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GROWTH AND DEVELOPMENT OF THE EASTERN HARVEST MOUSE, REITHRODONTOMYS HUMULIS

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GROWTH AND DEVELOPMENT OF THE EASTERN HARVEST MOUSE, *REITHRODONTOMYS HUMULIS*

JAMES N. LAYNE [1]

SYNOPSIS: Observations were made on the breeding history, growth and development of the young, and parental care in captive eastern harvest mice, *Reithrodontomys h. humulis*.

Breeding occurred throughout the year, gestation was presumably 24 days or less, and mean litter size was 2.2. The sex ratio at birth was even.

The curves for body weight and total length became essentially asymptotic by the 7th week. Tail length increased only slightly after the 5th week, and the curve for hind foot length leveled off at 3 weeks. Mean ear length showed no significant increase after the 4th week. A marked slowing at 3 weeks of the initially rapid growth in weight, total length, and tail length coincided with the period of weaning.

Newborn young are pinkish and possess both vibrissae and a sparse scattering of hairs over the middorsal region. The pelage is sufficiently developed by the end of the first week to exhibit the typical juvenile coloration, and by the second week the juvenile coat is apparently fully grown. The postjuvenile molt takes place between the 3rd and 9th weeks. Full adult pelage is not attained until at least one further partial or complete molt.

The eyes open from the 7th to the 9th or 10th days of age. The pinnae unfold on the 1st or 2nd day of age, and the external auditory meatus becomes patent from the 7th to 10th days. Claws are present at birth and are noticeably better developed by the 4th day.

Incisors were above the gums on the 4th day in one mouse, but typically did not appear until the 6th or 7th day. They are faintly yellowish by the end of the 2nd week. All molars were apparently functional in a specimen 4 weeks of age.

Weaning occurs between the 2nd and 4th weeks. The vulvas of females opened between the 4th and 7th weeks, and two females became pregnant for the first time at 11 and 20 weeks of age. The testes and cremaster of the males enlarged by the 7th or 8th week.

The young have little coordination at birth. When 4 days old they can sit upright, and the prehensile nature of the tail is apparent. Week-old young scratch and attempt to wash. With the opening of the eyes they become more active and exploratory, and by 2 weeks of age their behavior is similar to that of adults. Most individuals were nervous and wild. The young and adults were generally highly tolerant of one another, although some fighting occurred among males in one cage.

Increased nest building and food storing activities may precede parturition in females. Mothers exhibited concern for their young through the 3rd week of age, although the intensity of parental care declined after the 2nd week. In-

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stances of paternal care were observed, and behavior assumed to represent a weak retrieving response was noted in 4-week-old young.

Comparison of the growth and development of *R. humulis* and *R. megalotis* indicates a close similarity of postnatal developmental patterns, although *megalotis* may have a somewhat slower growth rate.

Introduction

Comparative data on postnatal growth and development in different species and subspecies of mammals are often of interest from a taxonomic, genetic, physiological, behavioral, or ecological standpoint. Knowledge of such aspects of the reproductive biology of mice of the genus *Reithrodontomys* is apparently limited to only 3 of the 17 Recent species. Two accounts (Svihla, 1931; Smith, 1936) apply to *R. megalotis*. Svihla (1930) gives weights and a short description of the newborn young of *R. fulvescens*, and Audubon and Bachman (1849) mention the birth in captivity of two litters of the eastern harvest mouse, *R. humulis*, noting that the young were blind and naked at birth, became covered with hair in a few days, and were seen peeping out of the nest when a week old. Holding and Royal (1952) present more extensive data on the development of a single young *R. humulis*.

An adult female and juvenile male *Reithrodontomys h. humulis* (Audubon and Bachman) captured by hand 16 December 1956, near Gainesville, Alachua County, Florida, served as the nucleus of a small laboratory colony. This colony was studied actively for about a year. During this time 11 litters were produced and observations were made on breeding, growth and development of the young, and parental care.

Methods

The mice were first kept in a large aquarium with a hardware cloth top. Several inches of dry sand served as a substrate, and dried grasses were supplied for cover and nesting material. Later, wire cages with a litter of sawdust or wood shavings and cotton for nesting material were used. Shelled whole corn was the principal food given. This diet was supplemented with sunflower seeds, crimped oats and oat flakes, Purina lab chow, and various fresh fruits and vegetables. Water was provided in open dishes or in standard water bottles.

When litters were expected, the nests were usually examined for young in the morning and evening. Young born during the period between the evening and morning checks were considered as being newborn on the day discovered, even though the exact time of parturi-

tion was not known. No differences in the degree of development of such litters as compared to those examined a short while after birth were apparent.

The intervals at which different litters were examined varied. The young of all litters, except two for which the date of birth was doubtful, were examined on the day of birth. In one litter the young were examined daily up to the 10th day and weekly to 11 weeks of age. One litter was examined at 1- to 3-day periods for the first 9 days and weekly to the 4th week, while another was observed at 2-day intervals for 2 weeks and once a week up to the 16th week of age. Four litters were handled only at weekly intervals up to 10, 11, 12, and 17 weeks, respectively. Two litters were examined only at birth. In one of these the single young found shortly after parturition was missing from the nest the next day. One young of the other litter of three was preserved at birth as a permanent record, and the mother destroyed its nest mates the following day. When examinations at weekly intervals were discontinued, the mice were observed at longer and more irregular intervals. For better observation of critical details, a stereoscopic microscope was used in examining the young at early ages.

Weights were ordinarily taken each time the litter was handled, while measurements were generally taken only at weekly intervals through the 10th week and usually more sporadically thereafter. Three newborn young were sacrificed to obtain measurements at birth. In all other cases measurements were taken on anesthetized young. Mice 1 to 3 weeks of age were anesthetized by placing them in a covered finger bowl containing a small piece of ether-soaked cotton. Older young were anesthetized in a similar fashion in a gallon glass jar. The animals were removed from the dish or jar as soon as movement ceased. If they became active during measuring or examination they were returned to the container until unconscious again. As the same state of relaxation was not always attained, this method sometimes resulted in slight discrepancies in measurements of the same individual from week to week. However, as the errors were ordinarily small and tended to cancel each other out and the number of measurements for each age is fairly large, the values obtained are considered sufficiently reliable to reflect growth rates accurately.

Breeding History

All litters studied were the result of matings in captivity. Births occurred in every month of the year except February, May, and

November. The original female produced 8 litters totaling 15 young in an 11-month period. She gave birth to her first litter in captivity 31 March 1956, and six litters followed at 28-, 49-, 31-, 26-, and 24-day intervals. The last litter was born in January 1957. Although she was kept with her original mate for 15 months afterwards, this female did not breed again. The three other litters were born to her offspring.

The 24-day minimum time between successive litters recorded for the original female indicates that the gestation period in *Reithrodontomys humulis* is 24 days or less and that mating may take place shortly after parturition. Gravid females appeared noticeably swollen in the abdominal region several days before parturition. The original female, whose nonpregnant weight varied from about 6.5 to 7.0 grams, weighed 9.5 grams 3 days before the birth of one litter of two and 10.1 grams 4 days prior to the birth of another litter of two.

Litter sizes ranging from 2 to 5 have previously been reported for the eastern harvest mouse (Audubon and Bachman, 1849; Brimley, 1923; Holding and Royal, 1952). In this study the exact number of young at birth was known for nine litters; there were three litters of 3 young, five of 2, and one of 1, giving a mean litter size of 2.2. The size of two other litters was questionable, for evidence suggested that the mothers might have destroyed some of the young. The sex ratio at birth was even.

Growth

The mean weight of 20 young at birth was 1.2 grams, with extremes of 0.8 and 1.6 grams. Figure 1 shows the weights of individual young plotted at weekly intervals from birth through 10 weeks; the curve connects the average weights at each week. Two growth phases, characterized by distinctly different relative growth rates, seem evident from these data. During the initial phase, from birth to 3 weeks, weekly weight increments average 1.03 grams, or approximately 86 percent of the birth weight. Weight gain averages about .42 grams (35 percent of the birth weight) per week during the second growth phase, which extends from the 3rd to the 7th week. By the latter age, the curve for weight becomes essentially asymptotic.

The freshly-killed newborn mice had the following measurements before being preserved: Total length, 37, 37, 38 mm.; tail length, 10, 11, 11 mm.; and hind foot length, 5, 5, 6 mm. Holding and Royal (1952) give measurements of 35 mm. total length and 11 mm. tail length for a single *R. humulis* at birth.

Figure 2 shows measurements of young at weekly intervals from birth to 10 weeks. Growth in total length and tail length shows two rather distinct phases, as in the case of weight. From birth to 3 weeks of age total length increases an average of approximately 20 mm. per week, or 54 percent of the length at birth. Growth from the 3rd to the 7th weeks averages only about 5 mm. (12 percent of mean total length at birth) per week, and there is no significant increase in total length after the 7th week. The initially high growth rate of the tail from birth to the 3rd week is approximately 118 percent (12.6 mm. per week) of the tail length at birth per week. The tail increases only about 1.2 mm. per week (10 percent of its length at birth) from the 3rd to the 5th week. The mean tail length at 6 weeks is less than a millimeter longer than at 5 weeks and no further growth is evident after the 6th week.

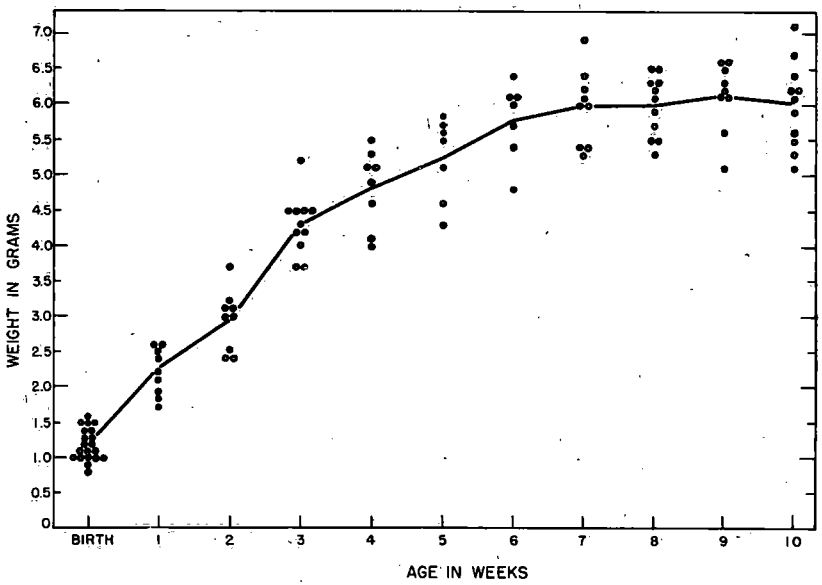


Figure 1.—Growth in weight of *Reithrodontomys humulis* from birth to 10 weeks of age.

The growth of the hind foot levels off at 3 weeks of age at a mean length of 14.3 mm. There is a slight increase, to an average length of 14.7 mm., by the 6th week, after which no further change is recorded. Increase in hind foot length during the first week is approximately 88 percent of its size at birth, and it grows at a rate of about 32 percent of its length at birth per week in the next 2 weeks.

As the pinna is folded over at birth, the first ear measurements (from notch) were made at one week of age (mean 4.4 mm.). The ear is 34 percent larger at 2 weeks, and during the 3rd and 4th weeks shows a weekly increase of approximately 19 percent of its length at 1 week of age. No significant difference in the weekly means for ear length is apparent after the 4th week.

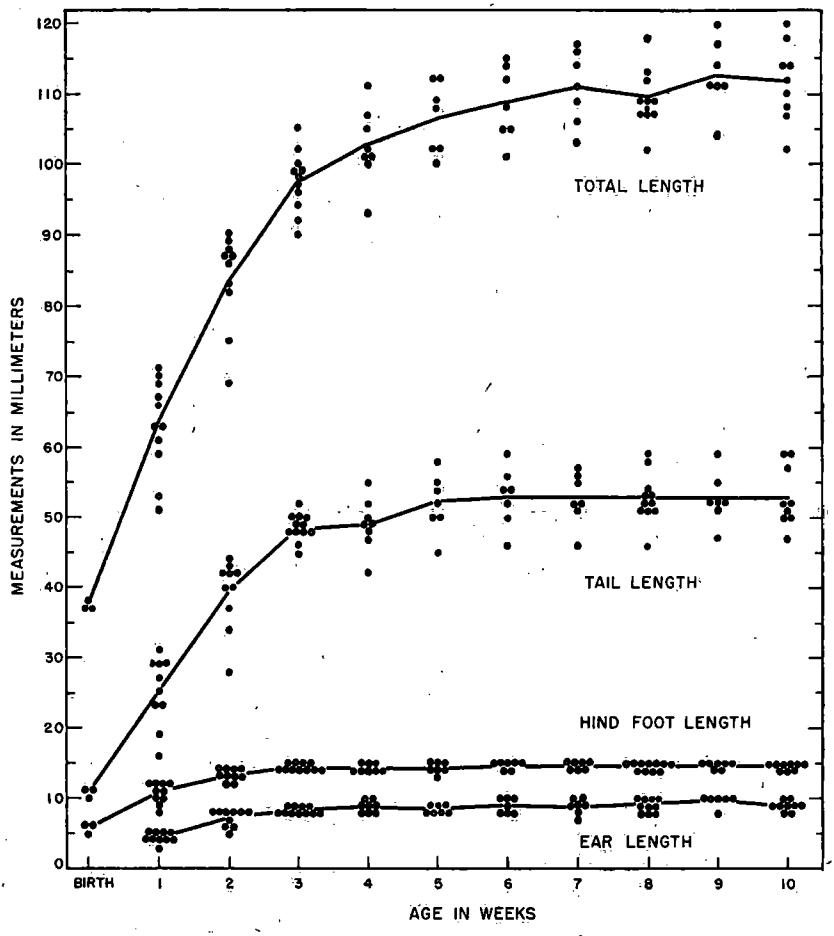


Figure 2.—Growth in four linear measurements of *Reithrodontomys humulis* from birth to 10 weeks of age.

The termination of the period of rapid initial growth, which is clearly evident at 3 weeks in the curves of weight, total length, and tail length, is correlated with the period of weaning.

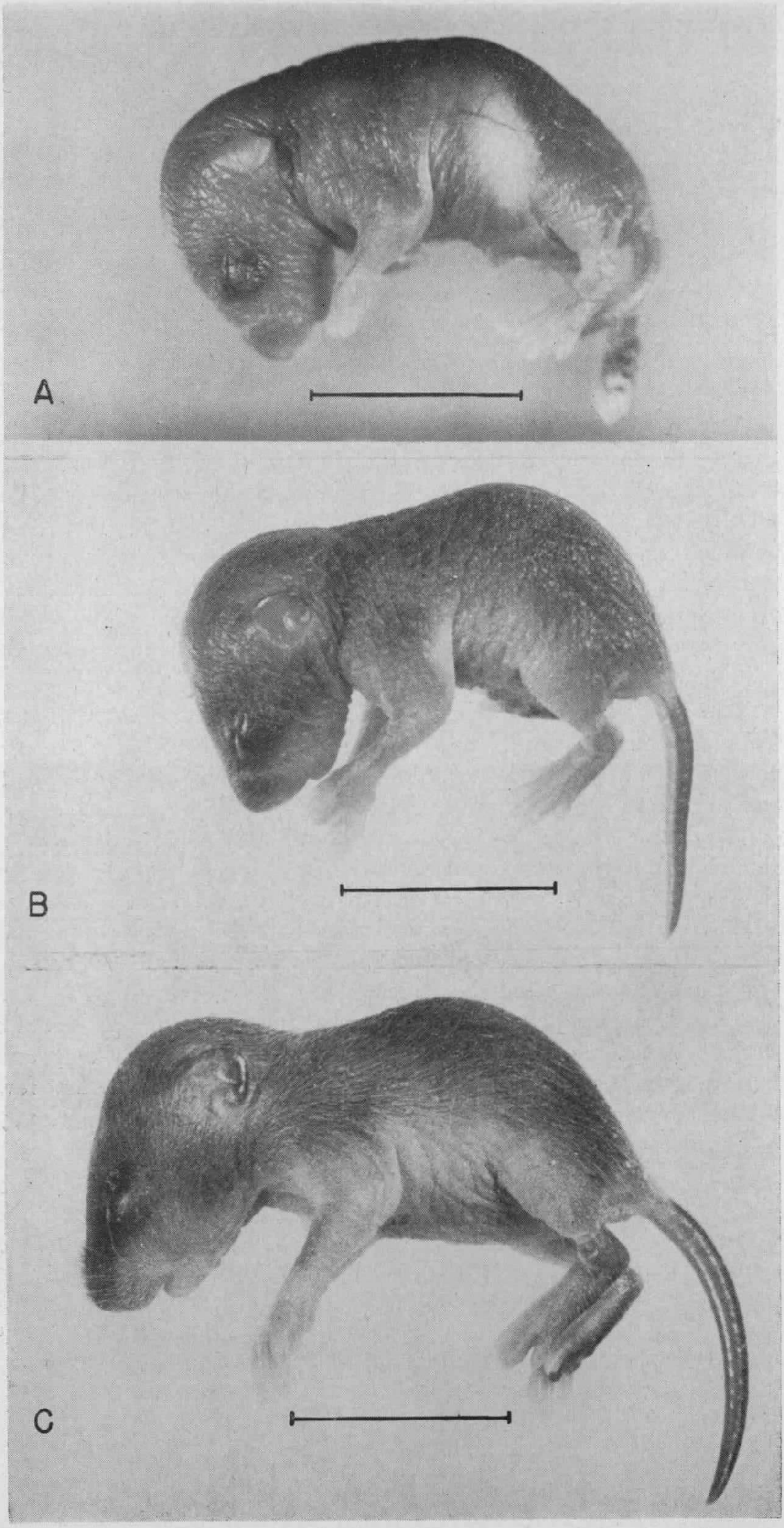
The present data do not indicate any significant differences between intralitter and interlitter variability in growth rates, nor any apparent correlation between growth rates and litter size. In several cases a young in a given litter was noticeably smaller than its litter mates at the time of birth. Such individuals continued to lag behind the others in size and development throughout the period of growth, although the differences were most pronounced at the earlier ages.

Physical Development

Pelage. Young examined within several hours of birth (Fig. 3A) are pinkish in color all over, although tiny, discrete, dark pigment spots, apparently associated with developing hair follicles, impart a slightly dusky tinge to the middorsal region. The skin is rather loose, wrinkled, and somewhat transparent, particularly on the lower sides and venter. In these areas blood vessels are quite prominent, and the lower portions of the ribs, the costal cartilages and sternum, and the abdominal viscera are visible through the skin. Nipple sites are faintly evident on the venter.

The vibrissae are relatively well developed, the mystacials being the most conspicuous. Fine, widely scattered, short hairs are also present on the middorsal region and are most abundant on the head. Short bristles are visible on the chin; otherwise the lower sides, limbs, tail, and venter are devoid of hair. Although no young were examined immediately after birth, the assumption is made that the pelage development observed in mice several hours after parturition is similar to that at birth. Audubon and Bachman (1849) and Holding and Royal (1952) have stated that newborn *humulis* are hairless at birth. The latter did not record the appearance of hair until 5 days of age. The discrepancies between these observations and the present are most likely the result of differences in the manner in which the young were examined at the earlier ages. I found that during the first few days of development the hairs on the body could be seen clearly only under magnification.

In day-old young the dorsum is slightly darker and the hairs are noticeably more abundant. Both short dark hairs and longer lighter ones are now evident. The short dark hairs are denser than the widely scattered long ones and are best developed on the head and shoulders. Whitish hairs are visible on the sides of the body and on the limbs to the wrists and ankles; a few also appear widely spaced on the venter. The tail is hairless but slightly bicolor from the development of pigmented follicles on the dorsal surface. Patches of dusky pig-


A
B
C

ment are visible on the ankles, and the soles and plantar tubercles of the hind feet have become noticeably darker.

By the 2nd day of age the longest hairs of the developing pelage are approximately 1 mm. in length. The dark hairs are still most abundant on the crown and rostrum. The upper surface of the fore and hind feet now have a covering of hair, but none is yet visible on the digits. Although still sparse, hairs are more abundant on the venter. The tips of the hairs have appeared above the skin on the dorsal surface of the tail. The skin is definitely more opaque, and blood vessels are visible only on the lower sides, belly, and limbs.

At 3 days of age, hairs appear on the digits and on the lower surface of the tail. Dandruff-like scales are also visible on the dorsum.

By the 4th or 5th days (Fig. 3B) the dorsal pelage has assumed a faintly brownish tinge, particularly on the head and shoulders. A patch of dark hairs has developed on the front of the wrists and ankles. The liver is still faintly visible through the abdominal wall, although the ventral pelage is better developed. Epidermal scales are still conspicuous.

The pelage is sufficiently developed by the end of the first week (Fig. 3C) to exhibit the general juvenile color pattern, the upperparts being dark grayish brown and the underparts grayish white. A faint pale yellowish tinge is evident on the cheeks, on the sides of the head anterior to the base of the ears, and along the extreme lower sides. The wash along the lateral line is suggested in some individuals as early as the 4th day, whereas the yellowish patch of hairs in front of the base of the ear is apparent by the 6th day. Epidermal scales are noticeably fewer on the 6th day and disappear a day or two later.

Development of the pelage after the first week chiefly involves further growth in the length of the hairs (Fig. 4A). By the end of the 2nd week the juvenile pelage is essentially fully developed (Fig. 4B). The coat has lost its earlier sleek appearance and is now looser and more fuzzy.

Data on the postjuvenile molt were obtained from 6 litters comprising 11 young examined at weekly intervals (Fig. 5). Molting was first observed at the 4th week, and all individuals had essentially completed the molt by the 9th week of age. Although individual

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Figure 3.—Stages in the development of *Reithrodontomys humulis*. A. Young at birth, B. Four days of age. C. One week of age. Scale in each case equals 1 cm.

variation in the timing and sequence of the replacement was rather marked, the general pattern appeared to be for the molt to begin on the venter and then spread to the upperparts, beginning first on the lower sides, extending dorsally at midbody, and then proceeding anteriorly and posteriorly onto the head and lower back. In some individuals a patch of juvenile pelage persisted on the crown after the remainder of the body had completed the molt. As the molt was completed rather rapidly, the times at which the young were examined were too far apart to provide a detailed picture of the molt pattern. The sequence observed was, however, in general agreement with that established by Hooper (1952) through the study of conventional museum skins of various species of *Reithrodontomys*.

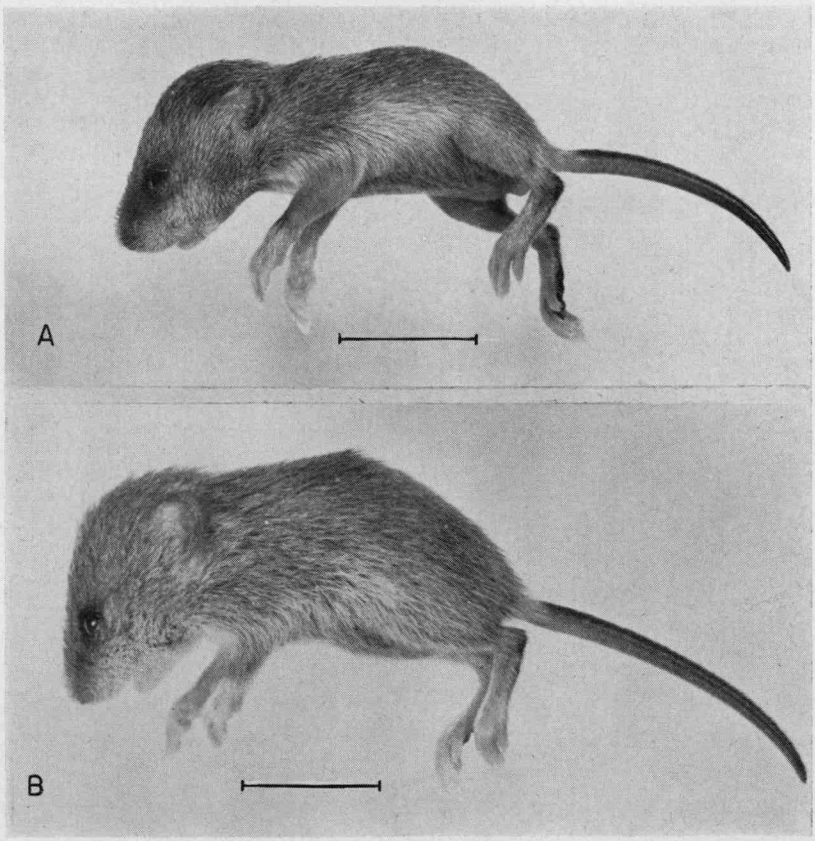

Figure 4.—Stages in the development of *Reithrodontomys humulis*. A. Ten days of age, B. Two weeks of age. Scale in each case equals 1 cm.

The postjuvenile or subadult pelage is browner above and more distinctly buffy along the lower sides than the juvenile coat, but not as bright or rich as the full adult pelage. The venter of the subadult animal also appears more thickly haired and less grayish than in the juvenile. Mice in the postjuvenile pelage frequently exhibited a faint buffy wash on the breast and occasionally along the midline onto the belly. It was not determined whether this coloration is due to pigment in the hairs or to a stain from some glandular secretion.

Five of 11 individuals completed the postjuvenile molt between the 3rd and 6th weeks, while in 6 the molt occurred in the interval between the 5th and 9th weeks. The duration of the molt was calculated from the last week that no molt was observed to the first week that complete postjuvenile pelage was present (including some specimens that retained a small patch of juvenile pelage on the crown). On this basis the maximum period of molting ranged from 1 to 3 weeks, with an average of 2 weeks.

Full adult pelage apparently is not attained until one or more additional complete or partial molts. Data obtained on molts after the postjuvenile, though incomplete, do indicate another molt, and perhaps two in some individuals, before 30 weeks of age. One mouse was molting at 15 weeks and completed what was apparently a second molt phase between 24 and 26 weeks. Another completed a molt between 20 and 22 weeks, and a third was undergoing a molt at 17 weeks. One individual of a litter of two began to molt at 13 weeks of age and was in an advanced stage of replacement of hair when killed the following week. Its litter mate was molting when examined at 17 weeks. The pattern of these molts was not clearly evident. However, replacement seemed in general to proceed as in the postjuvenile molt, as also indicated by Hooper (1952), although it appeared to be even more diffuse and variable. The pelage following these molts was grossly like that of the majority of adults, being a richer brown than the postjuvenile coat. Adult *humulis* are believed to undergo two partial or complete molts a year (Hooper, 1943).

Eyes, ears, and claws. The eyes of the newborn young are covered with the sealed lids, which are so transparent that the iris is distinctly visible as a dark ring and the lens as a pinkish center. The crease marking the line of fusion of the upper and lower lids is not well marked. By the 2nd day the eyes are less prominent, as pigment is forming in the lids, and by the 4th day they are completely obscured. At this time the slit between the lids is considerably more noticeable. The eyes opened between the 7th and 10th days of age.

Of 9 young in which the opening of the eyes was recorded, the eyes were visible on the 7th day in 6, on the 8th day in 1, and on the 9th or 10th day in 2. The eyes of the single *humulis* individual studied by Holding and Royal (1952) opened between the 10th and 11th days of age.

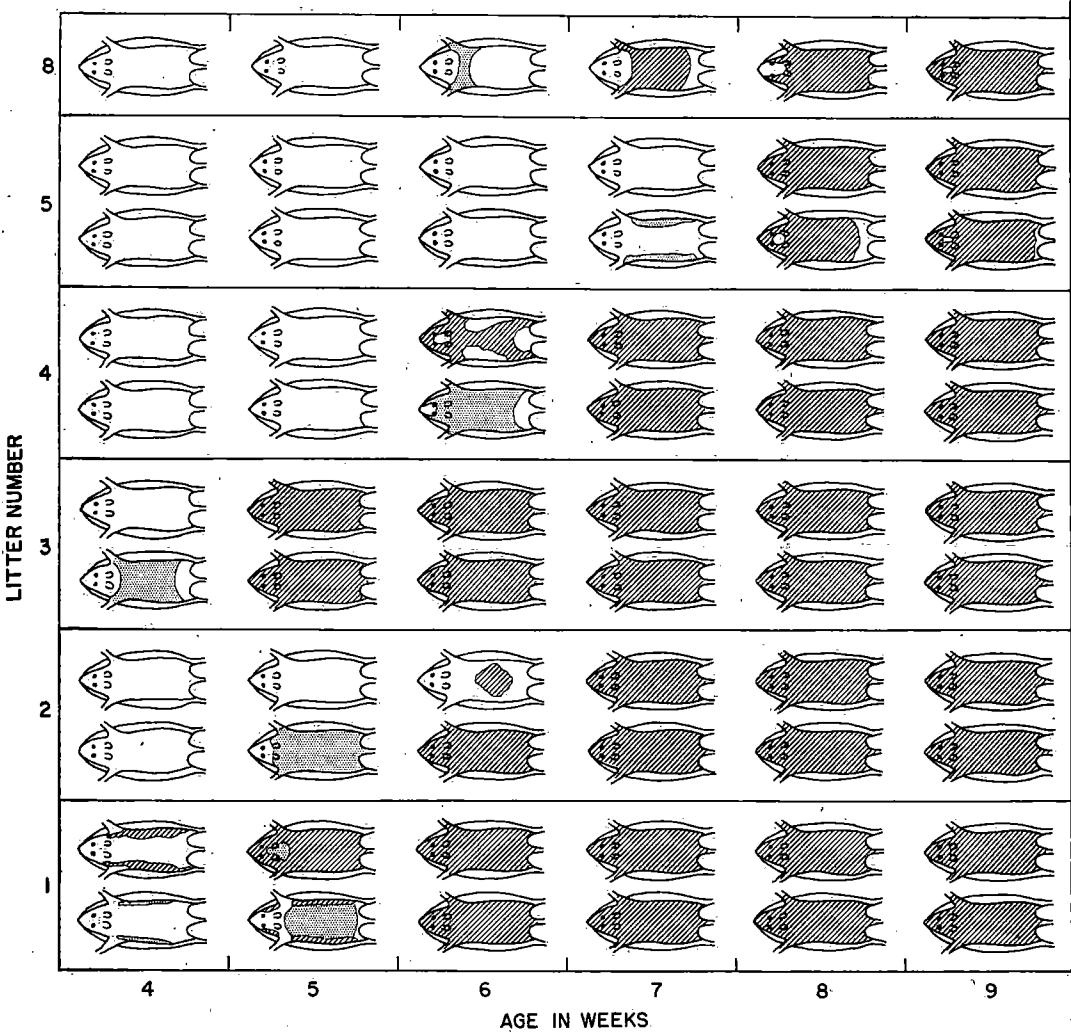

Figure 5.—Postjuvenile molt patterns in six litters of *Reithrodontomys humulis* examined at weekly intervals. Molt on the upper-parts only is shown. Clear area indicates juvenile pelage, stippled area intermixture of juvenile and postjuvenile pelage, and hatched area postjuvenile pelage.

At birth the pinnae are tightly folded over and conceal the opening of the external auditory meatus. The posterior margins are slightly more elevated than the anterior ones. The pinnae unfolded in most of the young on the day following birth, though in some this did not occur until the next day. At first the pinnae stand out from the side of the head but within a day lie flat against the head. The pinnae are fleshy and but lightly pigmented during the first week of development. Hairs appear on the anterior portion of the lateral surface of the ears in some individuals by the 4th day of age, and by the end of the first week a sparse coating of hair covers the entire lateral surface.

The external auditory meatus remains tightly closed until at least the 7th day of age. Five of 10 young had the meatus open on the 7th day. In 2 it was open on the 8th or 9th day, and in 3 others, on the 9th or 10th day. No reaction to sound was recorded for any young before the meatus opened. In several instances the typical reaction to a sharp sound, a convulsive start, was not elicited until the day after the meatus appeared to be open.

The digits of the fore and hind feet are well separated at birth, and short, blunt, more or less translucent claws are present. The claws become noticeably sharper by the 3rd day and by the 4th are seemingly more opaque and harder.

Dentition. In one young the lower incisors were visible on the 4th day of age, but in the rest the incisors were not clearly above the gum line until the 6th or 7th day. The lower incisors seemed to erupt before the uppers in some individuals, whereas in others both pairs appeared above the gum line about the same time. The incisors are white and chalky at first, but by the end of the 2nd week have taken on a faintly yellowish tinge. At this age the upper incisors are from .5 to .8 mm. in length and the lowers from 1.0 to 1.5 mm. At the end of the 3rd week the upper incisors are about 1 mm. long, the lowers 2.0 to 2.5 mm., and both pairs are brighter yellow than at 2 weeks of age. Little change in the size of the incisors is apparent after the 3rd week. The grooves in the anterior faces of the upper incisors are evident as soon as the teeth have extended beyond the gum.

In one mouse sacrificed at the end of the 4th week the cheek teeth were all in position, although the last molar in both upper and lower jaws was slightly below the level of the others.

Weaning. One individual was observed still nursing at the end of the 2nd week; another at this age was seen feeding on fresh corn

and was apparently fully weaned a week later. Other young were noted outside the nest with the parents at night by the end of the 2nd week, and most were foraging regularly outside the nest at 3 or 4 weeks of age. A mouse killed at the end of its 4th week had only solid food in the stomach. It thus appears that weaning occurs between the 2nd and 4th weeks, and that most of the young probably take mainly solid food by the end of the 3rd week of age.

Sexual maturity. Although the vulvas of females opened for the first time between the 4th and 7th week, records of two pregnancies in captive-born young suggest that full breeding status may not be reached until several weeks later. Although caged with fully adult males, these two young females did not become pregnant for the first time until 11 and 20 weeks of age. A female sacrificed at 4 weeks had a small, undeveloped genital tract showing no evidence of reproductive activity.

The testes of males showed slight enlargement, on the basis of external examination, by the end of the 4th week, but it was not until the 7th or 8th week that the testes conspicuously filled out the cremaster and the latter was sparsely haired. Two males killed at 10 and 14 weeks of age each had testes 5 mm. long and 3 mm. wide. The accessories were fully developed, and the cauda epididymal tubules were enlarged and contained spermatozoa.

Behavioral Development

The young are capable only of relatively uncoordinated movements at birth. When disturbed they writhe and twist the body and move the limbs about aimlessly. If they chance to roll onto the venter they can drag themselves a short distance, but soon topple over. During the efforts to crawl the fore limbs seem to provide most of the power and to be under better control than the hind limbs. The young sleep or rest on their sides and at brief intervals give involuntary convulsive twitches. They utter very high-pitched, insectlike peeping notes.

When 2 days old some young reacted quickly to a slight touch on the side by giving a sudden jerk, sometimes throwing themselves so violently that they landed on their backs; other individuals at this age did not react similarly. It is not possible to say whether this is because of individual variation or simply that the relatively short periods of time the animals were out of the nest for examination precluded the possibility of observing the full range of behavioral capacities of any litter on a given date.

By the 4th day of age the young begin to utter a louder, more insistent squeak when disturbed. At this age they are able to crawl somewhat better and also begin to offer resistance when held in the hand. As earlier, the propulsive force seems to be mostly supplied by the fore limbs which now exhibit better coordination than before. At this age the tail begins to show its semiprehensile nature, moving in a wormlike fashion when the animal is active and responding quickly to a slight touch by bending toward the stimulus. The young rest on the venter more frequently and are apparently able to assume this position at will.

When 1 week old the mice show considerable improvement in their crawling ability, although they still drag the venter on the ground and their legs still splay out to the sides. The hind limbs now function more smoothly, but are still less well coordinated than the fore limbs. The young can scratch the body with a hind leg and attempt to sit up and wash but, although they support themselves on the fore arms, are unsteady and fall over easily. When disturbed in the nest they exhibit a defense reaction similar to that sometimes observed in adults—lying on the back and kicking violently. Convulsive twitches are still noted when the young are sleeping or otherwise motionless.

The opening of the eyes and ears signals a marked change in behavior. The young become more active and responsive to their environment. At 10 days they walk more or less normally. They hold the legs fairly well beneath the body and no longer drag the venter. They sit up to wash more steadily than before and can lift the fore limbs off the ground during the washing process, although they occasionally lose their balance when doing so. They exhibit a definite tendency to remain together, crawling over and under one another in a wriggling mass. They show more fear of the observer and struggle hard to escape when grasped. Convulsive twitches are no longer noted when they are still.

By 12 days of age the young have grown very active. If removed from the nest they scamper about with the typical "hitching" gait of the full grown animal and are difficult to capture. They still tend to remain together but wander about more. The use of the tail for support and balance when the animal is climbing is quite evident. The young can now sit erect on the hind legs to wash in the manner typical of the adults. They wash the snout first, then the fur behind the ears, bringing the fore feet briskly forward over the backs of the pinnae. Next the flanks receive attention, the mouse

twisting from one side to the other and stretching down and back to reach the pelage with mouth and paws. Finally, they groom the entire tail from the base to the tip.

The young are venturing from the nest and look and behave like miniature adults at 2 weeks of age. When in the nest they tend to be difficult to flush and when outside run quickly back to the nest when alarmed.

Most of the harvest mice composing the colony were nervous and jumpy in temperatment. If disturbed they usually dashed and leaped wildly about the cage or aquarium in a frenzy of excitement. Frequent handling appeared to have no effect on the disposition of the young, and after the eyes and ears opened they soon became as wild as the adults. The one exception to the generally nervous temperament of the animals, at least at first, was the original female. Immediately after capture she was extremely tame and would sit on the hand and allow herself to be stroked gently without showing any inclination to escape. Although her mate was seldom seen during the day and remained hidden in the nest, she spent many hours sitting in the top of a dried clump of brome sedge stalks with her back pressed against the top of the aquarium. However, after several months in captivity this female also grew quite wild and as difficut to catch and handle as the others. Coincident with this change in temperament, she also abandoned her diurnal activity to a large extent.

Both the young and adults were highly tolerant of other individuals. All animals in a cage or aquarium usually shared a communal nest and newly introduced individuals were readily accepted without apparent antagonism. The original female and her mate often occupied a single nest with recently born young and those of a previous litter or litters. However, several observations suggested that the adult female might be somewhat antagonistic to other individuals for a short period just before or after the birth of a litter. In several cases the male or young of a previous litter who were sharing a nest with a female in advanced pregnancy were noted outside the nest near the time when parturition was believed to have occurred. Such aggressive behavior, if it actually was, was apparently of short duration, for the other individuals would soon be found back in the nest with the female and her young.

The only fighting among the captives was recorded in a cage housing several males and females of older litters. Most of the fighting apparently took place between the males. Evidence of strife,

such as torn ears, patches of hair missing, and tooth marks in the skin, was not noted until the mice were obviously sexually mature, at about 11 or 12 weeks of age.

Parental Care

One observation suggests that the nest-building drive in pregnant females may be intensified shortly before the young are born. A gravid mouse housed in an aquarium for several days made no attempt to build a typical nest until suddenly one night she was noted actively so engaged. She bore her litter between 9 and 10 a.m. the following day.

This female was also seen moving corn into the completed nest the night before parturition, which suggests that pregnant females may tend to provision the nest before bearing young. What might possibly be further evidence of this was noted in the original female before her first litter in captivity was born. About a week before parturition, a cache of corn was discovered in a small depression at the base of a clump of dried grass. The kernels had been carried from a foot away. Although this female and her mate had been kept in the same aquarium for 3 months, no food storage had been noted previously.

Females exhibited concern for their young through the 3rd week after birth. Mothers often were extremely reluctant to abandon the nest and attempted to ward off fingers or forceps with boxing motions when the young were being secured for examination. In one case a female, using her mouth and fore feet, attempted to pull her week-old young back into the nest as they were being lifted out. Sometimes a mother would rapidly repair the nest wall from within as the observer began to open it from the outside to get at the young. On one occasion a female frequently interrupted her defense of 10-day-old young to push them deeper into the bottom of the nest, giving them a quick, nervous grooming each time. Mothers were not recorded as actively defending the young after the 2nd week, although during the 3rd week they often stayed around the nest when the young were being handled and appeared to show concern.

On several occasions mothers flushed from the nest carried along a 7 or 8 day-old young clinging to a nipple. In one instance the young mouse was dragged roughly about the cage for some 30 seconds and even hung on when the mother ran upside down across the wire cage top. Audubon and Bachman (1849) did not observe the young being carried on the nipples in the captive harvest mice they

studied and believed this to be a behavioral difference between *Reithrodontomys* and *Peromyscus*.

Females readily retrieved small young placed up to 6 inches from the nest. Before picking up the young, they performed a ritual of thoroughly sniffing and washing it while vigorously rolling it around with the fore feet. Females were seen to carry small young either by the nape of the neck or the skin of the belly. Often when young were removed from the nest to observe the retrieving response, the mother, though the young might be in full view only a few inches away, would seem to ignore their presence until they began to squeak.

A female was twice seen trying to get older and more active young back to the nest. Once she seized a 10-day-old individual moving about near the nest by the shoulder and tried to push it through the wall of the nest. Failing in this, she went into the nest and pulled the young unceremoniously through the side. Several days later when a young of the same litter was returned to the aquarium still unsteady from anesthesia, the mother came up to it, straddled and cleaned it, then went directly to the nest. The young followed her and when it reached the nest began to push against it. The female came partly through the side, seized the young with her mouth and fore feet, pulled it inside, and then repaired the nest wall.

The original pair was kept together throughout the observations and the one male fathered the 8 litters the female produced. Several instances of apparent solicitude toward young in the nest by this male were observed. Although he generally left the nest quickly when it was disturbed by removing the young, he did occasionally remain with the family and engage in defensive behavior, but was always more easily driven away than his mate. On one occasion he was seen to come part way out of the nest and retrieve a 4-day-old young that had been placed about an inch away. After dragging the young into the nest chamber he proceeded to clean it thoroughly in the same manner as the female and then set about repairing the opening in the nest. Examples of paternal care in other genera of cricetids (*Baiomys* and *Peromyscus*) have been given by Blair (1941) and Horner (1947).

Twice, what appeared to represent a weak retrieving response in young of an older litter to those of a younger litter was observed. A pair of adults and litters of 2-day and 4-week-old young were housed in the same cage and shared the same nest. One night when the adults and older young were outside one of the babies was placed a few inches away from the nest. Soon one of the older young came

over to it and sniffed and rolled it about to wash it in the same way as the mother. A few moments later it was joined by its litter mate and both washed and rolled the baby around but made no effort to carry it back to the nest. One of these two older young showed the same behavior when the experiment was repeated the following night.

COMPARISON OF THE DEVELOPMENT OF *REITHRODONTOMYS HUMULIS* AND *R. MEGALOTIS*

The descriptions given by Svihla (1931) and Smith (1936) of the development of *Reithrodontomys megalotis* provide a basis for at least a limited comparison of the developmental patterns of that species and *R. humulis*. As variations in certain aspects of growth and development in different species or subspecies in some mammalian genera, notably *Peromyscus*, have been shown to have taxonomic, behavioral, or ecological implications, such a comparison is of interest.

The breeding seasons, gestation periods, and fecundity of the two species appear to be comparable. Smith (1936) indicates that breeding occurs in wild *R. m. longicaudus* nearly every month of the year, with peaks in April and October. The present data on captive eastern harvest mice suggest a similarly prolonged breeding cycle, although this is not as yet well corroborated with field data. The gestation period calculated for *megalotis* by Svihla (1931) was 23 or 24 days, whereas the evidence for *humulis* indicates an equal, if not shorter, period. Twenty-seven litters reported for *megalotis* (Svihla's and Smith's data combined) range from 1 to 7 with a mean of 2.5, while the average of 11 *humulis* litters (present study and Audubon and Bachman, 1849) is 2.4 with extremes of 1 and 4. Brimley (1923) gives a range of from 2 to 5 embryos for *humulis* in North Carolina but does not include individual counts or the mean. These samples show no significant difference in litter size between the two species. Adequate information on average and maximum fecundity in the two species is lacking, but Svihla's (1931) record of a female *megalotis* producing 7 litters totaling 17 young in a year's time is equalled by a *humulis* female who gave birth to 8 litters totaling 11 young in an interval of 11 months.

The weights of newborn *megalotis* and *humulis* agree closely, ranging from 1.0 to 1.5 grams in the former and from .8 to 1.6 grams in the latter. Weights of 1.07 and 1.15 grams have been given for the young at birth of a third species, *R. fulvescens* (Svihla, 1930).

There is some disagreement in the descriptions of the newborn young of *fulvescens, humulis,* and two subspecies of *megalotis* and of the time of first appearance of body hair in the last two species. Svihla (1930) describes *R. fulvescens* as being naked at birth. *R. humulis* has also been considered to be hairless at birth, with the first body hair not appearing until the 5th day of age. Svihla (1931) states that the newly born young of *R. m. megalotis* are without hair, which first becomes visible on the head at 5 days, while Smith (1936) claims that vibrissae are present at birth in the subspecies *longicaudus* and that the first body hair is visible at 3 days. As mentioned above, the present study found both vibrissae and scattered body hairs in *humulis* examined shortly after birth, and the lack of agreement with previous accounts is considered as possibly the result of differences in observational techniques. A similar explanation may also account, at least in part, for the alleged variations reported in the other species.

Data given on further pelage development in *megalotis* by Smith can probably be compared more confidently with those obtained for *humulis.* In the former, the first hair on the tail and the first suggestion of coloration of the body hair was noted on the 4th day, while in *humulis* hairs were barely visible on the tail at 2 days of age, and coloration was evident by the 4th or 5th days.

In Svihla's (1931) study the eyes of *R. m. megalotis* young opened at 12 days of age, whereas the progeny of *R. m. megalotis—R. m. nigrescens* crosses opened their eyes a day earlier. Although the latter form has since been synonymized with *megalotis,* these data, if consistent, may be indicative of at least some degree of genetic divergence between the two populations. Smith noted eyes opening in one litter of *R. m. longicaudus* at 10 days. There appears to be an average difference of about 3 days between the opening of the eyes in *megalotis* and *humulis,* in which most of the young observed had their eyes open on the 7th day.

Only Smith gives data on the development of the ears in *megalotis.* He notes that the pinnae became erect on the 2nd day and the auditory meatus opened on the 9th day in one litter, each event about a day later than the average for *humulis.*

Smith notes that the lower incisors were visible in *megalotis* at 4 days, whereas in *humulis* the eruption of the incisor teeth was not recorded in most individuals until the 6th or 7th days. The discrepancy here may be more apparent than real, since in the present study the incisors were not considered as erupted until they appeared

above the gum line, although they may have been visible at the gum line a day or so earlier.

The completion of weaning at about 3 weeks in *megalotis* falls well within the period of weaning in *humulis*. Thus, there appears to be no significant difference in this aspect of the development of these species.

The two subspecies of *megalotis* that have been studied appear to differ in temperament. Svihla (1931) indicates that mice of the nominate subspecies had generally pugnacious dispositions, whereas Smith (1936) found *longicaudus* individuals highly tolerant of one another. In this respect, *humulis* seemingly agrees with the latter. Similar differences in temperament between various species and subspecies of deer mice, *Peromyscus*, have been noted by Svihla (1932), King (1958), McCabe and Blanchard (1950), and others.

Comparison of behavioral development on the basis of general written descriptions is difficult. However, the chronology of behavioral development described by Smith for *R. m. longicaudus* appears to correspond rather well to that of *humulis*.

In summary, to the extent that the data available permit comparison, development is closely similar in the species *humulis* and *megalotis*, although the latter may develop at a slightly slower rate, perhaps in keeping with its somewhat greater size. The apparently close similarities in developmental patterns and chronologies in the two species are in accordance with their morphological likenesses, on the basis of which the two forms are placed in the same species group under the subgenus *Reithrodontomys*.

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