REPRODUCTIVE BIOLOGY OF
TYLOMYS AND OTOTYLOMYS

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ABSTRACT

REPRODUCTIVE BIOLOGY OF TYLOMYS AND OTOTYLOMYS

By

John Daniel Helm III

The major concern of this paper is to describe and compare the reproductive biology of two Neotropical climbing-rats, Tylomys and Ototylomys. The Tylomys were descended from animals caught from Rio Grande and Valle Nacional, Oaxaca, Mexico and from captives donated by R. Tesh from El Acquacate, Panama. The Ototylomys were offspring of animals live-trapped from Campeche, Mexico. All of the animals were maintained in the Michigan State University Live Animal Colony. Date collected from both genera included determination of the estrous cycle, gestation length, occurrence of postpartum estrus, and prenatal and post-natal development.

Vaginal smears were collected from Tylomys exposed to two lighting conditions. The average interval between cornified cell periods was 6.8 ± 0.4 days under natural lighting and 12.0 ± 2.5 days when exposed to 12 hours of light and 12 hours of darkness. Ototylomys kept in 14 hours of light and 10 hours of darkness had an average estrous cycle of 8.8 ± 0.5 days. A postpartum estrus was observed for all littering females of both genera, as evidenced by the presence of sperm in smears taken within 24 hours after the discovery of new litters.

The earliest recorded mating for female Tylomys was 90 days of age while the earliest recorded mating for female Ototylomys was 29 days of age. The earliest recorded mating for males was 144 days for Tylomys and 175 days for Ototylomys.

The gestation period for Tylomys was 40.6 ± 0.5 days and 52.8 ± 2.1 days for Ototylomys. No statistical difference was found between the mean gestation lengths of lactating and non-lactating females for either genus. Both the minimum and maximum extremes in gestation length were observed in lactating females of both Tylomys and Ototylomys. Embryos were first detected by palpation of Tylomys on day 7 of gestation and of Ototylomys on day 14 of gestation. The fetal head was initially distinguishable at 28 days in both genera.

The ratio of males to females at birth was 95.6:100 and 115:100 for Tylomys and Ototylomys, respectively. Tylomys had an average of 2.3 young per litter and Ototylomys had an average of 2.4 young. The range in litter size was 1-4 in both genera. Statistical analysis of the standard measurements at birth for the Mexican and Panamanian Tylomys populations did not reveal any differences at day one; therefore, the data were pooled. The standard measurements, in millimeters, for Tylomys were: total length, 134.1 ± 1.0; tail length, 50.0 ± 0.7; hind foot, 18.0 ± 0.2; ear, 8.5 ± 0.04. For Ototylomys they were: total length, 119.5 ± 0.9; tail length, 47.1 ± 0.8; hind foot, 16.4 ± 0.2; ear, 9.4 ± 0.2. Tylomys weighed 20.2 ± 0.3 grams and Ototylomys 10.2 ± 0.3 grams at birth. The least variance over time was observed in the length of head and body, without tail, and was therefore most valuable for comparisons of growth rates over time. At birth, Tylomys measured 84.3 ± 0.7 mm and Ototylomys measured 67.0 ± 3.2 mm. Head and body length of Tylomys from Mexico was 34.9 per cent of adult body length; those from Panama were 35.8 per cent and Ototylomys were 46.4 per cent of their adult body lengths. No statistical differences were found between males and females at birth for either genus.

For approximately 30 days after birth, the neonates of both genera adhere tenaciously to their mother's inguinal teats. Both Tylomys and Ototylomys young are precocial, with Ototylomys young being the more precocial. The greatest number of Tylomys were initially able to respond to loud noises between days 8 and 9 while the largest number of Ototylomys initially responded by day 2. Eye opening occurred for the greatest number between days 10 and 11 in Tylomys and day 6 for Ototylomys. Hearing preceded eye opening in all but four cases.

Tylomys from Mexico have attained 50 per cent of adult body length by day 14 and those from Panama between days 12 and 14. Ototylomys reach 50 per cent of their adult body length by day 2. Ninety per cent of adult body length is reached at 120 days in the Mexican Tylomys while the Panamanian group grew to 90 per cent of their adult body length by 116 days. Ototylomys grew to 90 per cent of their adult body length by 58 days of age.

REPRODUCTIVE BIOLOGY OF TYLOMYS AND OTOTYLOMYS

By

John Daniel Helm III

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INTRODUCTION

The purpose of this paper is to describe and compare the reproductive biology of two Neotropical climbing-rats, Tylomys and Ototylomys. Within the framework of these comparisons, considerations will be made of the possible ecological and evolutionary significance of this biology.

Mossman (1953) and Keys (1954; 1958) proposed that the physical mechanisms of implantation and subsequent development of placental membranes have possibly more evolutionary significance than do the morphological criteria now being used, since adaptation to external environment contributes little to the development of placentation. Within the genus Peromyscus, Layne (1966) found that body size and environment were the most influential factors governing gestation length and postnatal development. To further illucidate evolutionary and reproductive relationships found in rodents, two closely related animals found in similar environments, Tylomys and Ototylomys, were examined and the results are described herein.

Tylomys and Ototylomys belong to an assemblage of Neotropical cricetine rodents of obscure ancestry. The genera, Tylomys and Ototylomys were considered to be related to Neotoma by Hooper and Musser (1964) and have been placed in the same subfamily as Neotoma. A later study by Lawlor (1969) shows that Tylomys and Ototylomys are probably more closely related to each other than to Neotoma or Nelsonia, the other two members of the subfamily Neotominae. The latest compilations (Cabrera, 1961: 435;

Hall and Kelson, 1959: 573-6) list eight species in the genus Tylomys. However, some of these species may ultimately be reduced to subspecific status (see Goodwin, 1969; Handley, 1966; and Schaldach, 1966). On the other hand, Ototylomys is monotypic, with all populations assigned to O. phyllotis (Lawlor, 1969). Only generic names will be referred to in this paper.

Tylomys and Ototylomys are generally considered to be scansorial, but their autecologies are poorly known. Figure 1 shows the distribution of both Tylomys and Ototylomys. They are found in both moist and arid forested areas, along rocky ledges, and from sea level to 1820 meters above sea level (Anthony, 1916; Baker and Petersen, 1965; Burt and Stirton, 1961; Disney, 1968; Goodwin, 1931, 1942, 1946, 1955, 1969; Hall and Dalquest, 1963; Hall and Kelson, 1959; Handley, 1966; Lawlor, 1969; Peters, 1866; Schaldach, 1966; Tesh, 1970; Ramírez-Pulido and Sánchez-Hernandez, 1971). Animals of both genera are thought to be nocturnal, although activity-wheel performances show Tylomys to also have diurnal activity. The animals of both genera used in the present study are from seasonally dry localities. Tylomys have been reared in captivity by Tesh (1970) in Panama. Baker and Petersen (1965) reported on some laboratory behavior of Tylomys, and postnatal development of five male and three female Ototylomys were described by Disney (1968).

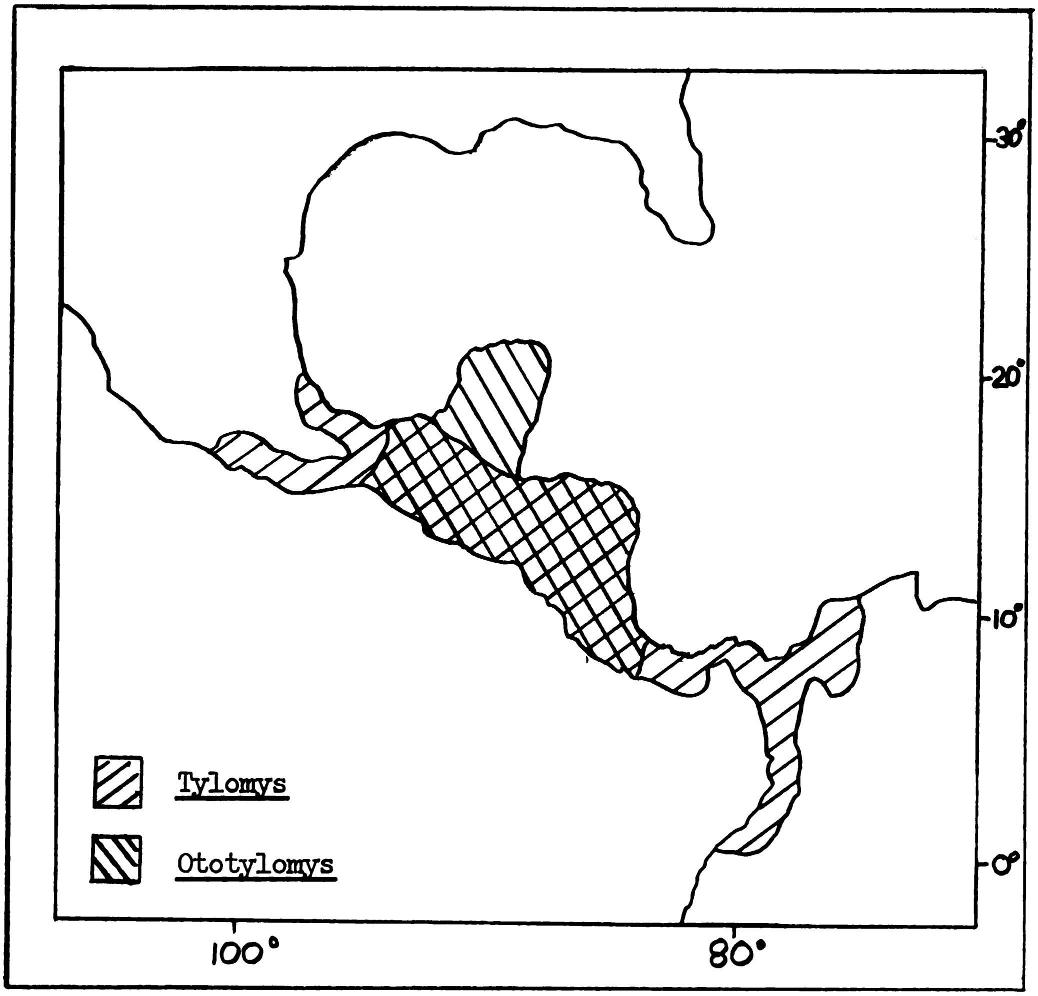

Figure 1. Distribution of Tylomys and Ototylomys

MATERIALS AND METHODS

The *Tylomys* used in this study were descended from Mexican animals caught 8 kilometers east of Rio Grande at an altitude of 30 meters, Oaxaca; 16 kilometers south of Valle Nacional, at an altitude of 1280 meters, Oaxaca; and from captives donated by R. Tesh from El Acquacate, Panama. The *Ototylomys* were all offspring of animals live-trapped by James A. Lackey and Thomas Nelson, 7½ kilometers west of Escarcega, Campeche, Mexico. The animals were maintained in the Michigan State University Museum Live Animal Colony in cages measuring 91.5 cm x 45.5 cm x 45.5 cm. Sawdust was used as bedding, and each pair of animals was furnished with a nest-box. Their diet consisted chiefly of Zimmerman Laboratory Rat Chow which was supplemented periodically with fruits. Room temperature was 21 degrees Centigrade. From September 1970 until March 1971, the colony was subjected to natural lighting. From March 1971 until December 1972, the controlled lighting was 12 hours of light and 12 hours of dark. Each animal was toe-clipped at birth for easy identification.

Data for postnatal development were obtained from 95 individual *Tylomys* (including more than 45 litters) and 86 individual *Ototylomys* (including 36 litters). Total length, tail length, hind foot length, ear length, and body weight were measured weekly for all animals from the day of birth (day 1) to three months of age and then monthly until six months of age. Timing of incisor erruption, of first hearing response (flinching to finger snapping), and separation of eyelids were also recorded for these animals. Mean measurements of *Tylomys* from Mexico and Panama were compared by one-way analysis of variance to evaluate the significance of differences.

Vaginal smears were obtained from 33 _Tylomys_ and 14 _Ototylomys_ in an effort to measure the lengths of the estrous cycle and gestation and as an aid in the determination of the onset of implantation. Smears were scored by the methods of Long and Evans (1922) and Papanicalou, as modified by Wachtel (1969) and Zarrow (1964). Vaginal smears were taken during four different time periods. The first were collected from 29 October 1970 to 15 April 1971, when samples were obtained daily from 22 female _Tylomys_ between 0900 and 1100 and stained with Geimsa Solution (Zarrow, 1964).

The second collection period was between 16 July 1971 and 1 October 1971 and involved 11 _Tylomys_. Six males and five females were put into Unifab Rat Activity Cages, Series 450, in an isolated room. The cage dimensions were 24 cm x 19 cm x 19 cm, with a freely rotating wheel 36 cm in diameter and 13 cm deep. The lighting schedule was 14:10, light:dark. The animals were disturbed only between 0800 and 0900 and 1700 and 1800 daily when food and water were checked. Smears of the six females were taken each morning from 6 September 1971 to 1 October 1971. The samples were stained with toluidine blue and scored as to cell types, i.e. -- nucleated epithelial cells, cornified epithelial cells, combination of cells, or predominately leucocytes (Long and Evans, 1922). Comparisons of estrous phenomena and cycles of running activity were made.

The third collecting period involved only _Ototylomys_. Between 17 October 1971 and 9 February 1972, six male and six female _Ototylomys_ were placed in activity cages and subjected to the same procedures as the _Tylomys_ in the previous period. Vaginal smears were taken only between 27 December 1971 and 9 February 1972.

The fourth collecting period extended from 21 October 1972 until 21 December 1972. Vaginal smears were taken from eight non-pregnant and one lactating _Tylomys_ and from eight non-pregnant _Ototylomys_, between 1400 and 1600. All animals were kept in the same room in the Museum Live Animal Colony with a lighting schedule of 14:10, light:dark. The smears were stained by the Papanicalou method (Wachtel, _op. cit._). Each smear was observed under the microscope at 150X. A representative section of the slide was selected and the total number of cells seen in the field of vision was counted. The calculated percentages of red, orange, blue, and green cells were plotted against time to see if any cyclical patterns existed.

Females with sperm in their vaginal smears were considered bred. The date of sperm discovery was designated as day 1 of gestation. Animals were palpated weekly until parturition, and the neonates were measured at this time. Thirty _Tylomys_ litters (including 51 individual offspring) and 15 _Ototylomys_ litters (including 35 individual offspring) were sampled by this method.

Five _Tylomys_ females were examined to determine the time of implantation, three by laparoscopy (Dukelow _et al._, 1971), two by laparotomy. Three _Ototylomys_ were examined by laparotomy.

RESULTS

Tylomys

Estrous Cycle

The vaginal cytology of *Tylomys* does not show predictable cyclicity. Leucocytes are present at all times. The average interval between cornified cell stages was found to be 6.8 $\pm$ 0.4 days when the animals were exposed to natural lighting. Exposure to a lighting schedule of 12:12, light:dark, resulted in an average interval of 12.0 $\pm$ 2.5 days between cornified cell periods. An increase in the duration of smears with predominately leucocytes was attributed to the increase in overall cycle length (Table 1).

On the day immediately preceding the finding of cornified cells in vaginal smears, only leucocytes and nucleated epithelial cells could be found in varying ratios. Sperm was found in smears which consisted predominately of nucleated epithelial cells and leucocytes. No specific vaginal smear could predict when a female would accept a male for mating.

The handling of the animals when vaginal smears were obtained did not seem to disrupt their use of the exercise wheel. The length of time between maximum periods of wheel activity varied in a fashion similar to that found in the smears (Table 2). The model intervals were two and three days for all *Tylomys* females sampled. No predictions about running activity could be made from vaginal cytology.

Tylomys females have a postpartum estrus, and mating occurs within 24 hours, as indicated by the presence of sperm in smears taken at this time.

Table 1. Vaginal cytology (days: $\overline{X} \pm S_x$) of 15 _Tylomys_ and 14 _Ototylomys_.

Cell type	_Tylomys_ 29 October 1970 to 1 March 1971	_Tylomys_ 2 March 1971 to 15 April 1971	_Ototylomys_ 21 October 1972 to 21 December 1972
Cornified	1.4 ± 0.2	1.3 ± 0.1	2.3 ± 0.2
Combination	1.6 ± 0.1	1.3 ± 0.2	1.3 ± 0.1
Leucocytes	2.4 ± 0.3	5.6 ± 2.8	2.8 ± 0.7
Nucleated epithelial	1.8 ± 0.1	1.9 ± 0.3	2.6 ± 0.4
Total elapsed time between the onset of cornified periods	6.8 ± 0.4	12.0 ± 2.5	8.8 ± 0.5

Table 2. Revolutions per day ($\overline{X} \pm S$) for 5 *Tylomys* and 6 *Ototylomys*.

	Undisturbed			During vaginal smearing		
Animal number	Days between activity peaks	Peaks	Lows	Days between activity peaks	Peaks	Lows
			TYLOMYS			
1088	4.8 ± 1.0	6507 ± 734	3406 ± 513	6.4 ± 1.0	4703 ± 341	2214 ± 578
1034	3.6 ± 0.6	4740 ± 611	2750 ± 245	3.7 ± 0.5	4178 ± 177	2573 ± 158
1027	4.2 ± 0.4	1926 ± 131	1360 ± 87	3.5 ± 0.3	1918 ± 148	1190 ± 94
1065	4.2 ± 0.8	1160 ± 73	550 ± 41	5.4 ± 0.5	1711 ± 156	665 ± 113
1087	3.8 ± 0.4	5283 ± 645	2783 ± 469	3.9 ± 0.5	6648 ± 579	2481 ± 571
Total	4.3 ± 0.3			4.6 ± 0.4		
			OTOTYLOMYS			
100	4.3 ± 0.8	3803 ± 394	1665 ± 399	2.0	2475 ± 426	1092 ± 132
900	4.2 ± 0.6	2744 ± 224	1133 ± 196	3.3 ± 0.9	1270 ± 248	543 ± 159
198	4.9 ± 0.6	2925 ± 346	762 ± 110	4.7 ± 0.7	1121 ± 353	134 ± 61
600	3.3 ± 0.3	5128 ± 399	2626 ± 223	3.6 ± 0.3	781 ± 222	282 ± 108
303	3.8 ± 0.8	4095 ± 523	586 ± 138	4.1 ± 1.0	796 ± 88	183 ± 48
721	3.8 ± 0.6	3979 ± 278	1363 ± 210	4.6 ± 1.0	950 ± 235	307 ± 61
Total	3.9 ± 0.4			4.1 ± 0.4		

Sexual Maturity

The earliest recorded mating for females occured at 90 days of age and for males 144 days. This compares favorably to the age of earliest sexual maturation observed by Tesh (1970). Small (5 x 3 mm) copulatory plugs were discovered discharged into the litter in only four instances. Sperm was found in all of the vaginae, and two of the four females carried their litters to term.

Gestation

The overall gestation period for *Tylomys* is 40.6 ± 0.5 days with a range of 35-51 days (including 47 litters). For non-lactating females the gestation period is 39.2 ± 0.5 days with a range from 37-43 days (including 18 litters). For lactating females the gestation period is 40.6 ± 0.7 days with a range from 35-51 days (including 29 litters). There is no statistical difference between the means implying no delayed implantation due to lactation. Tesh (1970) found a minimum gestation length of 39 days for one lactating female.

Prenatal Development

The earliest noticeable indication of implantation observed by laparotomy or laparoscopy in *Tylomys* was four days after sperm were first found in the vagina. Day 7 of gestation was the earliest time that embryos could be detected by palpation. The fetal head was first palpatable at 28 days. Fetal growth, as determined by palpation, was approximately 10 mm per week (in crown-rump length) until birth at about 40 days. At that time, the crown-rump length was 50-60 mm. Table 3 summarizes the embryo size distribution through time.

Table 3. Prenatal development of 51 _Tylomys_ and 35 _Ototylomys_ individuals as determined by palpation (mm). *

Day of gestation	Crown-rump length	
	Tylomys	_Ototylomys_
1		
7	5 - 9	
14	11 - 19	5
21	21 - 24	6 - 9
28	26 - 29	11 - 14
35	31 - 39	16 - 19
42	41 - 45 **	21 - 24
49		36 - 40 **
Parturition	50 - 60	41 - 45

* Measurements represent a range of accuracy which could be detected by palpation

** Measurements taken one or two days prior to parturition

Birth

The ratio of male to female neonates in my colony was 95.6:100 and for 68 neonates in Tesh's colony, 46:100. The average litter size was 2.3 young with a range of 1-4 in my colony and 2.67 in Tesh's colony. Statistical comparisons of the measurements taken on the Tylomys populations from Panama and Mexico revealed no difference at day 1; therefore data were pooled.

Weight at birth was 20.2 ± 0.3 gm. Birth weight for animals examined by Tesh (1970) ranged from 15-25 gm, with an average of 19.9 gm. Measurements at birth were: total length, 134.1 ± 1.0; total length of tail vertebrae, 50.0 ± 0.7; length of hind foot, 18.0 ± 0.2; height of ear from notch, 8.5 ± 0.04. The length of head and body without tail measured 84.3 ± 0.7 mm. At birth the length of head and body without tail was 34.9 per cent of the mature body length in Tylomys from Mexico and 35.8 per cent for Tylomys from Panama. There were no significant differences in body weight or linear body dimensions between males and females at birth.

The skin of Tylomys at birth is gray-black on the dorsum and pink on the venter. The dorsum is finely furred at birth. The guard hairs measure about 2 mm in length, while the underfur is less than 1 mm. The length of verbrissae at birth ranges from 18-22 mm. The internal organs are not visible through the skin. The ears are erect at birth. The toes are not fused, and the tubercles on the feet of some animals are pigmented. Incisors have errupted at birth and are separated by almost 1 mm.

The neonates adhere tenaciously to their mother's teats and remain in the fetal position. Young which are separated at birth from the mother are capable of self-locomotion.

Hearing and Eye Opening

The newborn do not respond to loud noises and have closed eyelids. First ability to respond to finger snapping varied from day 6 to day 13 with the greatest number of *Tylomys* being able to hear first on day 8 or 9. Eye opening occurred between days 8 and 14 with the greatest number occurring on days 10 and 11. The hearing response preceded eye opening in all instances. Figure 2 is a histogram representation of the timing of eye opening and hearing.

Growth

Changes in body weight and linear measurements are shown in Figures 3 and 4. The measurements from day 84 to day 180 for the two populations are represented separately, since statistical differences between the samples from Mexico and from Panama are found for body length and weight at 180 days. *Tylomys* from Mexico attain 50 per cent of adult body length by day 14. The Panamanian population attains 50 per cent of adult body length between days 12 and 14. Ninety per cent of adult length is reached at 120 days in the Mexican *Tylomys* while the Panamanian *Tylomys* reach 90 per cent adult body length about seven days earlier.

Pelage

Hair coloration changes from gray and white to a mottled gray-brown-white between 10 and 17 days. The guard hairs are white along the sides and black on the dorsum. The underfur is gray with black, brown, and white tips. By 46 days, coloration of the dorsum has become a uniform gray-brown. The sides are paler brown than the dorsum; the guard hairs tend to be pale in color while the underfur is gray with brown tips. By 3 months, the change to adult pelage is complete with no specific molting sequence noted.

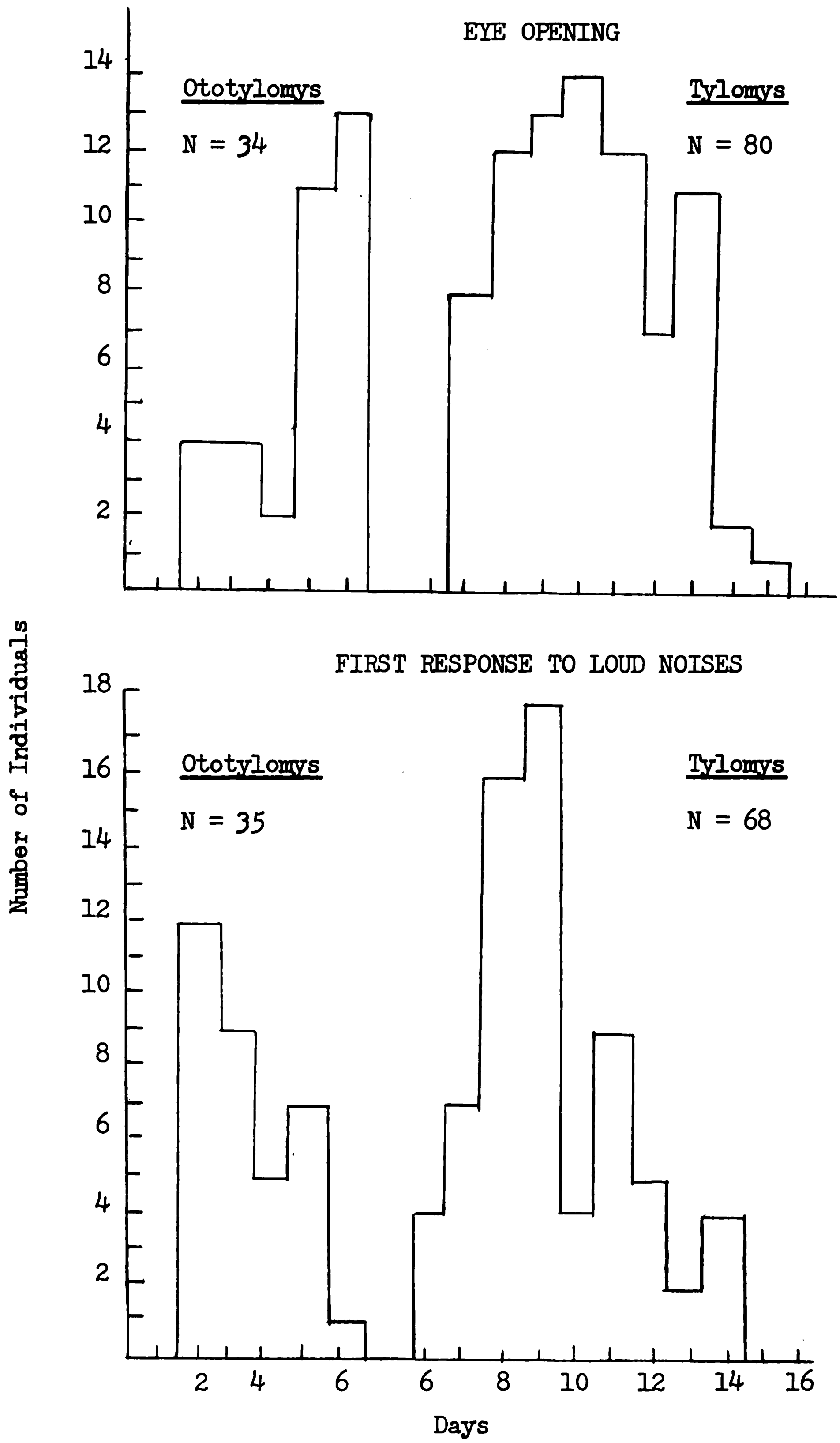

Figure 2. Eye opening and first response to loud noises.

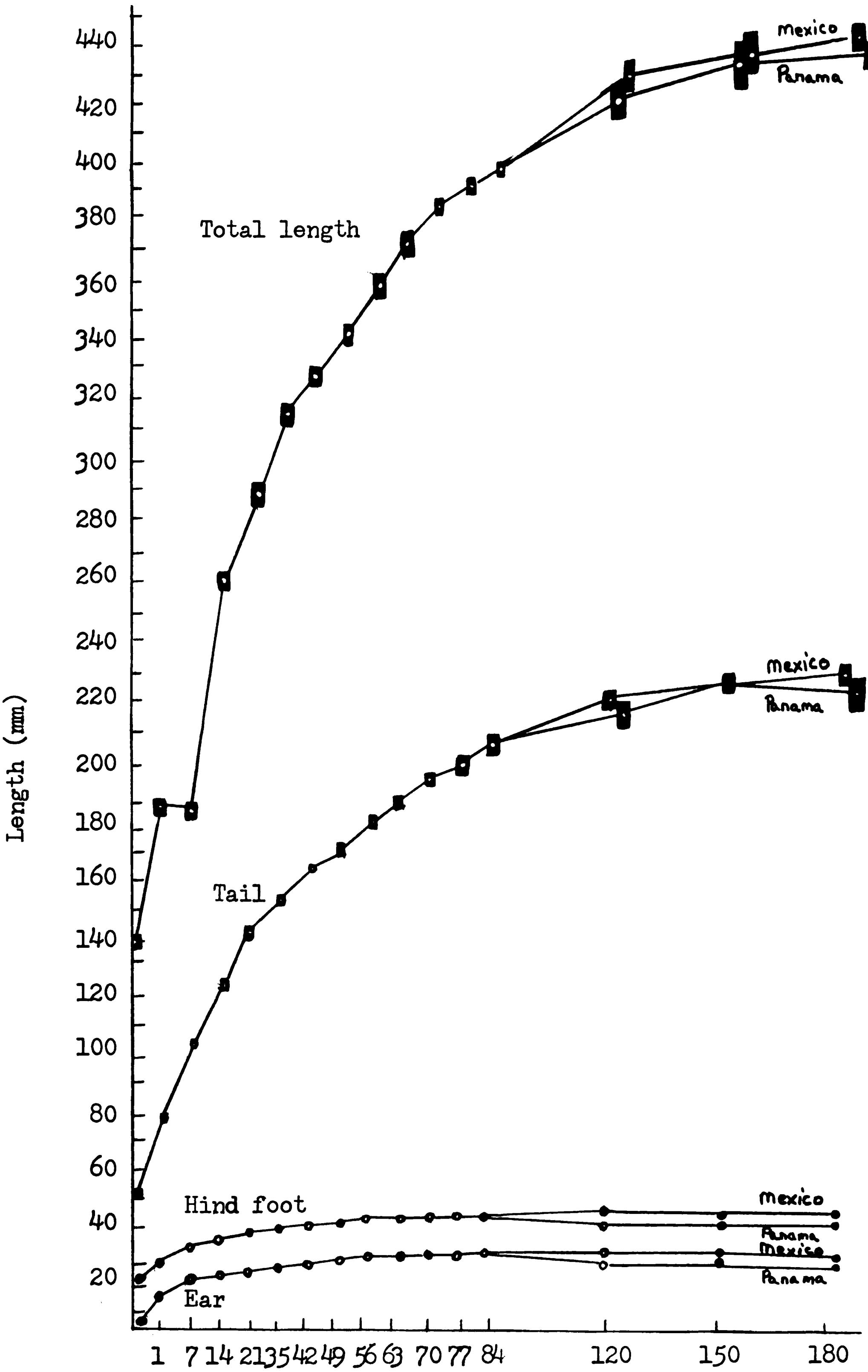

Figure 3. Growth of *Tylomys* from Mexico and Panama ($\overline{X} \pm S_x$).

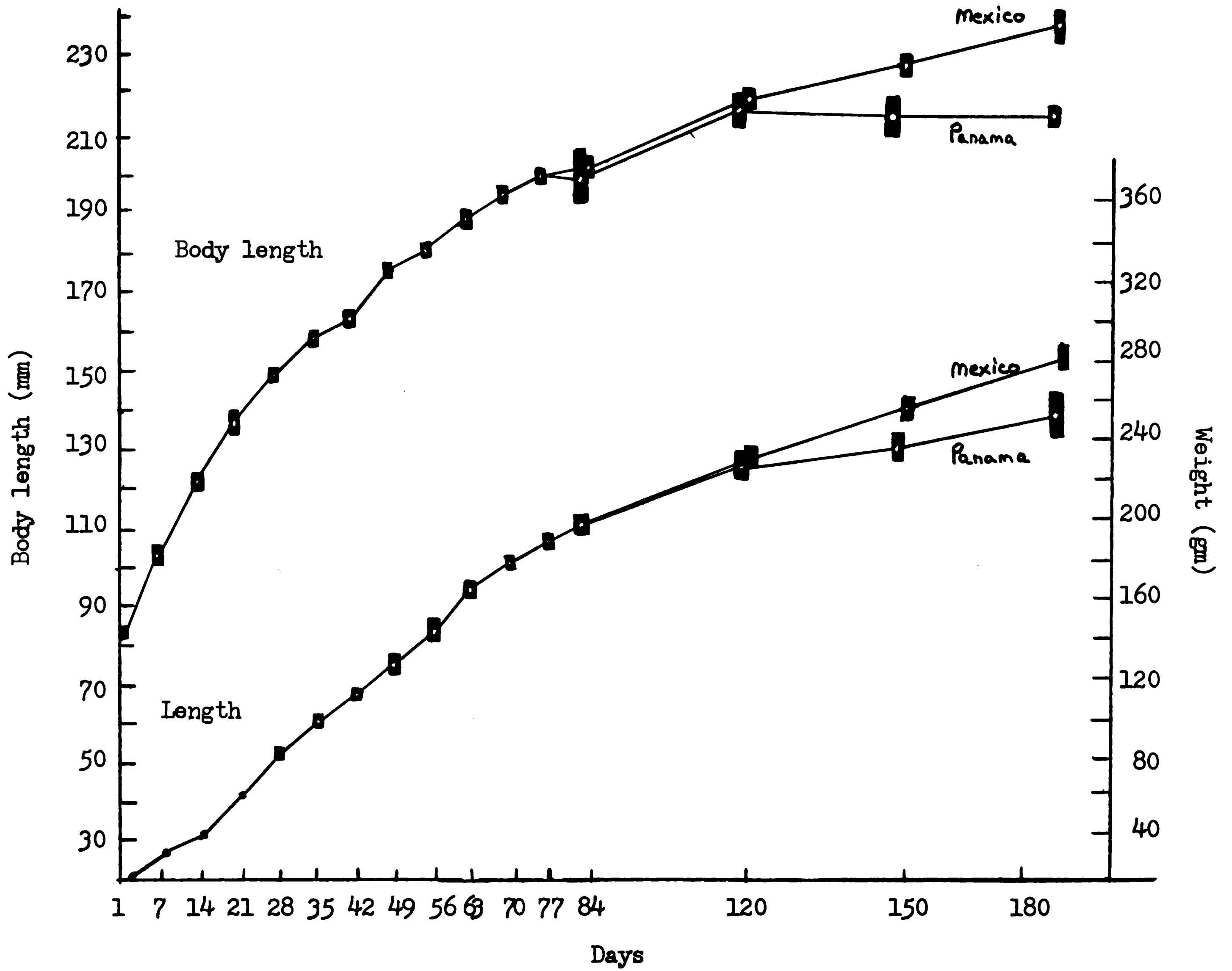

Figure 4. Body length (head and body minus tail) and weight of <u>Tylomys</u> ($\overline{X} \pm S_x$).

Ototylomys

Estrous Cycle

The vaginal cytology of *Ototylomys* does not show predictable cyclicity. The average interval between cornified cell stages was found to be 8.8 ± 0.5 days (Table 1). On the day immediately preceding the finding of cornified cells in vaginal smears, leucocytes and nucleated epithelial cells in varying ratios and mucosal secretions could be found.

For all animals, activity decreased markedly when the vaginal smears were taken (Table 2). The average interval between activity peaks in the six females studied was 3.9 ± 0.4 days when the animals were permitted to run undisturbed and 4.1 ± 0.4 days during the period when vaginal smears were being collected. No predictable sequential activity pattern was found for any of the animals, nor was vaginal cytology predictive of running activity.

The only consistent vaginal phenomenon was that smears with sperm present stained red using the Papanicalou staining method. Other cells present with the sperm varied from 100 per cent leucocytes to a mixture of nucleated epithelial cells, cornified epithelial cells, and leucocytes.

Ototylomys females have a postpartum estrus. Mating had taken place within 24 hours after delivery, as indicated by the presence of sperm in these smears.

Sexual Maturity

Vaginal opening occurred from day 21 until 70 days. The earliest recorded mating for a female occurred at 29 days of age. This resulted in a pregnancy which terminated 52 days later. Testicular descent occurred between 15 and 38 days. The earliest recorded mating for a male was at 175 days. Disney (1968) indicated both sexes reached sexual maturity within 30 days. In two instances, a small (less than 5 mm x 2 mm) vaginal plug was discovered while taking vaginal smears. Additional efforts were unsuccessful in discovering copulatory plugs.

Gestation

The overall gestation period for Ototylomys is 52.8 ± 2.1 days. For non-lactating females, the range is 50-52 days (including 6 litters) and for lactating females this range is more variable and is 49-69 days (including 9 litters). There is no statistical difference between the average of 51 ± 0.6 days for non-lactating and 53.6 ± 7.6 days for lactating females. Disney (op. cit.) reported a gestation length of 52 days for a captive-born female. He also suggested that delayed implantation might occur since another female was isolated in the laboratory for 174 days after which she had a litter of two.

Prenatal Development

The earliest noticeable enlargements of the uterus observed by laparotomy were at day 8 of gestation. Day 14 was the first day when embryos could be palpated. At this time the embryos were about 5 mm long. Weekly development thereafter was 5-10 mm until parturition at 52 days. The head was first distinguishable by palpation between 21 and 28 days of gestation. Table 3 gives the size distribution of both Ototylomys and Tylomys.

Birth

The ratio of males to females at birth was 115:100. The average litter size was 2.4 with a range of 1-4. Disney (op. cit.) reported average litter sizes to be 2.3 and 2.2 for two groups of wild-trapped <u>Ototylomys</u>. No sex ratio was reported. Disney also noted that larger females tended to have larger litters; however, this was not confirmed by data from my colony.

At birth, <u>Ototylomys</u> weigh 10.2 ± 0.3 gm. Their standard measurements are: total length, 119.5 ± 0.9; total length of tail vertebrae, 47.1 ± 0.8; hind foot length, 16.4 ± 0.2; height of ear from notch, 9.4 ± 0.2. The length of the head and body (without the tail) is 67.0 ± 3.2. The least variance over time seems to be observed in length of head and body. This parameter is especially valuable when the animals get older since there is a tendency for tails of laboratory raised <u>Ototylomys</u> to become necrotic and fall off. At birth, the body is 46.4 per cent of the adult length. Males tend to be 1 or 2 mm shorter than the females although differences between means are not significant. Males and females weigh the same at birth. The length of verbrissae is about 20 mm and both pairs of incisors are present at birth. The tubercles of the forefeet do not tend to be pigmented, while those on the hind feet do tend to be pigmented. Both feet have unfused toes.

<u>Ototylomys</u> young are quite precocial at birth. They adhere strongly to one of the mother's four inguinal teats and assume a fetal position. When separated from the mother, the young can walk quite well and are able to hang suspended from objects.

<u>Hearing and Eye Opening</u>

The newborn <u>Ototylomys</u> do not respond to loud noises and have closed eyelids. The largest number of young <u>Ototylomys</u> respond to finger snapping (hear) by day 2. One animal could not hear until day 6. The largest number opened their eyes on day 6. The earliest eye openings were on day 2. With the exception of four animals, ability to hear preceded eye opening by at least one day. Both phenomena were observed on the same day in these animals. Figure 2 is a histogram representation of the timing of hearing and eye opening.

Growth

Figures 5 and 6 show growth rate measurements including total tail, body, hind foot, ear length, and body weight. Ototylomys reach 50 per cent of their adult body length between days 1 and 2. They have reached over 90 per cent of adult length by 58 days of age.

Pelage

The skin of newborn Ototylomys is gray-black on the dorsum and pink on the venter, and both the dorsum and venter are sparsely haired. The internal organs are not visible through the skin. Hair on the dorsum range from 2-4 mm in length and are black with white tips, giving an overall gray appearance to the hair. The hair on the venter is white and less than 1 mm long. The tail is also bicolored and is covered with fine hairs. The ears are erect at birth and a large white spot is found under each ear. These spots remain throughout adulthood.

At about 21 days, the gray hair of the sides begin to be replaced by brown hair. By 43 days adult coloration has been attained. No definite molting pattern was observed.

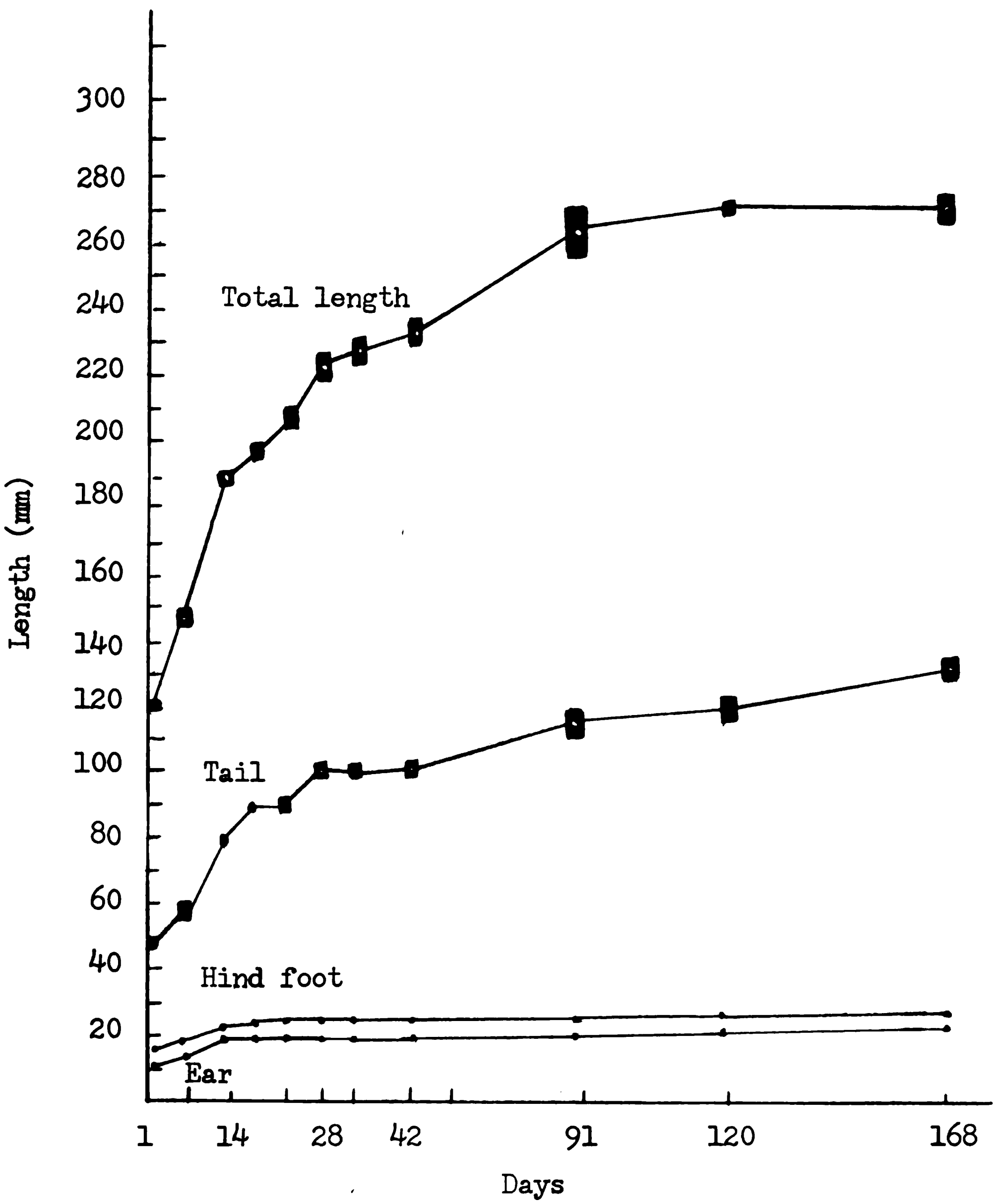

Figure 5. Growth of <u>Ototylomys</u> ($\bar{X} \pm S_x$).

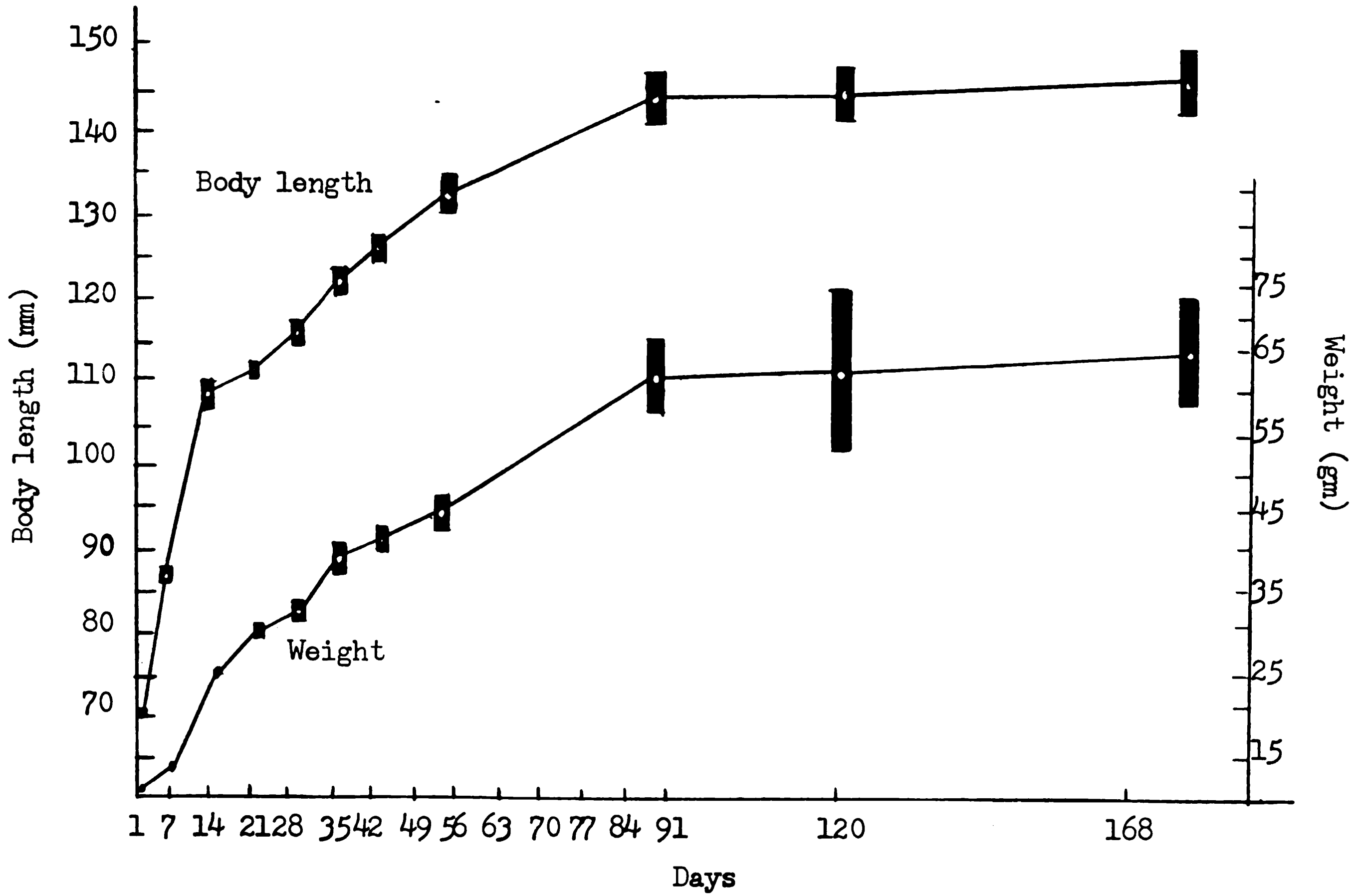

Figure 6. Body length (head and body minus tail) of Ototylomys ($\overline{X} \pm S_x$).

DISCUSSION

Tylomys and Ototylomys are members of a group of Central American cricetine rodents, Neotominae (based on phallic material: Hershkovitz, 1962; Hooper and Musser, 1964; Lawlor, 1969). The evolutionary trends for all of the Peromyscus-like rodents, including Neotominae and Peromyscinae, have been diagramed by Hooper and Musser (op. cit.: 55). Within the neotomines (including Xenomys, Neotoma, Nelsonia, Tylomys, and Ototylomys), Tylomys and Ototylomys are the most primitive. The neotomines are more primitive than the peromyscines (including Scotinomys, Baiomys, Onychomys, Ochrotomys, Neotomodon, Peromyscus, and Reithrodontomys).

My data indicate that neither Tylomys nor Ototylomys have a regular or predictable estrous cycle. Tylomys did not seem to be disturbed by being handled in the laboratory (as evidenced by the activity wheel experiment). On the other hand, manipulations of Ototylomys in the laboratory proved to be a traumatic experience (as evidenced by the activity wheel experiments). Another member of Cricetidae (but not a peromyscine or neotomine), Sigmodon hispidus was shown by Meyers and Meyers (1944) to have an increased estrous cycle length when exposed to a disturbed environment.

The only member of the neotomines whose cycle has been definitely determined is Neotoma floridana (Chapman, 1951). The most common cycle was from 4 to 6 days in length. Chapman found that increased frequency of handling the animals did not alter the length of their cycles. He also did not find any difference between the cycle of females kept in the laboratory and the cycles of females kept in outdoor enclosures. Peromyscus maniculatus, the only peromyscine whose cycle has been

determined, was found by Clark (1936) to have an estrous cycle of 4.8 days in the laboratory.

The significance which can be attached to the findings of my study and to the findings of other studies on estrous cycles of myormorph rodents is difficult to assess since so little information is available from which conclusions can be made.

The gestation lengths of Tylomys and Ototylomys are significantly different from each other and from those known for other genera of Peromyscus-like rodents (tested by the Mann-Whitney U-test, Sokal and Rohlf, 1969: 392). Within the neotomines, there is a slight tendancy toward reduction of gestation length as one proceeds along the branch which includes Tylomys and Ototylomys (Figure 7). Within the peromyscines, a similar reduction in gestation length is seen as one proceeds toward the more modern animals (Figure 7). The larger neotomines tend to have longer gestation lengths than do the smaller peromyscines.

There seems to be a correlation of gestation length with a decrease in body size within the neotomines. Tylomys is the largest animal, Ototylomys the smallest, and Neotoma the intermediate. Their gestation lengths parallel this trend in body size. The peromyscines, as a group, do not show such a trend, although Layne (op. cit.) did find that the larger members of the genus Peromyscus had shorter gestation lengths than the smaller animals. He postulated that some phylletic relationship was being expressed.

Examination of the suborder Myomorpha reveals that only five species have been reported as having gestation lengths as long as that found in Tylomys: Nyctomys sumichrasti (Birkenholz, 1966), Mystromys albicaudatus

References, Figure 7: *

1. Present study.

2. Present study.

3. Egoscue, 1957, 1962; Hamilton, 1953; Olsen, 1968.

4. Horner, 1968; Pinter, 1970; Taylor, 1968.

5. Brand and Rykman, 1968; Drickamer and Bernstein, 1972; Linzey, 1970; Layne, 1968; Rood, 1966.

6. Asdell, 1964: 259.

7. Linzey and Linzey, 1967.

8. Blair, 1941.

* Arrangement of neotomines and peromyscines from Hooper and Musser, 1964.

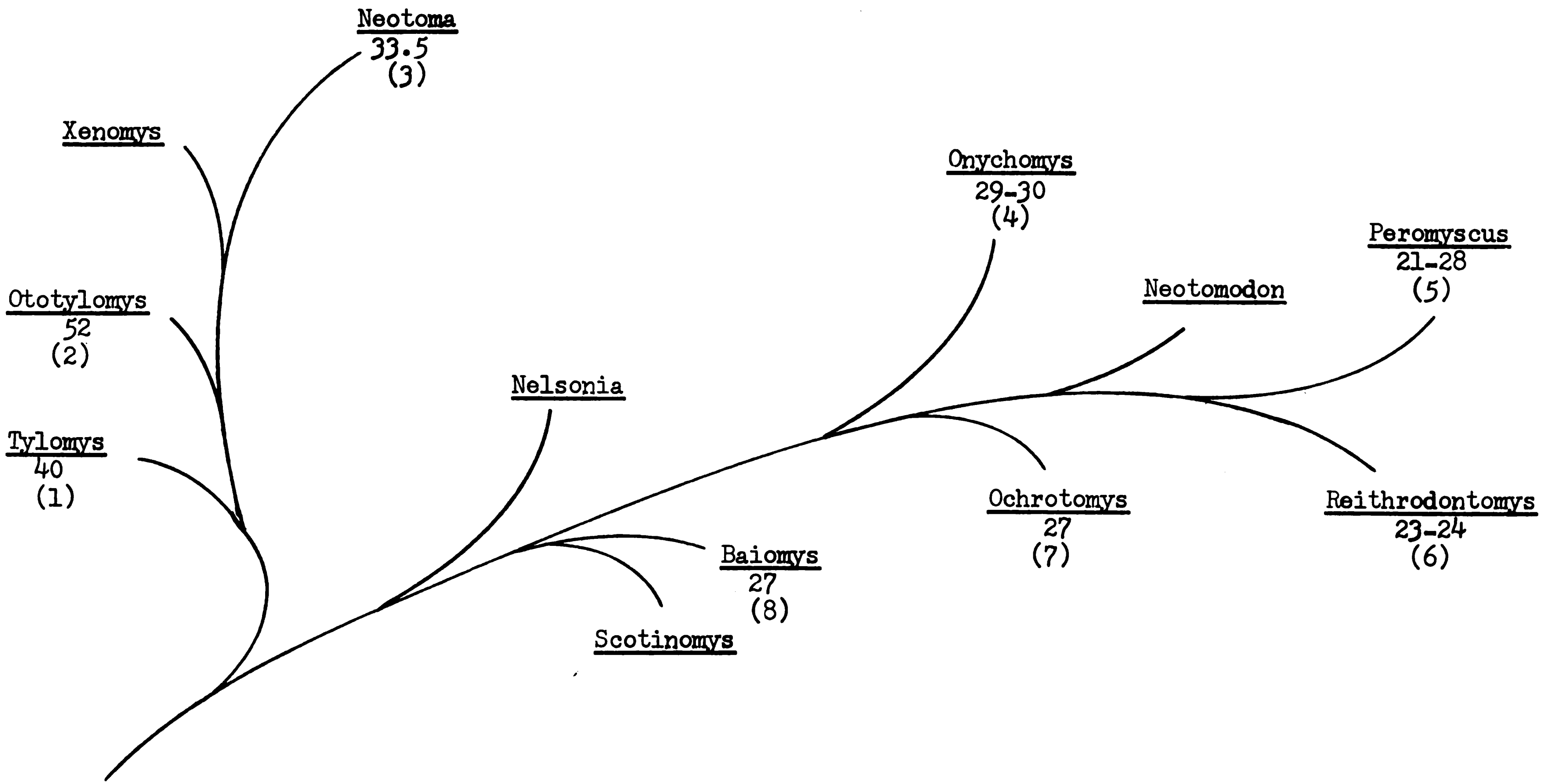

Figure 7. Gestation lengths of peromyscines and neotomines (References on page 25).

(Hall *et al.*, 1967), *Mesembriomys gouldii* (Crichton, 1969), *Acomys dimidiatus* (Walker, 1969: 935), and *Tachyoryctes ruandae* (Rahm, 1969). No phyletic trends are seen in this small group of rodents. The gestation length of *Ototylomys* is exceptionally long for the Myomorpha. The Hystrichomorpha is the only group of rodents where gestation lengths of 50 days or longer are found for animals whose body size is comparable to that of *Ototylomys* (*see* Tesh, 1970: 199; 1970: 201; Weir, 1970).

Ecological implications of the elongated gestation lengths found in *Tylomys* and *Ototylomys* are even more difficult to make than the phylogenetic ones. A prolonged gestation has been judged to be more of an advantage for animals living in xeric habitats than for those living in tropical habitats (Eisenberg and Isaac, 1963; Layne, *op. cit.*). The prolongation of gestation results in the production of more precocial young which are better able to cope with their environment while placing less strain upon the mother's resources (Layne, *op. cit.*; Smith and McGinnis, 1968). Similar adaptive significance has also been postulated for arboreal rodents living on specialized diets (Hamilton, 1962). Of those animals with gestation lengths as long as *Tylomys*, only *Mystromys* inhabits a xeric climate; the rest are of moist tropical origin. *Proechimys semispinosus* (Tesh, 1970: 201) and *Diplomys darlingi* (Tesh, 1970: 199) are two tropical Hystrichomorpha with gestation lengths similar to that of *Ototylomys*. Many more data are needed on the gestation lengths of tropical rodents before any conclusions can be made about the ecological implications of gestation length.

Comparison of the postnatal growth of the lengths of head and body (less tail) of *Tylomys* and *Ototylomys* for the first 28 days are represented in Figure 8. Growth rates are parallel. An F-test

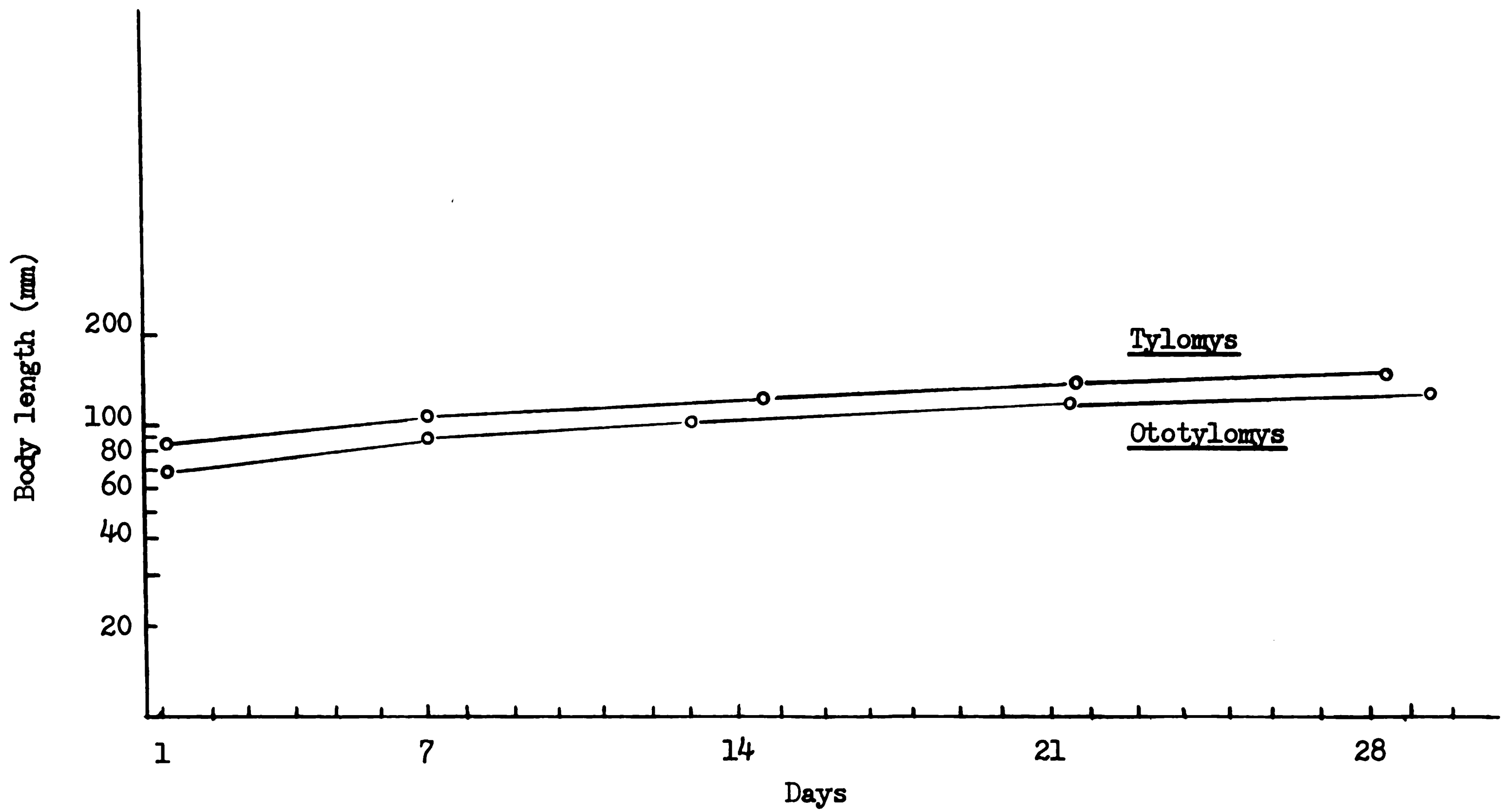

Figure 8. Growth of body length (semi-log) of Tylomys and Ototylomys through 28 days of age.

comparison of the regression coefficient ($b_{y.x}$) for these two lines shows these growth rates to be significantly different ($0.05 < p < 0.025$): $b_{y.x}=1.802 \pm 0.299$ for Ototylomys and $b_{y.x}=2.323 \pm 0.2045$ for Tylomys.

On the average, the eyes of Tylomys open at about the same time as do the various species of Neotoma while Ototylomys' eyes open from four to eight days earlier. Eye opening occurs between 12 and 18 days for all of the peromyscine group. Tylomys eye opening falls within this range while Ototylomys' eyes open 6 to 10 days earlier. All of the neotomines have erupted incisors at birth. The peromyscines show incisor eruption from 12 to 18 days of age.

Tylomys reaches 50 per cent of adult body weight at about the same time as all of the other peromyscine rodents, i.e. about 14 days of age. Fifty per cent of adult body weight is attained by Neotoma between 26 and 90 days of age. Ototylomys have attained 50 per cent of adult body weight by two days of age. Fifty per cent of adult body length was reached by Tylomys at about the same time time as other Peromyscus-like rodents while Ototylomys has grown to this extent at least four days earlier than any of the other species in this group. No attempt has been made to compare first response to finger snapping observed for Tylomys and Ototylomys to the other Peromyscus-like rodents, since this parameter is not reported by the authors used as references for this paper (for Neotoma, see Egoscue, 1957, 1962; Hamilton, 1953; Rainey, 1956; Richardson, 1943; for other peromyscines see: Blair, 1941; Brand and Ryckman, 1968; Drickamer and Bernstein, 1972; Horner, 1968; Horner and Taylor, 1968; Linzey, 1970; Linzey and Linzey, 1967; Layne, op. cit.).

Nipple-clinging observed in Tylomys and Ototylomys appears to be a common trait in Cricetidae and Muridae (Crichton, op. cit.; Horner and

Taylor, op. cit.). Crichton (op. cit.) hypothesized that this trait developed at an early time in the evolution of the murid group Pseudomyinae. That a similar trend also occurred in Cricetidae is evident by the fact that all members of the peromyscines and neotomines, whose reproductive biology has been reported, exhibit nipple-clinging. The adaptive significance would be two-fold. First, nipple-clinging young have access to an immediate supply of nutrients, a necessary factor for survival (Crichton, op. cit.; Horner and Taylor, op. cit.; Layne, op. cit.). Second, nipple-clinging young can be transported from one nest to another or from potential predators with little wasted energy (Birkenholz, 1965; Egoscue, 1962; Layne, op. cit.; Taylor and Horner, 1970). At the same time, it might be argued that the added burden of nipple-clinging young would hinder the mother's movements and therefore make her more vulnerable to predators. If the young are sufficiently precocial to be able to run along with the mother, rather than being dragged by her, the awkward locomotion would tend to be streamlined and thus reduce her vulnerability to predators. Ototylomys nest, have their young on the ground, and utilize the trees for food and protection (Disney, 1968; Williams, 1970). Laboratory observations have revealed that the young of Ototylomys do in fact run after their mother almost from birth.

Unfortunately, the field biology of Tylomys has not been examined as thoroughly as Disney and Williams did for Ototylomys. I can therefore only postulate that Tylomys occupies a more uniform environment than does Ototylomys, i.e. primarily in trees, or among rocks or on the ground. Species of Neotoma have been shown to occupy fairly uniform niches within their habitats (see: Egoscue, op. cit.; Finley, 1958; Murray and Barnes, 1969; Rainey, 1956). Tylomys postnatal development compares closely to that of Neotoma. However, Tylomys gestation is longer than that of Neotoma, and Tylomys young are somewhat more precocial than those of Neotoma.

The exact evolutionary significance of these findings is not clear. Tylomys and Ototylomys seem to be atypical forms within Cricetidae and, more specifically, within Neotominae. Their long gestation lengths appear to be primitive in form, especially as compared to other neotomines and peromyscines, as does the nipple-clinging behavior of their young. The reproductive biology of Tylomys is probably most adaptive for animals concentrating their activities in one dimension of their environment but still moving between two or more dimensions. Ototylomys has best adapted for scansorial living.

SUMMARY

To summarize, the reproductive biology of two Neotropical climbing rats, <u>Tylomys</u> and <u>Ototylomys</u>, were described and compared. Data collected from both genera included determination of the estrous cycle, gestation length, occurence of postpartum estrus, and prenatal and postnatal development.

Vaginal smears were collected from <u>Tylomys</u> exposed to two lighting conditions. The average interval between cornified cell periods was 6.8 $\pm$ 0.4 days under natural lighting and 12.0 $\pm$ 2.5 days when exposed to 12 hours of light and 12 hours of darkness. <u>Ototylomys</u> kept in 14 hours of light and 10 hours of darkness had an average estrous cycle of 8.8 $\pm$ 0.5 days. A postpartum estrus was observed for all littering females of both genera, as evidenced by the presence of sperm in smears taken within 24 hours after the discovery of new litters.

The earliest recorded mating for female <u>Tylomys</u> was 90 days of age while the earliest recorded mating for female <u>Ototylomys</u> was 29 days of age. The earliest recorded mating for males was 144 days for <u>Tylomys</u> and 175 days for <u>Ototylomys</u>.

The gestation period for <u>Tylomys</u> was 40.6 $\pm$ 0.5 days and 52.8 $\pm$ 2.1 days for <u>Ototylomys</u>. No statistical difference was found between the mean gestation lengths of lactating and non-lactating females for either genus. Both the minimum and maximum extremes in gestation length were observed in lactating females of both <u>Tylomys</u> and <u>Ototylomys</u>. Embryos were first detected by palpation of <u>Tylomys</u> on day 7 of gestation and of <u>Ototylomys</u> on day 14 of gestation. The fetal head was initially distinguishable at 28 days in both genera.

Only five other species included within the suborder Myomorpha were found to have gestation lengths similar to Tylomys. The gestation length of Ototylomys was exceptionally long for the Myomorpha, and only a few species of Hystrichomorpha were found to have equivalent gestation lengths. The sparsity of comparative information prevented speculation concerning the ecological ramifications of the prolonged gestation length observed for Tylomys and Ototylomys.

The ratio of males to females at birth was 95.6:100 and 115:100 for Tylomys and Ototylomys, respectively. Tylomys had an average of 2.3 young per litter and Ototylomys had an average of 2.4 young. The range in litter size was 1-4 in both genera. Statistical analysis of the standard measurements at birth for the Mexican and Panamanian Tylomys populations did not reveal any differences at day 1; therefore, the data were pooled. The standard measurements, in millimeters, for Tylomys were: total length, 134.1 ± 1.0; tail length, 50.0 ± 0.7; hind foot, 18.0 ± 0.2; ear, 8.5 ± 0.04. For Ototylomys they were: total length, 119.5 ± 0.9; tail length, 47.1 ± 0.8; hind foot, 16.4 ± 0.2; ear, 9.4 ± 0.2. Tylomys weighed 20.2 ± 0.3 gm and Ototylomys 10.2 ± 0.3 gm at birth. The least variance over time was observed in the length of head and body, without tail, and was therefore most valuable for comparisons of growth rates over time. At birth, Tylomys measured 84.3 ± 0.7 mm, and Ototylomys measured 67.0 ± 3.2 mm. Head and body length of Tylomys from Mexico was 34.9 per cent of adult body length; those from Panama were 35.8 per cent and Ototylomys were 46.4 per cent of their adult body lengths. No statistical differences were found between males and females at birth for either genus.

Semi-logarithmic plots of the regression coefficients for the lengths of head and body of _Tylomys_ and _Ototylomys_ for the first 28 days are parallel but significantly different.

For approximately 30 days after birth, the neonates of both genera adhere tenaciously to their mother's inguinal teats, as do the young of the neotomines and peromyscines. Both _Tylomys_ and _Ototylomys_ young are precocial, with _Ototylomys_ young being the more precocial. The greatest number of _Tylomys_ were initially able to respond to loud noises between days 8 and 9, while the largest number of _Ototylomys_ initially responded by day 2. Eye opening occurred for the greatest number between days 10 and 11 in _Tylomys_ and day 6 for _Ototylomys_. Hearing preceded eye opening in all but four cases. The timing of eye opening observed in _Tylomys_ is about the same as that observed for _Neotoma_ and for the peromyscines. _Ototylomys'_ eyes open four to ten days earlier than all other species examined.

Tylomys from Mexico have attained 50 per cent of adult body length by day 14 and those from Panama between days 12 and 14. This is at least ten days earlier than that observed for _Neotoma_ and about the same time as the other peromyscines. _Ototylomys_ reach 50 per cent of their adult body length by day 2, at least four days earlier than any other closely related species. Ninety per cent of adult body length is reached at 120 days in the Mexican _Tylomys_ while the Panamanian group grew to 90 per cent of their adult body length by 116 days. _Ototylomys_ grew to 90 per cent of their adult body length by 58 days of age.

The entire reproductive processes of _Tylomys_ and _Ototylomys_ were judged to be primitive in form and best adaptive for animals utilizing two or more dimensions of their environment.

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