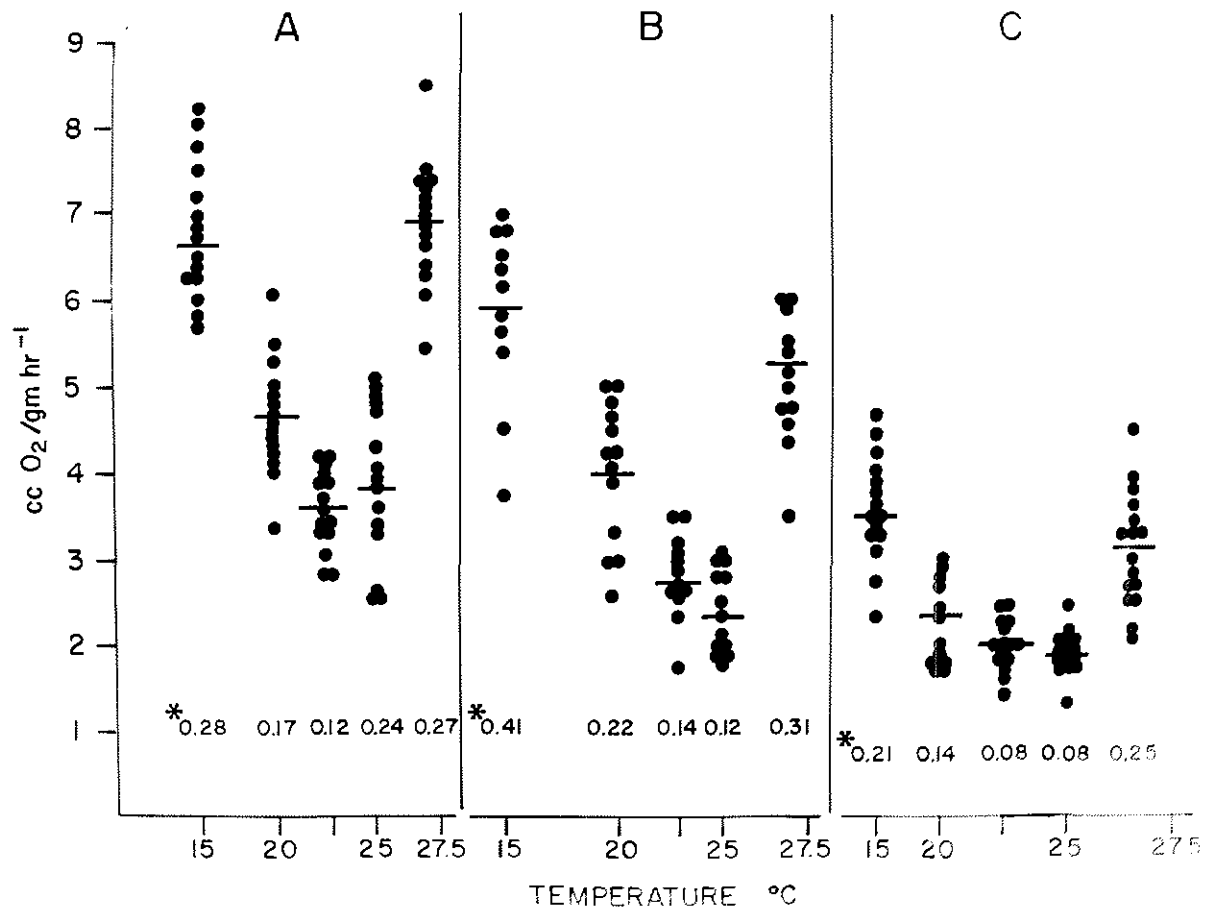


Figure 4. Mean metabolic activity at 25°C of litters of A) P. maniculatus (n = 4); B) P. boylii (n = 2) and C) P. californicus (n = 2). Open circles are the oxygen consumption record of one abnormally developing P. boylii.

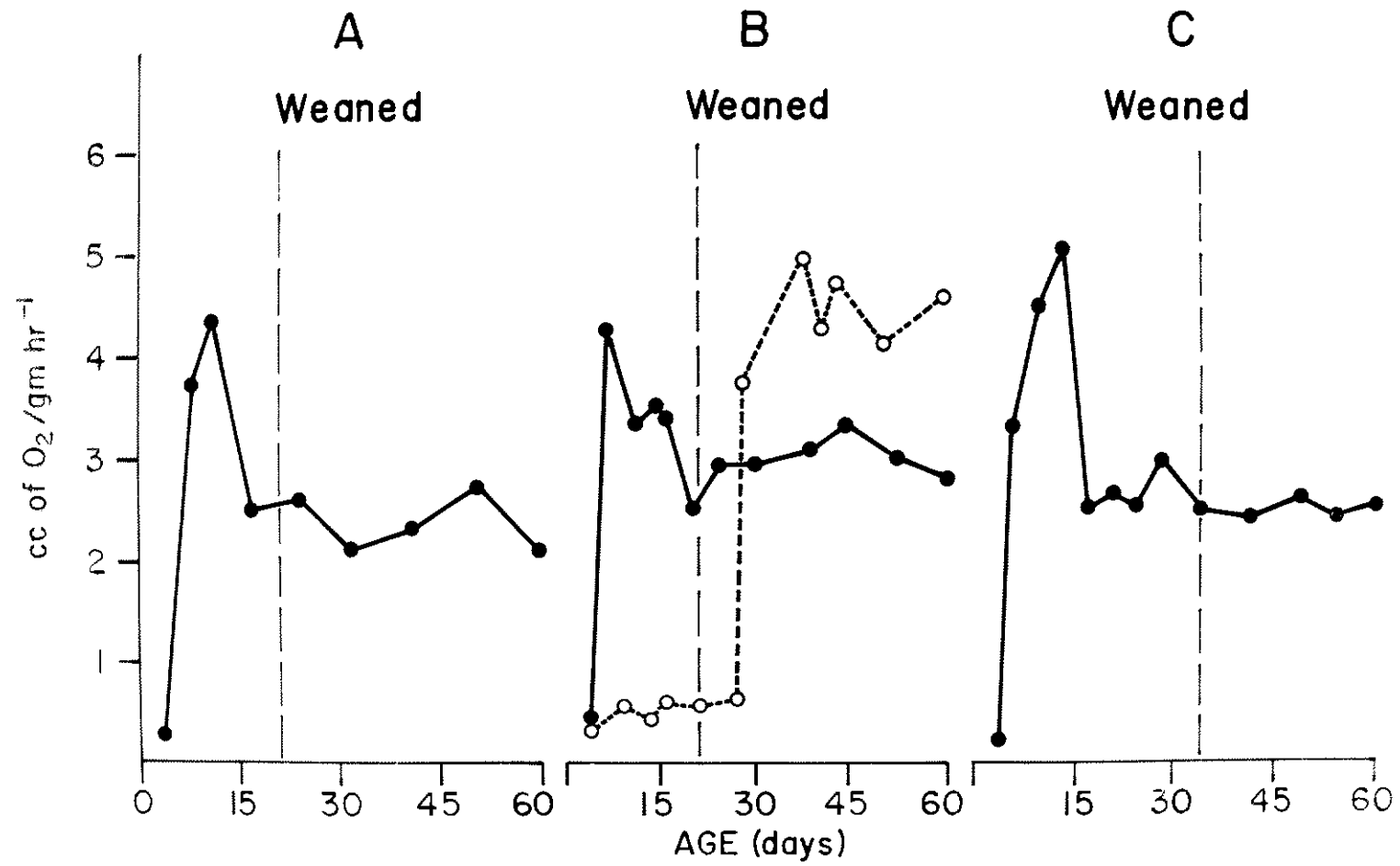


Figure 5. Growth in mean body weight of P. californicus (open circles, n = 15); P. boylii (dashed line, n = 10); P. maniculatus (long dashed line, n = 32); and one abnormally developing P. boylii (solid line).

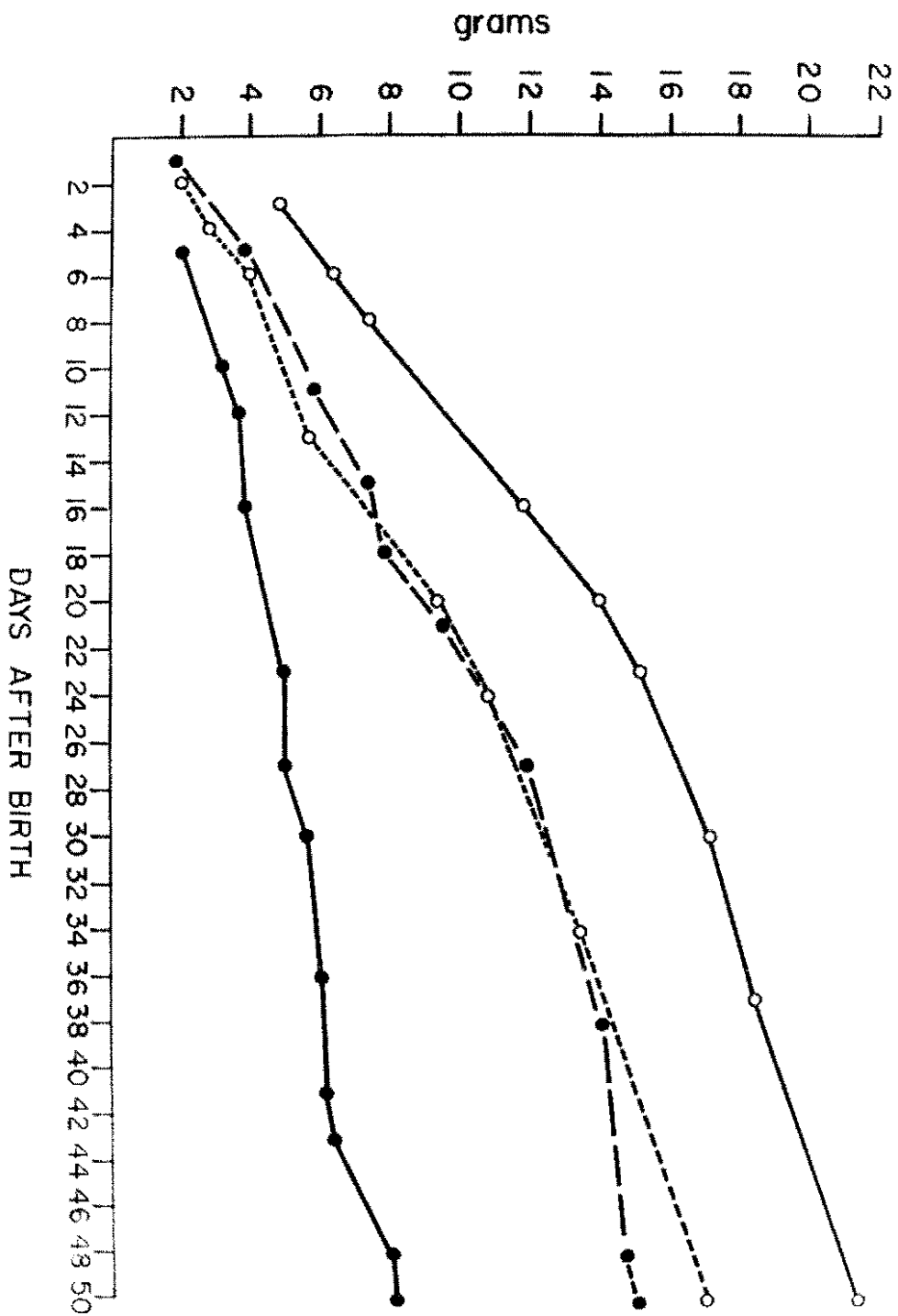


Figure 6. Linear regression correlation between oxygen consumption and early weight in A) P. maniculatus ($y = 1.4 x - 3.9$; $r = 0.81$; $P < 0.01$); B) P. boylii ($y = 0.9 x - 1.4$; $r = 0.74$; $P < 0.01$) and C) P. californicus ($y = 0.8 x - 1.8$; $r = 0.72$; $P < 0.01$).

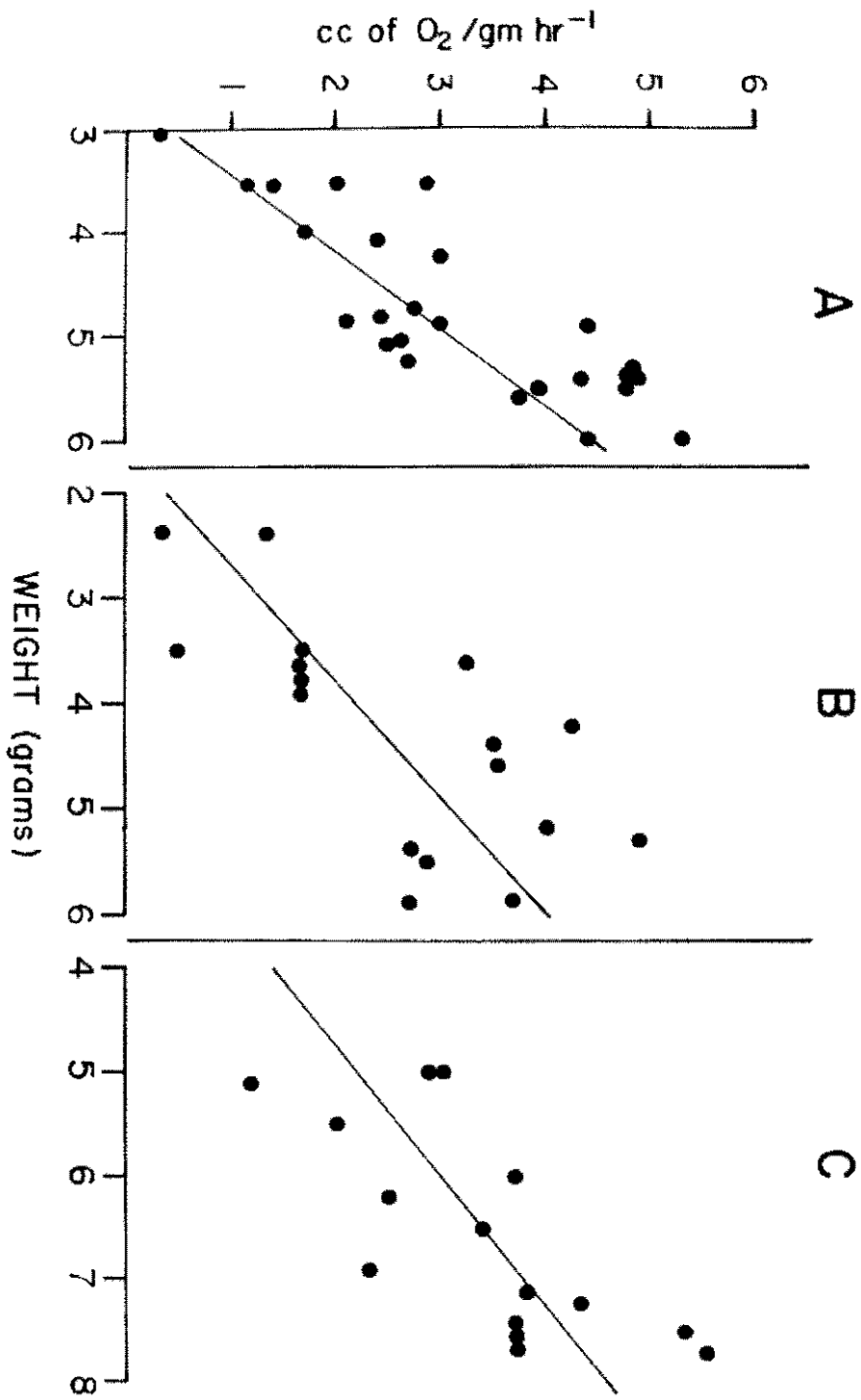


Figure 7. Number of individuals of young Peromyscus whose oxygen consumption for the first time falls within adult ranges. On the ordinate is the frequency of any metabolic study in which the metabolism of the animal was above 2.00 cc of oxygen per gm hr⁻¹ for A) P. maniculatus (n = 24); B) above 1.3 cc of oxygen per gm hr⁻¹ for P. boylii (n = 18) and C) above 1.25 cc of oxygen per gm hr⁻¹ for P. californicus (n = 20). See text for explanation.

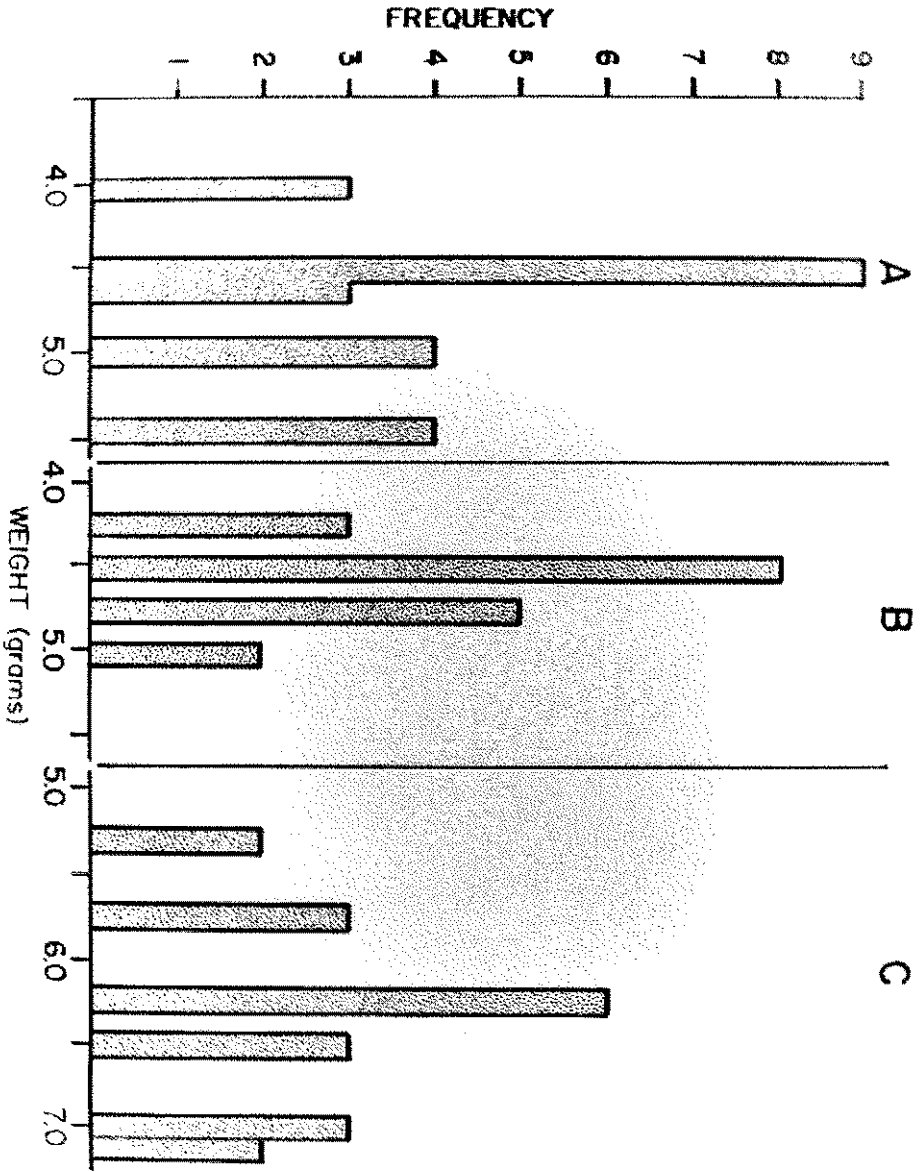
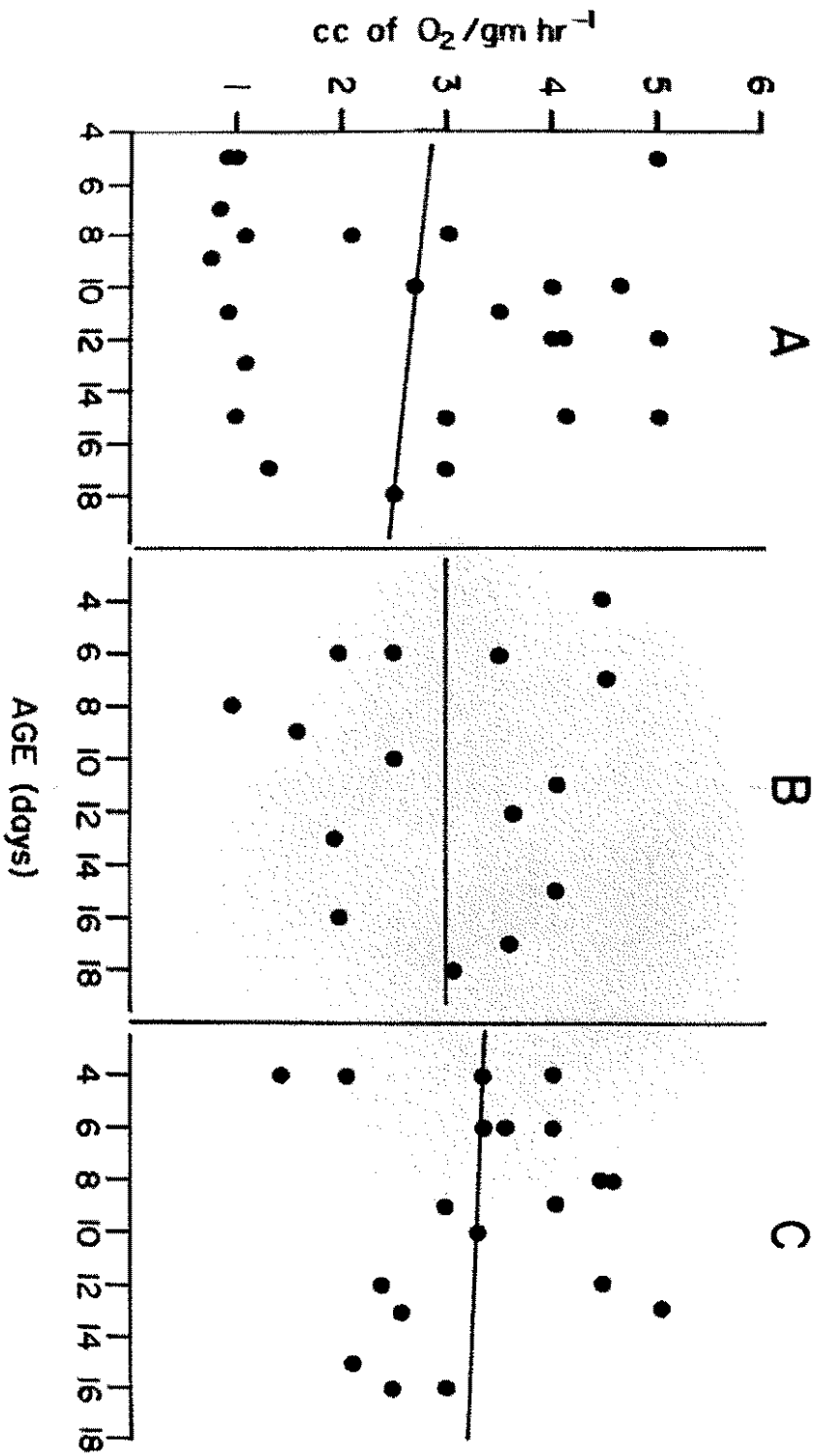


Figure 8. Linear regression correlation between oxygen consumption and age of A) P. maniculatus (n = 22); B) P. boylii (n = 15) and C) P. californicus (n = 17). See text for equations.



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